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FACTORS CONTROLLING THE DISTRIBUTION OF *CHITINOZOA* IN THE GLEEDON CHRONOZONE (WENLOCKIAN) OF NORTHERN EUROPE [1]

by

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(3 figures and 7 tables)

RESUME.- Nous avons voulu ici contrôler la répartition des Chitinozoaires suivant un même horizon chronostratigraphique en Europe occidentale, en l'occurrence la transition entre deux zones à graptolithes du Wenlockien-Gleedon : z. à *Gothograptus nassa* et z. à *Monograptus ludensis.* Nous pensons ainsi pouvoir évaluer l'influence du provincialisme d'une part et celle du milieu local d'autre part, sur la composition des assemblages. Nous avons soumis un ensemble de données analytiques, de variables paléontologiques et de paramètres physico-chimiques à l'analyse factorielle Q et R. Il ne s'en dégage aucune intervention marquante du provincialisme, milieu et mode de vie étant les facteurs prédominants. *Conochitina* voit sa distribution liée aux conditions du fond marin et était donc probablement benthique. *Linochitina, Ancyrochitina* et *Sphaerochitina* paraissent indépendants du milieu de sédimentation et étaient sans doute planctoniques. Enrichissement en *Linochitina* et transgression marine paraissent aller de pair.

ABSTRACT.- Samples were collected along a chronohorizon defined by the transition between the Wenlockian (Gleedon Chronozone) graptolite zones of *Gothograptus nassa* and *Monograptus ludensis* in several northern European localities to evaluate the influence of large scale provincialism and local habitat on the distribution of Chitinozoa. The distribution of Chitinozoa and several environmental parameters based on a number of palaeontological, chemical and physical variables were submitted to Q- and R-mode factor analyses. Provincialism does not seem to influence the distribution of Chitinozoa in the localities considered. The distribution of *Conochitina* is controlled by physico-chemical factors related to bottom conditions ; from this a benthonic habitat can be inferred. The distribution of *Linochitina, Ancyrochitina* and *Sphaerochitina* appears to be controlled by biological factors, independent of bottom conditions and thus indicating a planktonic habitat. The increase of *Linochitina* forms in a stratigraphic column is shown to represent a transgressive trend.

INTRODUCTION

Chitinozoans are marine organic microfossils of the Paleozoic. Composition of *Chitinozoa* associations in sedimentary strata is influenced, apart from stratigraphic position, by large scale provincialism and by local habitat. To evaluate the relative importance of the latter two, samples were collected in several European localities along a chronohorizon to exclude stratigraphic (evolutionary) differences.

METHODOLOGY

The chronohorizon chosen for this study was the transition between the graptolite biozones *Gothograptus nassa* and *Monograptus ludensis,* situated in the Gleedon chronozone of the Homerian stage of the Wenlockian Series, belonging to the Silurian System (fig. 1). This transition is well defined in several European localities.

Chitinozoans have been found in all kinds of marine sediments of the Paleozoic. Their resistant organic-walled vesicles make them less vulnerable than the common macrofossils to random destructive processes during fossilisation. These properties make *Chitinozoa* suitable for numerical data processing. To evaluate the influence of provincialism and habitat, *Chitinozoa* associations will be correlated in a multivariate way with environmental parameters defined by a number of paleontological, chemical and physical variables. A Q-mode factor analysis of the chemi-

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CHRONOSTRATIGRAPHY			LITHOSTRATIGRAPHY	BIOSTRATIGRAPHY
SERIES	STAGE	CHRONOZONE		GRAPTOLITE BIOZONES
WENLOCKIAN	HOMERIAN	GLEEDON	Much Wenlock Limestone Formation	*ludensis*
			Farley Member of Coalbrookdale Formation	*nassa*
		WHITWELL	Coalbrookdale Formation	*lundgreni*
	SHEINWOODIAN			*ellesae*
				linnarssoni
				rigidus
				riccartonensis
			Buildwas Formation	*murchisoni*
				centrifugus

Figure 1.– The stratigraphic subdivisions of the Wenlockian (after Bassett and al., 1975).

cal and physical variables and a second one of the paleontological variables will be used to verify if the resulting factors represent geographic groupings either identical or different. If geographic groupings of the paleontological variables are different of those of the chemical and physical variables, then this will be considered as an indication of provincialism. Finally a R-mode factor analysis of all variables will try to decipher the mutual correlations among the environmental parameters and *Chitinozoa* associations.

