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Calcareous nannofossils from the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn as palaeoenvironmental indicator, Kraków-Silesia Homocline, Poland

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ABSTRACT:

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Qualitative and quantitative studies on calcareous nannofossils have been carried out on the Middle–Upper Bathonian succession of Gnaszyn (Kraków-Silesia Homocline, Częstochowa region). The nannofossil assemblages are moderately or well-preserved and are dominated by *Watznaueria britannica*; also common are *Staurolithites lumina* and *Zeugrhabdotus erectus*. The presence of delicate nannofossil forms together with dissolution-resistant taxa shows that the changes in composition of some of the nannoplankton assemblages reflect original variations. The frequency and diversity changes of the calcareous nannofossil assemblages have been interpreted in relation to fluctuations of sedimentation rate versus changes in trophic conditions within the photic zone. The highest diversity assemblages contain a high percentage of palaeofertility indicators, and are impoverished in the genus *Watznaueria*. This is interpreted as a reflection of a lower sedimentation rate and more stable, possibly mesotrophic conditions within the photic zone. On the other hand, *W. britannica*-dominated assemblages with low species diversity may represent more unstable environments with a high influx of terrestrial material related to a high sedimentation rate and a high nutrient influx, i.e. eutrophic conditions in the photic zone.

Key words: Bathonian; Jurassic; Calcareous nannofossils; Palaeoenvironment; Kraków-Silesia Homocline; Poland.

INTRODUCTION

The oldest nannofossils have been reported from the Late Triassic and are known only from shallow-marine, low-palaeolatitude environments, mainly from the Tethys (Bown 1987). During the Early Jurassic, nannofossils expanded from the shallow Tethyan seas to other environments and underwent great taxonomic diversification, with the maximum diversity achieved during the Early Toarcian (Roth 1986; Bown *et al.* 1992, 2004; Bown and Young 1998a). Since that time, due to biocalcification, nannoplankton started to be the major primary producer of carbonates in oceanic realms. It has been responsible for the production of huge amounts of carbonates at least since the Early Cretaceous (Burnett *et al.* 2000; Rost and Riebesell 2004; Less *et al.* 2005). The nannoplankton ooze production in the oceanic pelagic zones may be considered the most important indicator of the primary surface water productivity since the Middle/Late Jurassic (Roth 1986; Brummer and van Eijden 1992). It also influenced the climate during the Mesozoic–Cenozoic with both positive and negative feedbacks (Burnett *et al.* 2000). Moreover, it is believed that

changes of climate influenced the nannoplankton phylogeny and its environmental adaptations. For example, cooling in the Mesozoic greenhouse caused diversification of calcareous nannoplankton and thus palaeolatitudinal differentiation (Bown *et al.* 2004).

The recognition of the environmental preferences of the nannoplankton is one of the main goals in recent studies on both extant and extinct assemblages. After preliminary agreement concerning the palaeoenvironmental preferences of particular taxa, it has been concluded that palaeoenvironmental interpretations based solely on nannoplankton are strongly biased. Moreover, analogies based directly on modern assemblages could have led to erroneous results, since the Creta-

ceous/Paleogene boundary extinction eliminated c. 93% of the species and there are no extant forms representing the main Mesozoic taxa (for discussion see Lees *et al.* 2005). Nevertheless, the latitude, surface oceanic water-currents, and temperature (e.g., Okada and Honjo 1973), as well as nutrient supply (e.g., Lampert *et al.* 2002; Andruleit *et al*. 2003), are considered the main factors controlling the distribution of modern and, by analogy, also the extinct nannoplankton (see also Lees *et al.* 2005).

The main purpose of this paper is the interpretation of the palaeoenvironment of the Bathonian clays in Gnaszyn, based on calcareous nannofossil assemblages and their dynamics.
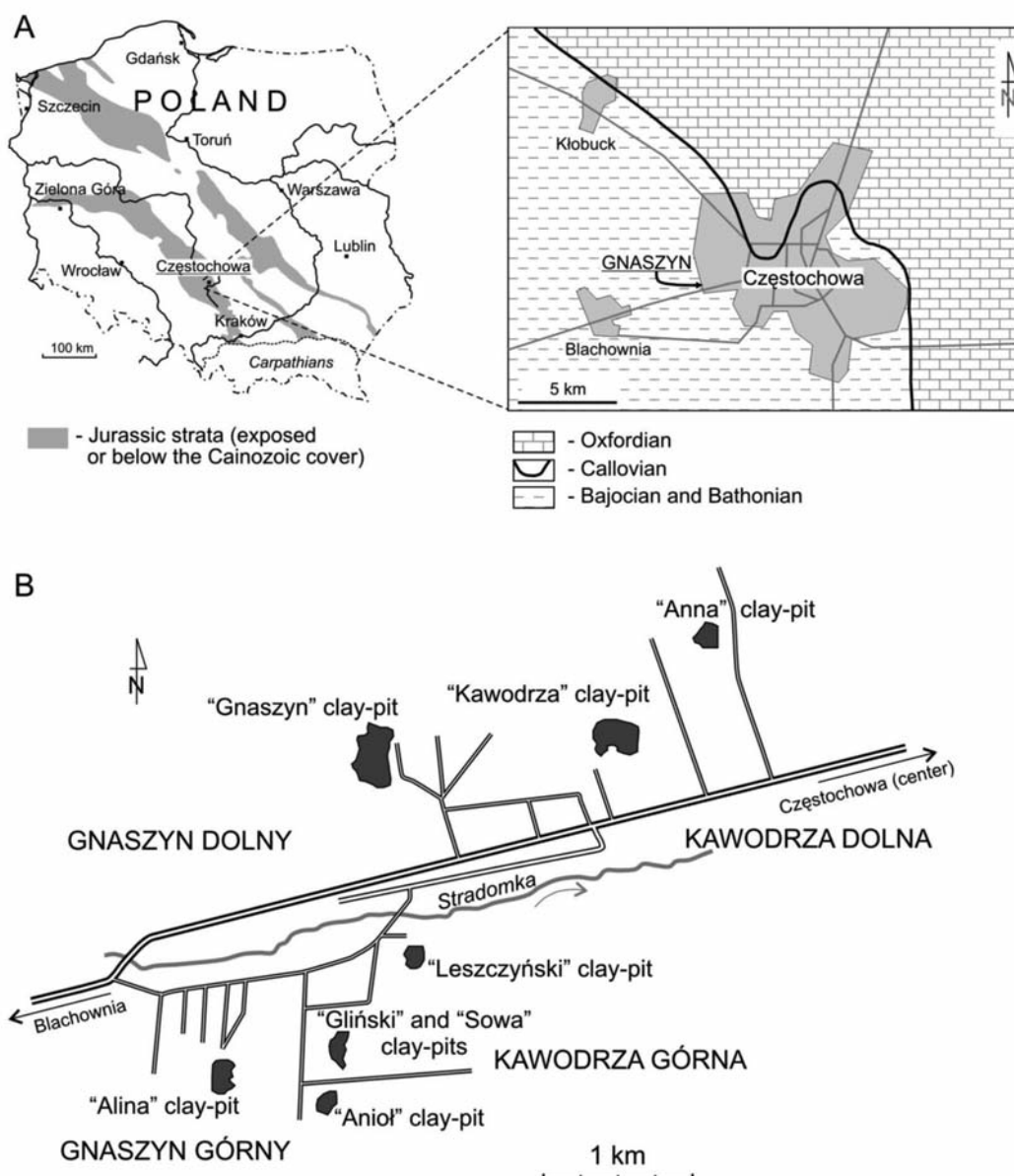
Text-fig. 1. Geological sketch-map of the Częstochowa area (A – after Majewski 2000) and location of the studied sections (B – after Matyja and Wierzbowski 2003)

CALCAREOUS NANNOFOSSILS FROM MIDDLE JURASSIC ORE-BEARING CLAYS

GEOLOGICAL SETTING

The Gnaszyn section is located in the western part of the town of Częstochowa (Central Poland) (Text-fig. 1). It is an active clay-pit, exposing a monotonous series of soft clays or clayey shales, black or dark grey in colour. The clays are strongly bioturbated with the primary lamination rarely observed (Leonowicz 2012, this issue). They are partially enriched in coarse-grained clasts, especially in the lower and upper parts of the succession. Distinctive horizons of large siderite concretions with common septarian structures (Majewski 2000; Witkowska 2012, this issue; Text-fig. 2) are scattered throughout the succession.

The Gnaszyn succession represents the offshore zone below the fair-weather wave base, commonly af-fected by storms and river input (Leonowicz 2012, this issue), rich in both benthic and nektonic macrofauna and plant fossils. The most common are bivalves, gastropods, cnidarians and ammonites (see also Majewski 2000; Gedl *et al.* 2003; Matyja and Wierzbowski 2003; Kaim 2004, 2008, 2011).

The calcareous nannoplankton was studied from sections A, B and C (Text-fig. 2). Sections A and B represent the Middle–Upper Bathonian Subcontractus through Retrocostatum ammonite zones. Section C represents the Upper Bathonian Retrocostatum Ammonite Zone (Gedl and Kaim 2012, this issue). In the nannoplankton scheme, the succession represents the NJ 11 *Pseudoconus enigma* Biozone, which spans most of the Bathonian, from the Parkinsoni up to the Hodsoni ammonite biozones (Bown and Cooper 1998).
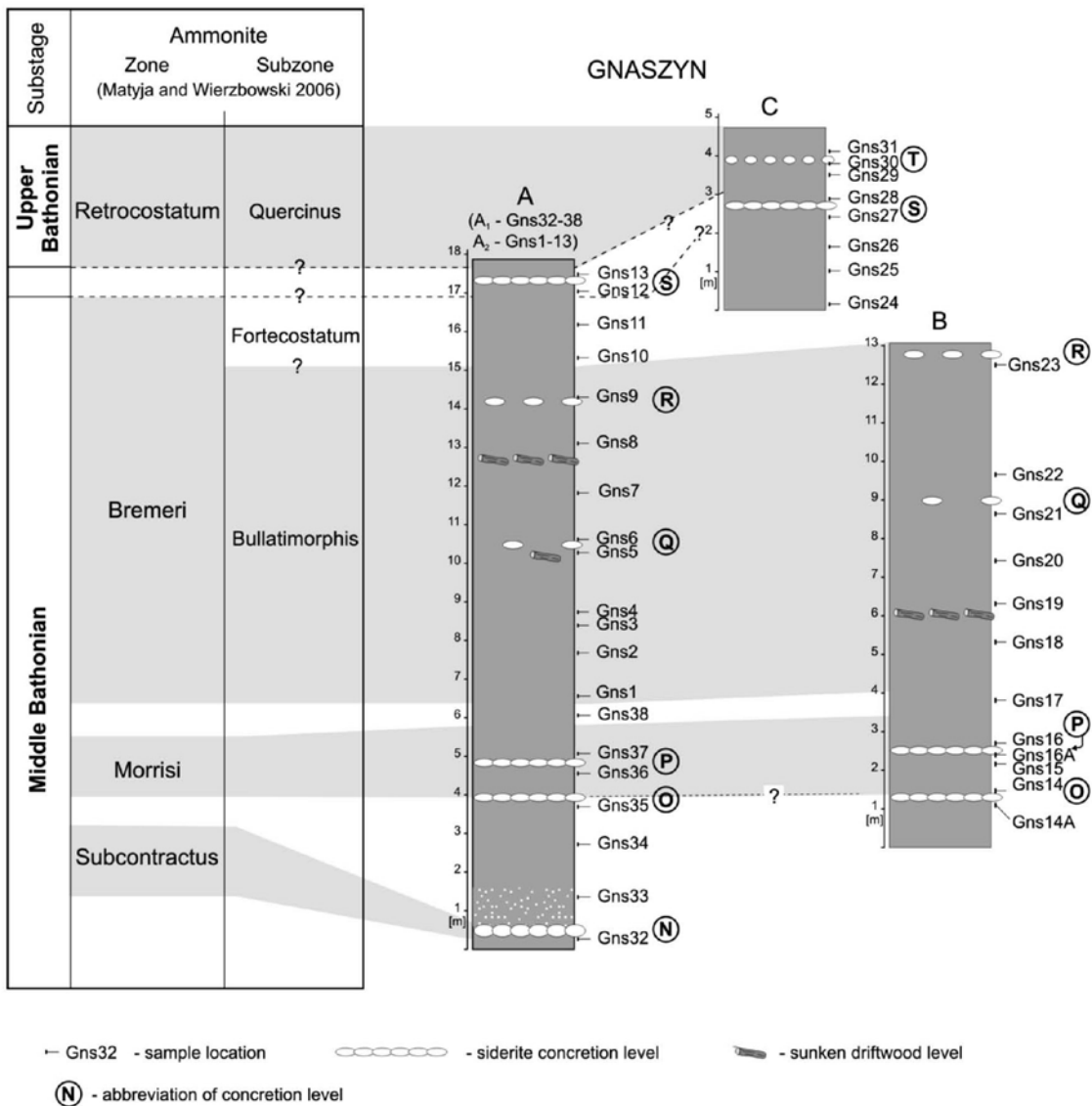
Text-fig. 2. Sketch-map of the Gnaszyn clay-pit with location of studied sections (from Gedl and Kaim 2012)

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MATERIAL AND METHODS

Forty rock samples were studied (Text-fig. 2). The light microscope slides were prepared using the simple smear-slide method; a small amount of rock-sample was scraped onto the slide and spread across its surface with a little water; after drying, the slide was covered with a cover-glass with a drop of Canadian Balsam (see also Bown and Young 1998b). The slides were then inspected under the polarised light microscope Nikon Eclipse 600 under cross polarised light or phase contrast at magnification x1000. The relative nannofossil abundance was determined based on c. 300 specimens calculated on a smear-slide (Thierstein *et al.* 1977; Bown and Young 1998b). In samples with total nannofossil abundance below 300, the percentage was computed based on 200 specimens available for analysis. The approximate abundance of nannofossil assemblages within a slide was measured as a mean content of specimens (of all taxa) per field(s) of view (abbreviated FOV). Three categories of abundance were distinguished: very rare – 1 specimen per 10 FOVs or less; rare – 1 specimen per 1 – 9 FOVs; frequent – 1 specimen per 1 FOV; common – 2 – 10 specimens per 1 FOV. The nannofossil state of preservation was estimated using the scale of Roth (1983) where E (weak E-1 to strong E-3) means the level of etching by dissolution; and O (weak O-1 to strong O-3) means secondary calcite overgrowth; X means excellent state of preservation.

RESULTS

Calcareous nannofossils, of moderate to poor preservation (E-2, on average), were found in all investigated samples. The samples with a coarse-
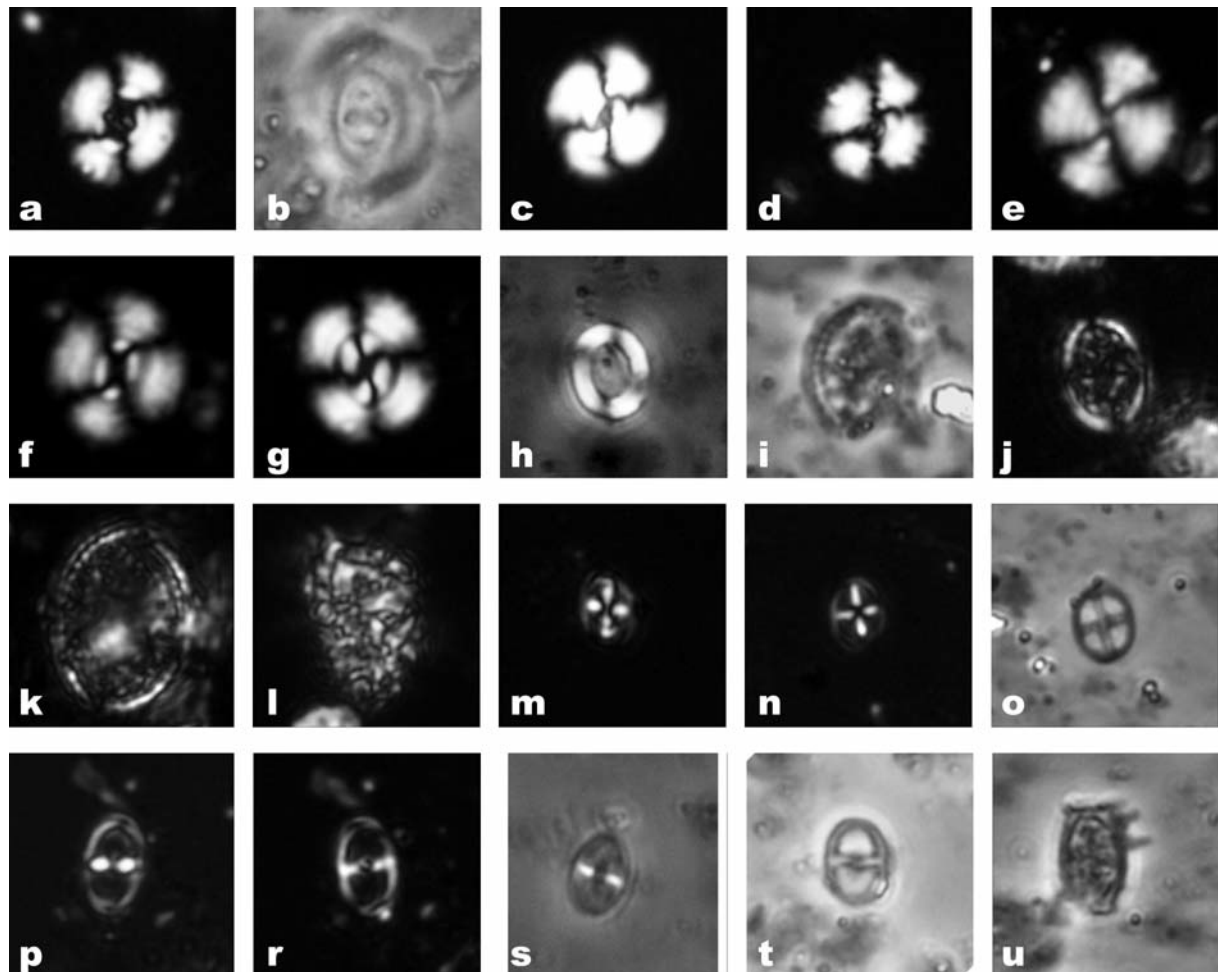
Text-fig. 3. Calcareous nannoplankton Gnaszyn (BF – bright field; XPL – cross polarised light; PC – phase contrast). a – *Watznaueria britannica* XPL, Gns30. b – *W. britannica* PC, Gns36. c, d – *W. barnesiae* XPL, Gns30. e – *W.* cf. *W. barnesiae* XPL, Gns36. f, g – *W. fossacincta* XPL, Gns36. h – *W.* cf. *W. ovata* PC, Gns36. i – *Octopodorhabdus decussatus* PC, Gns36. j – *O. decussatus* Gns36, XPL. k – *Ethmorhabdus gallicus* XPL, Gns36. l – *Pseudoconus* cf. *P. enigma* XPL, Gns14A. m, n – S*taurolithites lumina* XPL, Gns30. o – *S. lumina* BF, Gns36. p, r – *Zeugrhabdotus erectus* XPL, Gns30. s, t – *Z. erectus* PC, Gns36. u – *Stephanolithion speciosum* PC, Gns11. All figures are × 2200.