SAMPLES LOCATIONS

The transition between the *Gothograptus nassa* and the *Monograptus ludensis* biozones is well defined in Sweden (Gotland and Scania, Laufel *et al.,* 1975), in Poland (Holy Cross Mountains, Teller, 1969), in Germany (Thuringia, Jaeger, 1964), in Austria (Carnic Alps, Flügel *et al.,* 1977 ; Jaeger & Schönlaub, 1977), in Wales (Long Mountain, Palmer, pers. comm. 1976 ; and Colwyn Bay area, Warren, 1971 ; Rushton, pers. comm. 1976), in the Lake District (near Sedbergh and Town End, Rickards, 1969, and pers. comm. 1976) and in Shropshire (near Homer and Ludlow, Bassett *et al.,* 1975). For practical reasons sampling was confined to Gotland, Scania, the Holy Cross Mountains, Shropshire, the Lake District, the Long Mountain and the Colwyn Bay area.

In Gotland samples were taken along the transition between the Mulde Formation and the Klinteberg Formation at Fröjel 1 and 3 and at Mölner (sample location are as indicated in Laufel, 1974b). In Scania the transition between the *Cyrtograptus* Series and the *Colonus* Series was samplet in the Ö. Odarslöv quarry (Nyers & Nilsson, 1973 ; Laufel *et al.,* 1975). In the Holy Cross Mountains of Poland samples were taken in the Pragowiec Shales, outcropping in the Bardo–Pragowiec section (Teller, 1969 ; Tomczyk, pers. comm. 1977). In the Long Mountain samples were taken 400 m south of Breidden Station in the Trewern Brook Mudstone Formation (Palmer, 1970, and pers. comm. 1976), and in the Colwyn Bay area at Penrhiw-isaf, 5,5 km southwest of Colwyn Bay, along the transition from the Lower to the Upper Mottled Mudstones (Warren, 1971 ; Rushton, pers. comm. 1976). In the Lake District samples were taken at Town End, near Troutbeck, in the lower part of the Middle Coldwill Beds (Rickards, 1969, and pers. comm. 1976). In Shropshire samples were taken near Homer, along the road from Much Wenlock to Homer, in the Farley Member of the Coalbrookdale Formation (Bassett *et al.*, 1975), and near Ludlow, along the road from Ludlow to Aston, in the Wenlock Shales (Holland *et al.*, 1969). Figs 2 and 3 summarize the geographic and stratigraphic position of the samples taken.