grained organic matter fraction contain etched and/or broken nannofossils, with E-3 state of preservation. The better preserved assemblages (mainly E-2, but also E-1) contain some coccospheres. In the middle parts of sections A and B, and in the lower part of section A, calcareous nannoplankton is very rare or rare; 1 specimen per 10 FOV or less. Calcareous nannoplankton is more abundant (few to common) in the lower part of section B and in the uppermost parts of sections A and C.

Thirty-eight species-level taxa (with some left in open nomenclature) have been recognised (Table 1, Text-fig. 3), with their richness varying between 5 (Gns4, 32) and 22 (Gns9) per sample. The lowest richness is observed in the lower parts of sections A (Gns32, 35) and B (Gns16A, 16). Higher up the succession the richness gradually increases, although some exceptions are noticed (samples Gns35 to Gns4 in section A; or samples Gns20 and 21 in section B). As expected, the richness strongly correlates with sample size (Text-figs 4, 5).

The most common is genus *Watznaueria*, attaining a mean contribution to the calcareous nannofossil assemblages of c. 80%, reaching up to 97% of the total abundance in sample Gns4. This genus is represented mainly by *W. britannica*, which dominates all samples. The percentage of this species is the highest in the middle part of section A and in the lower and upper parts of section B (Gns3, 4 and Gns14, 21). Also common are *W. fossacincta* (26% in Gns5) and *W. barnesiae* (41% in sample Gns36). The former is also more abundant in the middle part of the studied sections (Gns1, 5 and Gns19). The latter is the most abundant in the lower part

of section A (Gns33, 36) and in the basal sample, Gns14A, of section B (Text-figs 4, 5).

Also common is *Staurolithites lumina*. It occurs in all samples, except Gns33, with relative abundance ranging from 1.3% (Gns32 and 14A) to 33.9% (Gns29) and mean abundance 8% (Text-figs 4, 5).

Zeugrhabdotus erectus occurs in abundances up to almost 11% (Gns29, 31). It is missing from several samples, particularly in the middle part of section A and in the lowermost part of section B (Tect-figs 4, 5). Its highest abundance was noticed in the upper part of section C and in the topmost part of section A (Text-figs 4, 5).

Biscutum dubium is also quite common, reaching 7.2% and 8.4% in samples Gns22 and 28 respectively; it is absent in the lower part of section B, and in the lower and middle parts of section A.

Pseudoconus enigma, *Ethmorhabdus gallicus*, and *Stephanolithion* spp. (represented mainly by *S. speciosum*) have been found in particular samples at percentages higher than 2%. However, their non-continuous occurrence (absence in some samples) remains statistically insignificant for the present analysis.

Percentages of the taxa mentioned above in relation to the calcareous nannoplankton assemblages are plotted against the lithological logs in Text-figs 4 and 5.

Based on abundance of the taxa in the studied assemblages, a cluster analysis and linear regression for selected pairs of variables has been performed, using the PAST software (Hammer *et al.* 2001). For the statistics, four additional variables were plotted: abundances of: (1) *Watznaueria* spp.; (2) *W. barnesiae*+*W. fossacincta*; (3) *Z. erectus*+*B. dubium*+*S. lumina*, and

Samples (Section A)	32	33	34	35	36	37	38	1	2	3	4	5	6	7	8	9	10	11	12	13
Taxa richness per sample	5	6	9	5	9	7	8	9	9	7	5	7	9	7	11	12	11	10	13	17
Anfractus harrisonii	0	0	0	0	0	0	0	0	0	0	0	0.395	0	0	0	0	0	0	0.412	2.007
Axopodorhabdus cylindratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.823	0
Axopodorhabdus atavus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.334
Axopodorhabdus sp.	0	1.852	2.941	0	1.835	1.031	1.13	0	0	0	0	0.478	0	0	0.749	0	0	0	0	0
Biscutum dubium	0	0	2.941	0	1.835	0	1.695	1.622	1.212	0.877	1.117	0	0.791	0	2.622	0.735	2.381	0.816	1.646	2.676
Biscutum finchii	0	0	1.471	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Biscutum sp.	1.299	0	0	0	0	0	0	0	3,03	0	0	0	0	0	0	0	0	0	0	1.672
Cribrosphaerella ehrenbergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.368	0	0	0	0
Cyclagelosphaera margarelii	0	0	0	0	0	0	0	0	0	0	0	0	0.375	0	0	0	0	0	0	0
Ethmorhabdus gallicus	0	0	0	2.222	1.835	0	0	0	0	0	0	0	0	0	0	0.735	0.397	0	0.412	0.334
Lotharingius sigillatus	0	1.852	0	0	0	0	0	0.541	3.636	1.754	0	0	1.186	0.69	1.873	0.368	0.794	0	0.823	1.338
Lotharingius sp.	0	0	1.471	0	1.835	1.031	1.13	0.541	0	0	0	0.957	0	1.379	0	0.735	0.397	0.408	0	2.341
Parhabdolithus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.669
Polypodorhabdus escaigii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.794	1.224	0	0
Podorhabdus grassei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.334
Pseudoconus enigma	1.299	1.852	4.412	3.333	0	3.093	0	0	3.636	0.439	0.559	0	0.791	0,69	0,749	0	2.381	0.408	1.235	0.669
Stephanolithion speciosum	0	0	0	0	0	0	0.565	0	0	0	0	0	0	0	0	0	0	1.633	0.823	0.334
Stephanolithion sp.	0	0	0	0	0	0	0	0	0.541	0	0	0	0	0	0	0	0	0	0	0
Staurolithites lumina	1.299	0	4.412	3.333	7.339	7.216	28.25	11.35	6.667	1.754	1.676	8.612	1.976	2.759	4.12	2.574	5.556	12.24	4.115	13.38
Tetrapodorhabdus shawensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.749	0.735	0	0	0	0
Tetrapodorhabdus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.334
Triscutum sp.	0	0	0	0	0	0	0.541	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubirhabdus patulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.368	0	0	0.412	0
Watznaueria barnesiae	31.17	37.04	13.24	33.33	41.28	17.53	6.78	10.81	1.818	3.07	0	1.435	0	0.69	1.873	1.838	0.794	0	2.469	5.017
Watznaueria britannica	64.94	55.56	58.82	57.78	41.28	51.55	56.5	49.19	60.61	74.56	83.8	62.2	79.05	82.76	71.16	82.35	75.4	65.31	65.84	43.48
Watznaueria fossacincta	0	0	2.941	0	1.835	17.53	0	24.86	18.79	17.54	12.85	25.84	15.81	11.03	14.98	7.353	7.937	16.33	20.58	16.72
Zeugrhabdotus erectus	0	1.852	7.353	0	0.917	1.031	3.955	0	0.606	0	0	0.478	0	0	0.749	1.838	3.175	1.633	0.412	8.361

Table 1a. Sample taxon-richness and relative abundance of taxa and calcareous nannoplankton abundance

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Samples (Section B)	14A	14	15	16A	16	17	18	19	20	21	22	23
Taxa richness per sample	10	10	9	6	7	9	16	16	15	10	14	15
Anfractus harrisonii	0	0	0	0	0	0	0	0,671	0	0,498	0,578	0
Axopodorhabdus cylindratus	0	0,424	0	0	0	0	0,338	0,336	0,352	0	0	0
Axopodorhabdus sp.	0,667	0	1,158	0	0	0,402	0	0	0	0	0	0,333
Biscutum dubium	0	0	0	2,985	0	1,606	1,351	4,362	4,225	0,498	7,225	2
Biscutum finchii	0	0	0	1,493	0	0	0	0	0	0	0	0
Biscutum sp.	0	0	0	0	0	0,402	0,676	0	0	0	0	0
Cretarhabdus cf. *conicus*	0	0	0	0	0,704	0	0	0	0	0	0	0
Cyclagelosphaera margarelii	0	0,424	0	0	0	0	0,338	0	0	0	0	0
Ethmorhabdus gallicus	0	0	1,931	0	0	0	0,338	1,678	1,408	0,995	0,867	0,667
Hexapodorhabdus sp.	0	0	0	0	0	0	0,338	0	0	0	0	0
Lotharingius hauffi	0	0	0	0	0	0	0	0	0	0	0	0,333
Lotharingius sigillatus	0	0	0	0	0	2,008	0,338	2,349	0,704	2,488	0	1,667
Lotharingius sp.	1,333	1,271	0	0	0,704	0	0,338	0,336	1,056	0	0,867	1
Polypodorhabdus escaigii	0	0,424	0	0	0	0,402	0,676	0	1,056	0,498	0,867	0
Pseudoconus enigma	6,667	4,237	0,772	1,493	2,113	0,803	1,014	1,007	1,056	0,498	0,867	1
Retecapsa sp.	0	0	0	0	0	0	0	0,336	0	0	0	0
Staurolithites lumina	1,333	3,814	3,475	4,478	4,93	22,09	11,82	11,74	12,32	8,955	18,79	10
Stephanolithion speciosum	0,667	0	0	0	0	0	0,338	0,671	0,352	0	0,289	0,333
Tetrapodorhabdus shawensis	0	0	0,772	0	0	0	0	0,336	0	0	0,289	0,667
Tetrapodorhabdus sp.	0	0	0	0	0	0	0	0	0,352	0	0	0
Triscutum sp.	0	0	0	0	0	0	0	0	0	0	0,867	0,667
Tubirhabdus patulus	0,667	0	0	0	0	0	0	0,336	0	0	0	0
Watznaueria barnesiae	30	1,271	4,633	11,94	2,113	0	3,041	2,685	0,704	0	0	1,667
Watznaueria britannica	41,33	85,17	69,5	77,61	77,46	60,24	67,57	48,99	70,42	79,6	57,8	76,67
Watznaueria fossacincta	16,67	2,966	17,37	0	11,97	12,05	11,15	21,48	4,225	4,975	8,96	2
Zeugrhabdotus erectus	0,667	0	0,386	0	0	0	0,338	2,685	1,761	0,995	1,734	1

Table 1b. Sample taxon-richness and relative abundance of taxa and calcareous nannoplankton abundance

| Samples (Section C)	24	25	26	27	28	29	30	31
Taxa richness per sample	13	13	18	15	16	22	18	16
Anfractus harrisonii	0	0	0,73	0,669	0	0	0,336	1,083
Axopodorhabdus cylindratus	0,324	0,42	0	0,669	0	0,424	0	0
Axopodorhabdus sp.	0	0	0	0	0,669	0,424	0,671	0
Biscutum dubium	4,854	2,101	3,285	4,682	8,361	5,085	3,02	3,249
Biscutum finchii	0	0	0	0	0	0,847	0	0
Biscutum sp.	0	0,42	0	0	0	0,424	0	0
Calyculus sp.	0	0	0,365	0	0	0	0	0
Cretarhabdus cf. *conicus*	0	0	0	0	0	0,424	0	0
Cribrosphaerella ehrenbergii	0	0	0	0	0	0	0	0,361
Cyclagelosphaera margarelii	0	0	0	1,003	0	0	0,336	0
Ethmorhabdus gallicus	0,324	0,42	1,095	0,669	0,669	0,847	0,671	0,722
Hexapodorhabdus cuvillieri	0	0	0,365	0	0	0	0	0
Hexapodorhabdus sp.	0	0	0	0	0	0,424	0	0
Lotharingius hauffi	0	0	0,365	0	0	0	0	0
Lotharingius sigillatus	2,913	0	1,825	1,338	1,338	0,847	1,342	1,444
Lotharingius sp.	1,942	2,101	2,19	0,334	3,679	1,271	2,013	3,249
Octopodorhabdus decussatus	0	0	0	0	0	0,424	0	0,361
Polypodorhabdus escaigii	0,647	0,42	0	1,672	1,338	0,847	0,336	0,361
Podorhabdus grassei	0	0	0	0	0	0	0	0
Pseudoconus enigma	0	0	0,365	1,672	0,334	0	0,336	0,361
Retecapsa sp.	0	0	0	0	0	0,424	0	0
Schizosphaerella sp.	0	0	0,365	0	0	0	0	0
Staurolithites lumina	16,83	23,95	18,25	12,37	20,4	33,9	20,13	14,44
Stephanolithion hexum	0	0	0	0	0	0	0,671	0
Stephanolithion speciosum	0,647	0,42	0,73	1,003	1,672	2,119	0	1,444
Stradnelithus sp.	0	0	0	0	0,334	0	0	0
Tetrapodorhabdus shawensis	0,647	0,84	0,73	0	0,334	0	0,336	0,361
Tetrapodorhabdus sp.	0	0	0	0	0	0	0,336	0
Triscutum cf. *sullivanii*	0	0	0,73	0	0	0	0	0
Triscutum sp.	0	0,42	0	0	0	0,424	0,671	0
Tubirhabdus patulus	0	0	0	0	0,669	0,847	0	0
Watznaueria barnesiae	1,942	0	0,73	4,013	0,334	4,661	1,342	1,444
Watznaueria britannica	55,02	63,03	51,09	54,52	41,47	21,19	53,69	50,54
Watznaueria fossacincta	9,061	2,101	8,394	9,03	10,03	13,14	8,054	9,747
Zeugrhabdotus erectus	4,854	3,361	8,394	6,355	8,361	11,02	5,705	10,83

Table 1c. Sample taxon-richness and relative abundance of taxa and calcareous nannoplankton abundance

(4) the number of taxa per slide. Variable (1) contains all the *Watznaueria* species, and variable (4) is the total sample taxonomic diversity. Tree cluster analysis shows four clusters (Text-fig. 6).

The linear regressions (described by the correlation coefficient – R) have been plotted to determine the relationship between pairs of selected variables. Table 2 shows the R values for all the variables with relatively continuous occurrence through the succession, signifi-cant similarity by means of cluster analysis and mean percentage value above 2. Most of the R values show weak ($0.1 = |R| < 0.3$) or average ($0.3 = |R| < 0.5$) linear correlations between the variables. Some of the pairs are extremely weakly correlated by means of the linear regression ($0 < |R| < 0.1$). Nevertheless, the most interesting are pairs with strong ($0.5 = |R| < 0.7$) and very strong ($0.7 = |R| < 0.9$) correlation coefficients, which have been noticed, among others, for the fol-
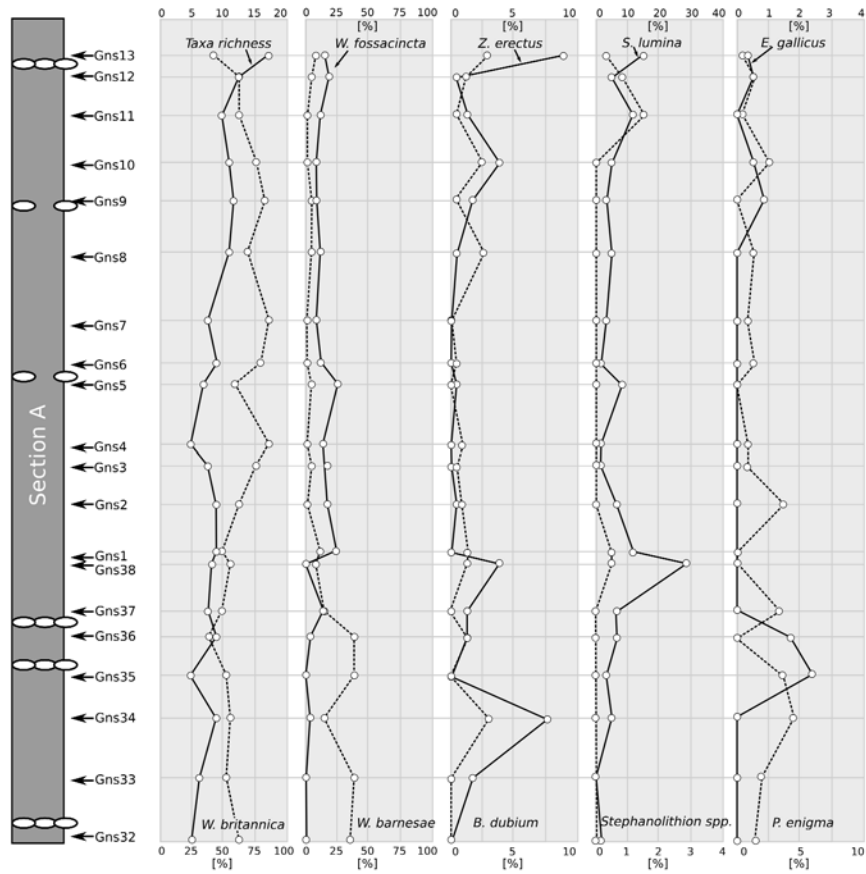
Text-fig. 4. Total richness and abundance of the most common calcareous nannoplankton taxa in section A
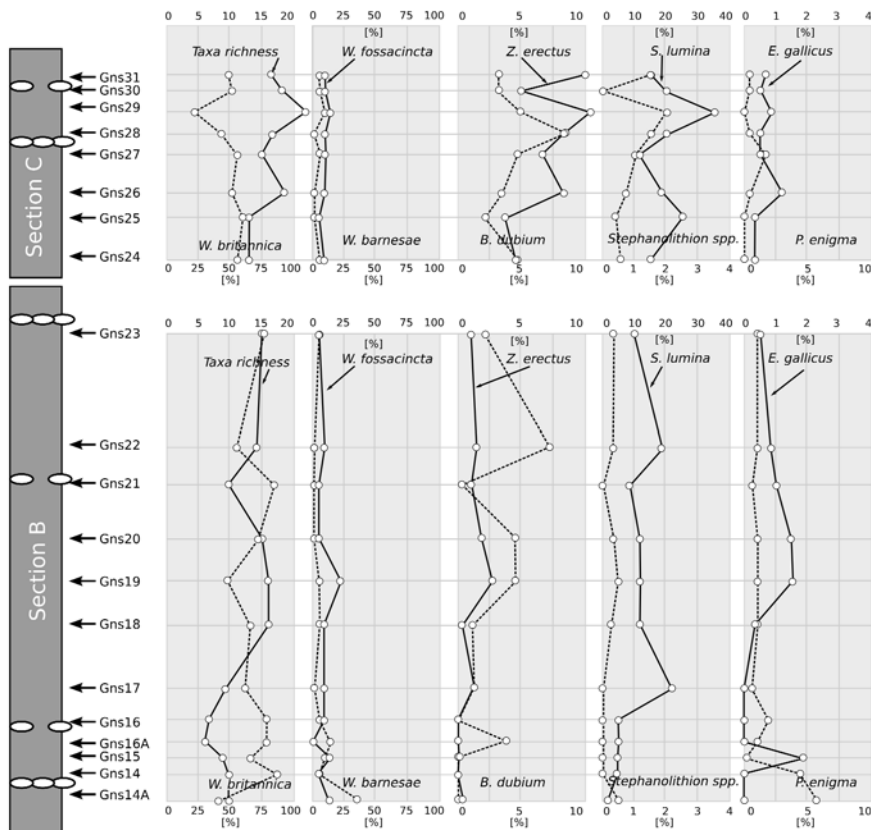
Text-fig. 5. Total richness and abundance of the most common calcareous nannoplankton taxa in sections B and C