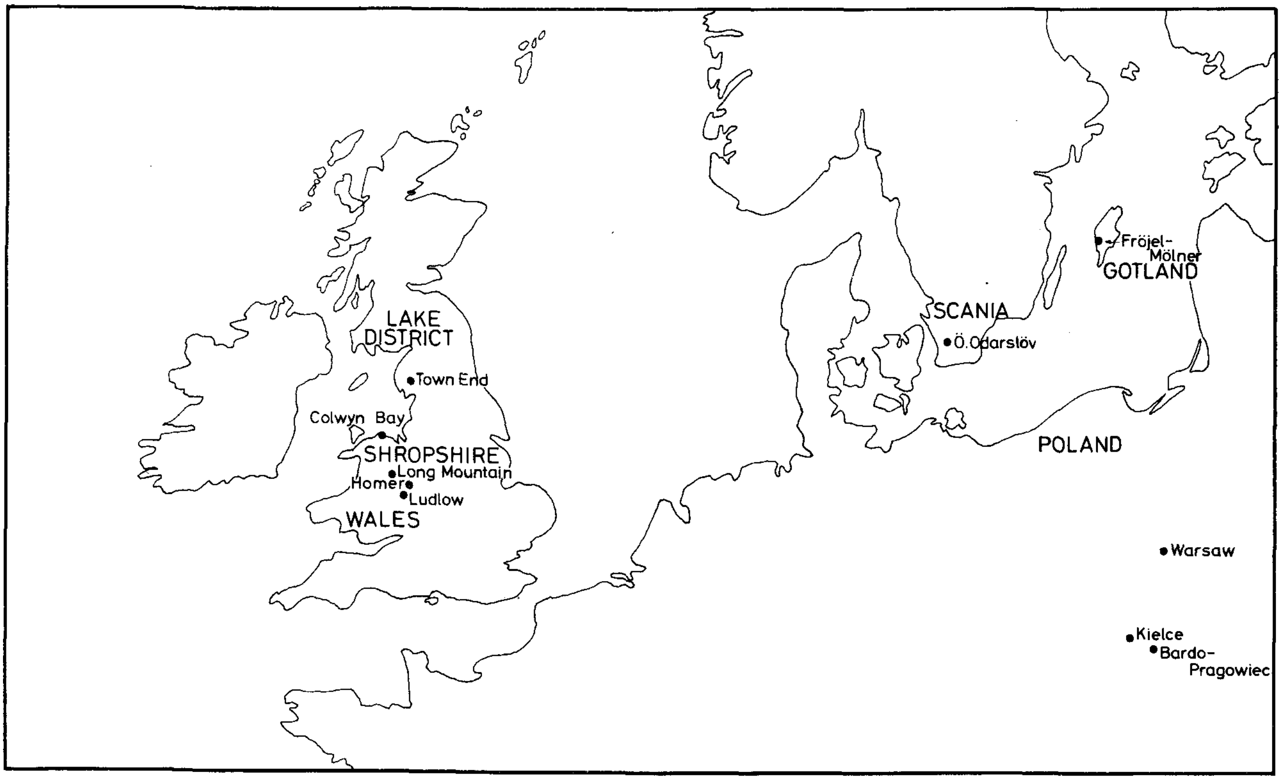

Figure 2.- Localisation of regions sampled.

CHRONOZONE	BIOZONE	GOTLAND	SCANIA	SHROPSHIRE HOMER	SHROPSHIRE LUDLOW	WALES LONG MOUNTAIN	WALES COLWYN BAY	LAKE DISTRICT	POLAND HOLY CROSS MTS
GLEEDON	*ludensis*	•F3E •F1A •F1C	•Sk3	•H7 •H6 •H2	•LU4	•LM6 •LM1	•W3 •W1	•T9	•P4 •P10
	nassa	•FX	•Sk2 •Sk1		•LU1	•LM4		•T7 •T3 •T1	•P9 •P13

Figure 3.- Stratigraphic position of the samples.

VARIABLES

Chitinozoan groups : Because of the highly variable degree of preservation of the *Chitinozoa* specimens, identification to the species level is not always possible with the same accuracy in all localities. For this reason, form groups were established on the basis of identification keys valid for all samples. The following form groups were defined :

- *Ancyrochitina ancyrea* group : specimens belonging to the species *Ancyrochitina ancyrea* and *Ancyrochitina gutnica* (Laufeld, 1974a).
- *Ancyrochitina* cf. *diabolus* group : specimens having the same characteristics as *Ancyrochitina* cf. *diabolus* (Laufeld, 1974a) and *Ancyrochitina diabolus* (Eisenack, 1977).
- *Ancyrochitina primitiva* group : specimens belonging to the species *Ancyrochitina primitiva* (Laufeld, 1974a ; Laufeld *et al.,* 1975).
- *Conochitina* aff. *elegans* group : specimens having the characteristics of *Conochitina* cf. *elegans* (Eisenack, 1964, 1968 and 1977) or of *Conochitina* aff. *elegans* (Laufeld, 1974a).
- *Conochitina pachycephala* group : specimens belonging to the species *Conochitina pachycephala* (Eisenack, 1964 and 1977) or resembling the form *Conochitina* sp., described by Jansonius (1964).
- *Linochitina cingulata* group : specimens belonging to the species *Linochitina cingulata* (Laufeld, 1974a).
- *Linochitina erratica* group : specimens belonging to the species *Linochitina erratica* (Eisenack, 1968 ; Laufeld, 1974a), *Linochitina* n. sp. aff. *Linochitina erratica* (Laufeld *et al.,* 1975, or *Linochitina odiosa* (Laufeld, 1974a).
- *Sphaerochitina lycoperdoides* groupes : specimens belonging to the species *Sphaerochitina lycoperdoides* (Laufeld, 1974a) and *Sphaerochitina concava* (Laufeld, 1974a).

The procentual frequencies of these form groups in each sample were used as variables in the multivariate data analyses (tab. 1).

Other paleontological variables : The following paleontological variables were also included in the factor analyses :

- Density of *Chitinozoa* : number of *Chitinozoa* specimens per 100 gram of dissolved rock sample.
- Diversity of *Chitinozoa* : the diversity of form groups in each sample was calculated by the formula:

$$H = - \sum_{i \times 1}^{k} \rho_i \ln \rho_i \text{ (Beerbouwer \& Jordan, 1969)}$$

with ρ_i = relative frequency of form group in the sample, expressed as a fraction between 0 and 1 ; k = number of form groups in the sample ; H = diversity of form groups.

- Density of *Scolecodonta* : number of *Scolecodonta* specimens per 100 gram of dissolved rock sample.

Chemical variables : Environmental parameters based on chemical analyses have the advantage of being numerical and expressed in the same scale for the different lithologies. The following parameters were selected :

- CO_2 content : represents the relative importance of carbonate sedimentation.
- Organic carbon content : represents the relative importance of anaerobic reducing sedimentary conditions.
- SiO_2 content : is used as a parameter for the detritic character of the sedimentary environment (Loring & Nota, 1973 ; Summerhayes, 1972 ; Wedepohl, 1968).
- MgO content : indicates the degree of diagenetic activity, dolomitization in the case of calcareous rocks, a slow ionic exchange resulting in a transformation to illite and chlorite in the case of argillaceous rocks.
- P_2O_5 content : was used in an exploratory sense, *data from literature being ambigious.*
- Na/K ratio : decreases with increasing ionic exchange, because of the higher mobility of sodium in sedimentary rocks and soils (Heier & Billings, 1970 ; Harriss & Adams, 1966). Sodium is mainly concentrated in the detritic fraction, potassium mainly in the authigenic clays. The sodium content increases with increaing geosynclinal character of the shales (Ronov *et al.,* 1965). Rapid deposition results in a high Na/K ratio (Hirst, 1962). The Na/K ratio is a parameter for sedimentation rate, making ionic exchange possible or not (Spencer, 1966), and for the detritic character of the shelfsediments (Loring & Nota, 1973).
- Fe^{II}/Fe^{III} ratio : Fe^{III} occurs relatively more in sands deposited close to the coast in comparison with pelitic sediments deposited in deeper seas (Loring & Nota, 1973).

Physical variables : Apart from the paleontological and chemical variables the following physical

Table 1.– Data matrix

SAMPLE \ VARIABLE	Chitinozoa Density	Chitinozoa Diversity	Chitinozoa Preservation	Scolecodonta	C. aff. elegans	C. pachycephala	L. cingulata	L. erratica	S. lycoperdoides	A. primitiva	A. ancyrea	A. cf. diabolus	CO_2	Organic Carbon	Na/K	Fe^{II}/Fe^{III}	P_2O_5	SiO_2	MgO	Time	Lamellation
Sk1	3140	63	1	0	0	0	10	81	0	10	0	0	13.9	1.60	0.33	1.71	0.14	46.7	3.76	1	1
Sk2	1394	81	1	0	0	0	15	74	2	10	0	0	9.3	1.82	0.32	1.53	0.22	48.3	4.11	1	1
Sk3	1050	97	1	0	0	0	10	67	6	17	0	0	10.0	1.11	0.34	1.39	0.26	47.6	4.23	2	0
T1	0	0	5	0	0	0	0	0	0	0	0	0	0.1	0.53	0.42	1.23	0.28	64.6	3.19	0	1
T3	0	0	5	0	0	0	0	0	0	0	0	0	0.2	0.66	0.49	1.11	0.28	62.8	3.14	0	1
T7	0	0	5	0	0	0	0	0	0	0	0	0	0.1	0.67	0.45	2.19	0.29	63.0	3.59	1	0
T9	0	0	5	0	0	0	0	0	0	0	0	0	4.1	0.77	0.50	4.70	0.15	54.4	5.55	2	0
F1A	8	0	1	0	0	100	0	0	0	0	0	0	41.1	0.40	0.35	0.82	0.04	1.7	0.48	2	0
F1C	4	0	1	0	0	100	0	0	0	0	0	0	41.4	0.35	0.19	0.83	0.03	1.5	0.93	2	0
F3E	0	0	1	0	0	0	0	0	0	0	0	0	41.7	0.39	0.30	0.80	0.02	2.4	0.68	3	0
FX	82	109	1	350	0	29	0	0	34	37	0	0	28.1	0.55	0.13	0.73	0.09	16.5	2.70	1	0
LU1	1038	171	2	32	11	18	31	17	9	14	0	0	27.5	0.55	0.41	1.27	0.09	21.4	1.26	3	0
LU4	2592	148	2	0	8	40	0	0	19	16	17	0	12.3	1.09	0.39	1.09	0.27	43.1	2.50	1	0
H2	174	0	2	36	0	100	0	0	0	0	0	0	9.5	0.58	0.38	0.33	0.33	49.3	2.18	2	0
H6	608	117	2	262	25	34	0	2	0	39	0	0	7.8	0.49	0.38	0.67	0.08	53.7	2.12	1	0
H7	322	137	2	32	5	8	9	4	21	53	0	0	7.7	0.62	0.48	0.63	0.11	54.3	2.05	1	0
LM1	1678	99	3	0	72	0	11	8	0	5	2	2	2.8	0.92	0.40	1.19	0.15	56.7	3.12	2	1
LM4	948	83	3	0	0	1	77	9	0	7	0	6	4.1	0.82	0.41	1.82	0.14	52.5	3.60	1	1
LM6	740	175	3	0	28	26	15	13	0	6	5	6	2.4	0.77	0.39	1.56	0.22	57.6	3.11	2	0
W1	82	144	4	0	15	44	12	10	0	20	0	0	0.2	0.64	0.33	2.72	0.12	60.8	2.59	2	0
W3	110	153	4	0	26	32	19	13	0	10	0	0	0.1	0.49	0.37	1.18	0.22	62.0	2.41	1	1
P4	116	60	1	0	71	0	0	0	0	29	0	0	4.2	4.23	0.26	1.06	0.27	54.1	3.55	4	0
P9	88	60	1	0	72	28	0	0	0	0	0	0	0.6	1.66	0.14	0.44	0.23	60.6	2.40	1	0
P10	383	114	1	0	43	41	11	6	0	0	0	0	1.1	3.16	0.18	0.65	0.26	60.9	2.41	2	0
P13	20	97	1	0	0	55	32	14	0	0	0	0	0.4	0.88	0.14	0.28	0.28	59.9	2.42	1	0