lowing pairs: *Watznaueria* spp. vs. *Z. erectus+B. dubium+S. lumina*; *Watznaueria* spp. vs. *S. lumina*; *Watznaueria* spp. vs. *Z. erectus*; *Watznaueria* spp. vs. number of taxa; *Watznaueria* spp. vs. *B. dubium*; *Z. erectus+B. dubium+S. lumina* vs. number of taxa; *Z. erectus* vs. number of taxa. The rest of the strong or very strong linear fits can be omitted due to one of the variables being a part of the other variable in the pair, e.g. *S. lumina* is part of the *Z. erectus+B. dubium+S. lumina* variable, so the very strong linear fit for this pair is strongly affected by self-fitting. R values taken into further considerations are shown in bold in Table 2.

DISCUSSION

Preservation

Analysis of the sedimentary environment based on nannofossil assemblages first requires an estimation of the effects of the secondary (taphonomic) changes on the assemblages. Delicate nannoplankton forms, such as holococcoliths of simple rim-like structure, are the most susceptible to secondary processes. In contrast, the robust forms, like cubic nannoliths or placoliths with a solid central area, are the most resistant. One of the most resistant to dissolution among the placoliths are species of *Watznaueria* (Hill 1975; Thierstein 1980). Delicate forms, e.g., muroliths, *Zeugrhabdotus* spp. or *Staurolithites* spp., and placoliths, *Biscutum* spp., are relatively more fragile and they may easily be dissolved (Roth and Bowdler 1981). This can be observed well in sediments with high carbonate (dissolution and then recrystallisation effects) or high organic matter (dissolution effect) contents (see also Bown and Young 1998b). Consequently, assemblages dominated by the dissolu-

tion-resistant taxa (e.g., *Watznaueria*) might be considered as strongly affected by diagenesis. Roth and Bowdler (1981) suggest that nannofossil assemblages composed of more than 40% of *Watznaueria* spp. may be regarded as strongly affected by diagenetic carbonate dissolution. However, this is not always the rule, and numerous, *Watznaueria*-rich assemblages may actually provide the primary environmental signal (e.g., Thomsen 1989). A good example was provided by Mattioli and Pittet (2002), based on early Jurassic limestone-marl alternations. They observed no significant difference in abundance of nannofossil assemblages between the marly and limestone parts of the cyclothems.

The state of preservation of the nannofossil assemblages is E-2 or E-3 (rarely E-1), what means that all of them were affected by dissolution. Nevertheless, the presence of delicate forms such as *Staurolithites lumina*, *Biscutum dubium, Stephanolithion speciosum* and *Zeugrhabdotus erectus,* indicates, that at least in some cases, the influence of diagenesis on the composition of the nannoplankton assemblages was insignificant.

Calcareous nannofossils as a palaeoenvironmental indicator

The coccolithophores producing the coccoliths belong to autotrophic microalgae (Billard and Inouye 2004). The light intensity, inorganic nutrients supply and other environmental factors (e.g., temperature or salinity) controlling the calcification and life processes of coccolithophores are similar to those preferred by other phytoplankton, including diatoms or dinoflagellates (Brand 1994). Coccolithophorids prefer low variability in N:P ratios in the upper 200 m of the water column, the shallower mixed layer depths, high surface ammonium concentrations, high N:Si ratios and low

	Taxa richness	B. dubium	S. lumina	W. barnesiae	W. britannica	W. fossacincta	Z. erectus	Watznaueria spp.	Z.erectus+ B.dubium+ S.lumina
Taxa richness	1								
B. dubium	**0.673**	1.000							
S. lumina	**0.647**	**0.603**	1.000						
W. barnesiae	-0.419	-0.313	-0.345	1.000					
W. britannica	-0.473	-0.454	**-0.563**	-0.339	1.000				
W. fossacincta	0.082	-0.065	-0.066	-0.338	-0.156	1.000			
Z. erectus	**0.712**	**0.625**	**0.611**	-0.182	**-0.62**	-0.099	1.000		
Watznaueria spp.	**-0.796**	**-0.767**	**-0.907**	0.292	0.684	0.085	**-0.850**	1.000	
Z. erectus+ B. dubium+ S. lumina	**0.752**	0.754	0.954	-0.339	**-0.632**	-0.083	0.798	**-0.984**	1.000
W. barnesiae+ W. fossacinta	-0.371	-0.359	-0.391	0.793	-0.444	0.305	-0.248	0.350	-0.397

Table 2. Correlation coefficients for selected, most common nannofossils and number of taxa

iron concentrations to grow and bloom (e.g., Lampert *et al.* 2002; Painter *et al*. 2010). Temperature and the accessibility of nutrients seem to have played the major role in controlling Mesozoic nannoplankton distribution (Burnett *et al*. 2000). The highest diversity assemblages of modern coccolithophores occur in subtropical oceanic gyres. Low-diversity assemblages with the highest total abundance are known from the subpolar or temperate regions (Winter *et al*. 1994). Such a pattern of distribution shows that the majority of modern coccolithophore species prefer moderately low turbulence, moderate nutrient supply, and moderate day-length (Brand 1994; Balch 2004). However, there are some modern species blooming in the fertile waters of coastal and/or equatorial upwellings. *Emiliania huxleyi,* in particular, is regarded as a typical eurytopic species that prefers meso- or eutrophic environments (Young 1994; Balch 2004). Similar ecological preferences are shown by other modern placolith-bearing coccolithophores (e.g., *Gephyrocapsa*), which occur in mass in environments with higher nutrient supply (high-mesotrophy to eutrophy) (e.g., Young 1994). These kinds of ecological preferences (among others: variable and uncertain climate, rapid development, and small body size) can be ascribed to *r*-selection (see Pianka 1970).

Species of *Watznaueria*, which dominated various Middle Jurassic and Cretaceous environments, are *r*-selected (e.g., Street and Bown 2000; Lees *et al.* 2004). Lees *et al.* (2004) interpreted *Watznaueria fossacincta/W. barnesiae*-dominated assemblages from the Upper Jurassic Kimmeridge Clay Formation (Dorset, UK), as nannoplankton blooms, representing the maximum stress of palaeoenvironmental condition. They found that the coccolith-bearing stone-band microlaminae in their studied succession recorded the seasonal blooms and peaks of eutrophy, while other non-watznaueriacean taxa were ecologically almost completely excluded. Subsequently, Lees *et al.* (2006) described an anomalously low-diversity assemblage dominated by Watznaueriaceae from the same formation, and interpreted it as the result of high trophic conditions that excluded most normal open-ocean taxa. They suggested that *W. britannica* was adapted to the highest nutrient concentration and therefore dominated in the lowest-diversity assemblages. Accordingly, the dominance of *W. barnesiae/W. fossacincta* in more diverse assemblages suggests their adaptation to slightly lower nutrient concentration. *Cyclagelosphaera margerelii* appears to be the most extreme r-selected species which may occurs in very high trophic conditions hostile even to *W. britannica* (Lees *et al.* 2006).