variables were included :

- Preservation of *Chitinozoa* : this variable was introduced to verify if certain form groups would be preferentially preserved after some detrimental diagenetic or metamorphic action. The following scale was established :

  1. All forms transparent and not flattened.
  2. *Ancyrochitina* and *Sphaerochitina* forms transparent, others not, but generally flattened.
  3. All forms opaque and flattened.
  4. All forms opaque, flattened and broken.
  5. No *Chitinozoa* preserved, other organic material strongly carbonized and fragmented.

- Time : a time dependent variable based on stratigraphic position of the sample was included to ascertain if the transition between the *Gothograptus nassa* zone and the *Monograptus ludensis* zone really is isochronous. To assess the possible influence of diachronism on the *Chitinozoa* associations, samples were also taken some meters below as above this transition and classified as follows :

0. middle *nassa* zone.
1. upper *nassa* zone.
2. base of the *ludensis* zone.
3. under *ludensis* zone.
4. middle *ludensis* zone.

- Lamellation : some samples exhibit a rythmic stratification not taken into account by the chemical variables. For this reason the following score was introduced :

0 = no lamellation ; 1 = lamellation present.

FACTOR ANALYSES

Q-mode factor analysis of physical and chemical variables : Eight physical and chemical variables, SiO_2, CO_2, organic carbon, P_2O_5 and MgO contents, Na/K and Fe^{II}/Fe^{III} ratios, and lamellation, were submitted to a Q-mode factor analysis towards the 25 samples. Only two eigenvalues were greater than 1.0000 and represent together 94 °/o of the total variance. The two corresponding factors were submitted to a Kaiser Varimax rotation. The resulting factor loadings and communalities are represented in table 2. The samples can be grouped by using logical operations on the numerical values of the two factor loadings. If f_1 is the loading on the first factor and f_2 the loading on the second, we can define the following four groups :

Table 2.- Loadings and communalites of the Q-mode factor analysis on the physico-chemical variables.