Giraud *et al.* (2009) recognised the spatial distribution of nannofossils in a Jurassic slope-to-basin tran-

sect, which corresponds to a decrease in nutrient concentration, lower turbulence and an increase in environmental stability. Small-sized *W. britannica* dominated the low-diversity assemblages in the slope settings and became less dominant in the more diverse assemblages of the basinal settings, being replaced with *W. barnesiae/W. fossacincta*. More detailed analysis of the influence of environmental conditions on morphology and abundance of *W. britannica* during the Late Jurassic was provided by Giraud *et al.* (2006). These authors concluded that low oligotrophic conditions in the surface water, connected with warm temperatures, were likely to be optimal for calcification of that species. Olivier *et al.* (2004) noted that small-sized *W. britannica* preferred high mesotrophic environments, *W. barnesiae* low-mesotrophic, whereas large-sized *W. britannica* and *W. manivitae* oligotrophic. Also Carcel *et al.* (2010) ascribed dominance of the smallest morphotype of *W. britannica* to higher trophic conditions, and similar results were reported by Pittet and Mattioli (2002), who concluded that *W. britannica* was more abundant in low-to-high mesotrophic conditions, whereas *W. barnesiae* and *W. manivitae* were more abundant in oligotrophic conditions. In contrast, the older results (e.g., Roth and Krumbach 1986; Herrle 2003) suggested that *Watznaueria* indicated low palaeofertility and/or pelagic palaeoenvironments (see also Perch-Nielsen 1985).

Generally, *Watznaueria* seems to be ubiquitous and dominant during the mid-Jurassic – Late Cretaceous, especially within the low and middle palaeolatitudes (e.g., Street and Bown 2000; Lees *et al.* 2004, 2005). The best proxy for the Mesozoic *Watznaueria* seems to be *Emiliania huxleyi*, one of the most opportunistic modern species (Lees *et al*. 2005).

Biscutum constans and *Zeugrhabdotus* spp. (< 5 µm) seem to have had a similar life strategy: their abundance usually increases in the upwelling zones and thus they may be regarded as good palaeofertility indicators (e.g., Roth and Bowdler 1981; Watkins 1989; Erba 1992; Street and Bown 2000). However, Giraud *et al*. (2009) and Giraud (2009) suggest that "these coccoliths were probably not competitive with respect to small-sized morphotypes of *W. britannica* in unstable and eutrophic surface waters for the Jurassic". On the other hand, Street and Bown (2000) noted that, although *B. constans, Zeugrhabdotus* sp. and *Watznaueria barnesiae* may have had a similar life strategy, their peaks of abundance are inverted. Abundances of *W. barnesiae* occur during periods of more muddy deposition while both *B. constans* and *Zeugrhabdotus* sp. are more common in more carbonate sediments. Despite the common use of these taxa as palaeofertility indicators neither

their ecological relationships nor preferences are un-equivocally clear (Lees *et al*. 2005).

Cluster analysis

Four clusters were revealed in the analysis, though only three of them may have significant similarity in terms of Euclidean distance (Text-fig. 6). The first cluster, of *W. britannica* and *Watznaueria* spp., has the highest similarity. However, as *Watznaueria* spp. consists mostly of *W. britannica* this cluster is almost *W. britannica* self-similarity. Similarly, the cluster grouping *W. barnesiae* and *W. barnesiae+W. fossacincta*. High similarity in this cluster is mainly *W. barnesiae*

self-similarity. The third cluster groups *S. lumina*, number of taxa per slide, and *W. fossacincta*. This grouping suggests that *W. fossacincta* is a species of *Watznaueria* that is more abundant in more diverse assemblages, where other *Watznaueria* species become rare. It is noteworthy that *S. lumina* has the most continuous occurrence (absent in only one sample Gns33). This is the second species besides *W. britannica* with such a complete record, what may suggest their similar environmental preferences. *S. lumina* becomes more abundant when *Watznaueria* spp. becomes rarer. The fourth cluster, of *Z. erectus* and *B. dubium*, indicates similar trends in abundance changes. Based on cluster analysis it may be concluded that, among the *Watznaueria*
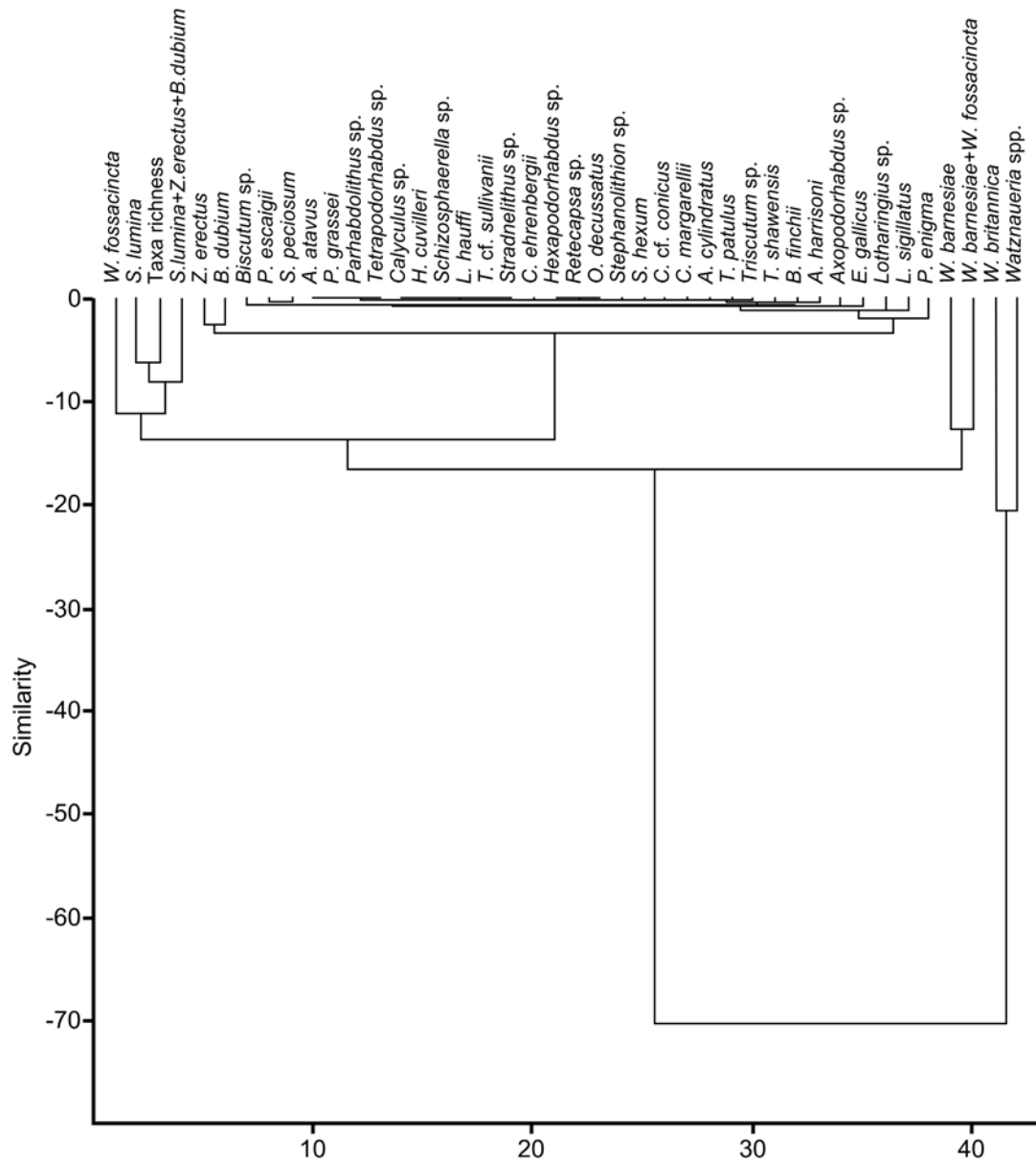
Text-fig. 6. Cluster analysis of studied assemblage of calcareous nannofossils

species studied herein, *W. fossacincta* has a pattern of occurrence more similar to the group of *S. lumina, Z. erectus* and *B. dubium* than to other *Watznaueria* species.

Interpretation of the correlation coefficient

The abundances of *B. dubium, S. lumina* and *Z. erectus* are proportionally correlated with assemblages richness, with similar R value. There are, most probably, some differences in the abundances between these three taxa, because their sum has an even higher R value. These differences, however, cannot be significant because R values in pairs between them are always at the same level, around 0.6. In conclusion, *B. dubium, S. lumina* and *Z. erectus* most probably occupied a similar ecological niche.

In contrast, abundances of all *Watznaueria* species show strong negative correlation with richness; they are more abundant in assemblages with lower diversity. Particular species of that genus show lower correlation with richness and among them the best fitted species is *W. britannica*, the next *W. barnesiae*, and no correlation was found for *W. fossacincta*.
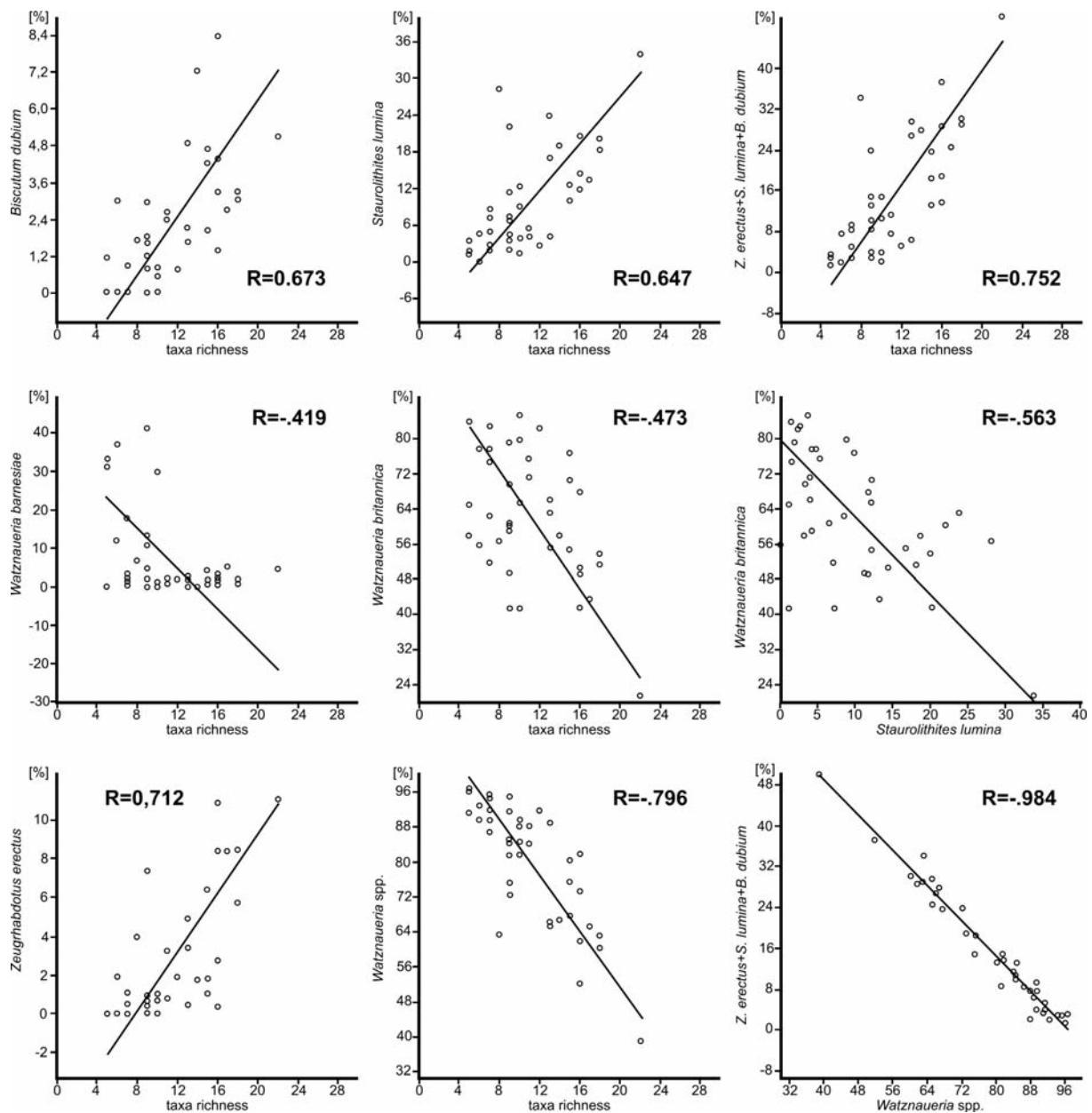
Text-fig. 7. Scatter diagrams plotted for selected pairs of variables. Section A is available in column on left side and sections B and C on right. Linear regressions are shown together with value of the correlation coefficient (R)

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A high |R| value for *Watznaueria* spp. and significantly lower |R| values for particular species of this genus suggest some shift in abundance between *W. britannica* and *W. barnesiae,* the most common species recorded in the samples. Their occurrences almost complement one another. Thus, they probably dominated in slightly different palaeoenvironmental conditions. This assumption is also supported by an average |R| value for that pair. *W. fossacincta* shows weak or no correlation in almost every pair of the variables. Also, *W. barnesiae+W. fossacincta* seems to have no significance for ecological considerations in term of correlation coefficient because its average |R| value is derived mainly from the *W. barnesiae* |R| values.

It is also noteworthy that *W. britannica* and *W. barnesiae* differ in their susceptibility to dissolution (Pittet and Mattioli 2002). *W. barnesiae* has the most solid central area of all the *Watznaueria* species reported herein, and seems to be the most resistant one. Nevertheless, the similar |R| values for these species (or even higher for *W. britannica*) in their correlations with richness values indicate rather the minor influence of dissolution on their share in the studied material.

The best correlation is revealed for *Watznaueria*

spp. and *B. dubium+S. lumina+Z. erectus*, with an almost perfect linear fit. As *W. fossacincta* shows no correlation to *B. dubium+S. lumina+Z. erectus*, it is clear that only *W. britannica* and *W. barnesiae* play a role in this fitting. It may be suggested that *B. dubium+S. lumina+Z. erectus* replace the ecological niche of *W. britannica* and *W. barnesiae.* Nevertheless, perfect linear regression with a negative slope between those two groups may be explained rather as a sign of selective dissolution than the effect of changes in ecological conditions. Such an explanation would be true if *W. barnesiae*, supposedly the most resistant species, had a high negative correlation to richness. Consequently, the rest of the Watznaueriacae should have a lower negative or no linear correlation. In fact, *W. barnesiae* has a lower negative |R| correlation to richness than *W. britannica* in the studied samples (Table 2). Therefore, evidence of strong selective dissolution cannot be confirmed in the studied sections.

In conclusion, the chosen variables show that *W. britannica* and *W. barnesiae* dominated in less diverse assemblages. This cause domination of *W. britannica* and *W. barnesiae* in the whole studied section. *B. dubium, S. lumina* and *Z. erectus* are more abundant in more diverse assemblages.
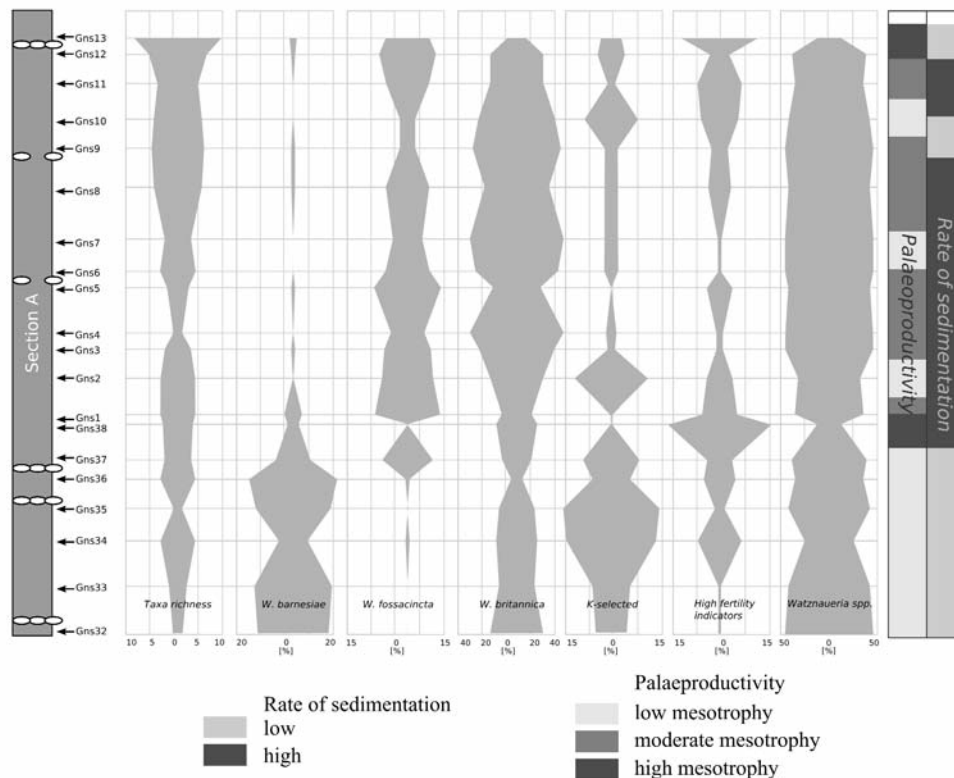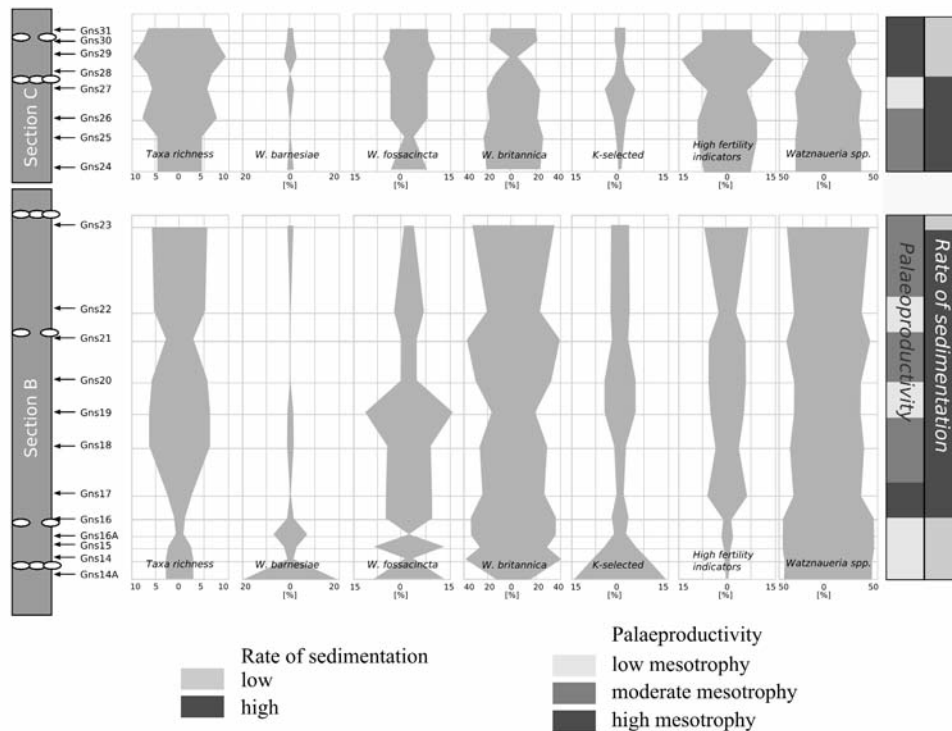

Text-fig. 8. Relative abundance of selected taxa or groups of taxa of calcareous nannofossils, with inferred palaeofertility and sedimentation rate in section A

Factors controlling calcareous nannofossil productivity

Although the analysis of correlation coefficients provides important information on the general trends in the frequency distribution of the studied assemblages, its resolution does not enable appropriate palaeoenvironmental interpretation. Additional information is supplied by the frequencies of the nannofossil taxa in particular samples (Text-figs 8, 9).

The lowest species richness, less than 10 taxa, is recorded in the lower parts of sections A (Gns32–Gns7) and B (Gns14a–Gns17); in the Subcontractus, Morrisi and lower part of the Bremeri zones (Text-figs 2). The richest assemblages, more than 15 taxa, occur in the upper parts of sections A (Gns13) and C, above sample Gns26. The latter is also characterised by a high contribution of species regarded as good palaeofertility-indicators (*Z. erectus* and *B. dubium*) and a higher abundance of *S. lumina* (in contrast to *Watznaueria* spp. which becomes rare) (Text-figs 7, 8). Such occurrence of palaeofertility-indicators suggests a higher availability of nutrients in the surface water during deposition of the upper part of the succession, i.e., during the Retrocostatum Zone. Similarly, the samples taken from the interval around the O and P siderite horizons (Gns34, Gns38 and Gns16a) are also slightly enriched in *Z. erectus* and *B. dubium.*

This pattern of nannofossil distribution partially corresponds to the pattern of sediment grain-size as observed in the succession (Leonowicz 2012, this issue): the lowermost part of the succession, between the N and O siderite horizons (samples Gns14a, Gns33–35) is characterised by the highest content of sand, suggesting the proximity of the source area, entailing delivery of clastic material together with fresh-water, making the marine surface-water hostile for most of the calcareous nannoplankton. Coarse-grained sediments are usually indicative of high energy environments with a high rate of accumulation, but this feature is not essential. A high rate of sedimentation may also characterize fine-grained sediments. In the studied succession, the rate of sedimentation can be estimated based on the presence of horizons with siderite concretions. Most of the concretions are of early diagenetic origin and some of them underwent early reworking (hiatus concretions). They are considered as levels of low sedimentation rate (Majewski 2000; Witkowska 2012, this issue). Formation of the concretions requires stable conditions when the sedimentation rate had been significantly decreased (Witkowska 2012, this issue). This may produce surface-water condition favourable for calcareous nannoplankton (Text-figs 2, 7, 8). The stable conditions occurring during concretion formation are evidenced by the enhanced occurrence of *Ethmorhabdus gallicus* and *Pseudo-*

Text-fig. 9. Relative abundance of selected taxa or groups of taxa of calcareous nannofossils, with inferred palaeofertility and sedimentation rate in sections B and C

conus enigma, which may be considered *K*-selected taxa. Their higher abundance is recorded in the lower part of sections A and B (around the concretion horizons O and P) (see Text-figs 2, 8, 9). In this case, the more frequent occurrence of *K*-selected taxa can be explained by a low dynamic water environment (low rate of sedimentation) and relatively low concentration of nutrients. This can be related to the (oligotrophic?) low mesotrophic palaeoenvironments (Text-figs 8, 9).

The middle part of the succession (generally between concretion horizons P and S) dominated by clays and/or clayey shales and with rare concretion horizons, most probably originated during a relatively high rate of sedimentation (Majewski 2000). The nannofossil assemblages from this part of the succession are of low diversity and dominated by *W. britannica*. This relationship may be explained by the generally unstable ecological conditions during periods of a high rate of sedimentation, habitable only for *r*-selected taxa. A higher rate of clastic deposition was connected with higher nutrient supply and destabilization of the environmental conditions. These periods could have also been characterised by a decrease in salinity caused by fresh-water input.

The nannofossil record from the upper part of the succession most probably reflects the highest fertility of the sea surface-water as the fertility-indicating taxa have their peak of abundance. It should also be emphasised that the rate of nutrient supply (regardless of sedimentation rate) was constantly moderate or high, indicating a low to high mesotrophic environment. Consequently, it seems that it was mainly water dynamics (stable or unstable conditions) that controlled the composition of nannoplankton assemblages.

Based on estimated fertility and sedimentation rate, inferred from nannoplankton assemblages, the following palaeoenvironments may be distinguished (Text-figs 8, 9):

• low mesotrophy and moderate (high?) rate of sedimentation (low frequency of palaeofertility indicators, high frequency of K-selected taxa); middle part of the Gnaszyn succession (samples Gns2; 6? –7?; 10; 19–20; 22; 27);

• low mesotrophy and low rate of sedimentation (dominance of *Watznaueria* spp. and high frequency of *K*-selected taxa); lower part of the Gnaszyn succession (samples Gns32-37; 14A-16A);

• mesotrophy and high rate of sedimentation (dominance of *Watznaueria* group); middle part of the Gnaszyn succession (samples Gns1; 3–5; 8–9; 11; 18; 21; 23–26)

• moderate/high mesotrophy with low rate of sedimentation (high frequency of palaeofertility indicators,

low frequency of *K*-selected taxa, high diversity); upper part of the Gnaszyn succession (samples Gns12–13; 28–31)

SUMMARY

The Gnaszyn succession contains poorly to moderately preserved calcareous nannofossil assemblages dominated by species of *Watznaueria* (especially *W. britannica*).

Although diagenetic processes may have enriched the samples in dissolution-resistant species to some extent, the assemblages seem to have been only weakly affected by dissolution and still record their primary composition.

Watznaueria britannica and *W. barnesiae* dominate assemblages with low diversity. There is some offset in their abundance which complemented each other in their dominance throughout the entire material studied.

Biscutum dubium, Staurolithites lumina and *Zeugrhabdotus erectus* are more abundant in assemblages with higher diversity and show the opposite trend in abundance to *W. britannica* and *W. barnesiae.*
Pseudoconus enigma and *Ethmorhabdus gallicus* may represent *K*-selected species.

The palaeoenvironment of sedimentation of the studied deposits may represent low through moderate/high mesotrophy. The unstable rate of sedimentation and nutrient supply (thus palaeoproductivity) together with changes in stability of the surface water dynamics were the main factors controlling the frequency of the taxa throughout the succession and the diversity of the assemblages. These factors most probably reflected climatic and/or bathymetric changes regulated by proximity of the coastline and/or the amount of the river-derived input.

The high amount of suspended organic matter reduces light availability so that only opportunistic species can survive in such conditions. Interruption or decrease in the rate of sedimentation and simultaneous high nutrient supply (a predominant mesotrophic palaeoenvironment) improved the ecological conditions, causing a decrease in the percentage of *r*-selected taxa and an increase in the diversity of the assemblages. On other hand, a low rate of sedimentation and low nutrient supply is reflected in an increase in abundance of *K*-selected taxa.

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