Group A : $f_2 > f_1$ and $f_1 < 0$
Group B : $f_2 > f_1$ and $f_1 > 0$
Group C : $f_1 > f_2$ and $f_2 > 0$
Group D : $f_1 > f_2$ and $f_2 < 0$

SAMPLE	FACTOR LOADINGS		GROUP	FINAL COMMUNALITY
	f 1	f 2		
SK 1	0.96402	0.16855	C	0.95775
SK 2	0.96371	0.06527	C	0.93300
SK 3	0.96157	0.10181	C	0.93498
T 1	0.98788	-0.09440	D	0.98482
T 3	0.98897	-0.09964	D	0.98799
T 7	0.98196	-0.08752	D	0.97190
T 9	0.83540	0.01151	C	0.69802
F1 A	-0.17261	0.97555	A	0.98150
F1 C	-0.12517	0.99157	A	0.99888
F3 E	-0.13585	0.98592	A	0.99050
FX	0.49879	0.79183	B	0.87578
LU 1	0.52960	0.82252	B	0.95701
LU 4	0.98628	0.15517	C	0.99683
H 2	0.96988	0.08384	C	0.94770
H 6	0.97576	0.04147	C	0.95383
H 7	0.97254	0.02726	C	0.94657
LM 1	0.99752	-0.05365	D	0.99793
LM 4	0.98636	-0.01323	D	0.97308
LM 6	0.99430	-0.05933	D	0.99216
W 1	0.95262	-0.09248	D	0.91603
W 3	0.97861	-0.10269	D	0.96822
P 4	0.85359	-0.10884	D	0.74046
P 9	0.96806	-0.11967	D	0.95145
P10	0.91097	-0.15186	D	0.85293
P13	0.97436	-0.10198	D	0.95978

(1) Group A : $f_2 > f_1$ and $f_1 < 0$
Group A contains the samples F1A, F1C and F3E of the *ludensis* zone of Gotland.

(2) Group B : $f_2 > f_1$ and $f_1 > 0$
Group B contains the samples FX and LU1 representing the *nassa* zone of Gotland and the *ludensis* zone of Ludlow.

(3) Group C : $f_1 > f_2$ and $f_2 > 0$
Group C contains the samples Sk1, Sk2, Sk3, LU4, H2, H6 and H7, representing the *nassa* and *ludensis* zone of Scania and Homer, and the *nassa* zone of Ludlow.

(4) Group D : $f_1 > f_2$ and $f_2 < 0$
This group contains all the remaining samples, representing the *nassa* and *ludensis* zone of the Lake District, the Colwyn Bay area, the Long Mountain and the Polish Holy Cross Mountain.

Looking at the factor scores (tab. 3) we notice that factor 1 is mainly characterized by the SiO_2-content and factor 2 mainly by the CO_2-content. Factor 1 can be interpreted as representing an environment characterized by a physical (detritic or authigenic) sedimentation, while factor 2 is characterized by a biogenic or chemical carbonate sedimentation. The influence of the carbonate sedimentation decreases in the following order : group A, group B, group C and group D, group D being almost exclusively characterized by physical sedimentation.

These results based on chemical parameters were compared with data obtained by conventional petrographic study. It allowed the following interpretation :

(1) Group A can be correlated with the biosparrudites and biosparrarenites of Gotland, except the biosparrarenites of Mölner (Sample FX), the clay content of which is too high.

(2) Group B can be correlated with the argillaceous limestones and the highly calcareous mudstones of Gotland (sample FX) and Shropshire (sample LU1).

(3) Group C can be correlated with the calcareous mudstones of Scania and shropshire.

(4) Group D can be correlated with the mudstones deficient in lime, the siltstones and sandstones of the Long Mountain, the Colwyn Bay area, the Lake District and the Holy Cross Mountains. Group D is an heterogenous group, having only abiogenic, physical sedimentation in common. The multivariate variances are too strongly determined by the CO_2 and SiO_2 contents, obliterating all other parameters. However if we look at the original data matrix (tab. 1) we see that chemical parameters as the Na/K ratio and the organic carbon content translate correctly the detritic character and the anaerobic conditions of the sedimentation, as would be expected from the petrographic data and the regional geologic context. We can deduce the following subdivisions :

- Detritic versus authigenic character (the Na/K ratio) : the detritic character is most important

Table 3.- Factor scores of the Q-mode factor analysis of the physico-chemical variables

VARIABLE	FACTOR SCORES 1	FACTOR SCORES 2
CO_2	-0.55719	2.32356
Organic Carbon	-0.19467	-0.42318
Na/K	-0.60930	-0.51149
Fe II / Fe III	-0.10640	0.00035
P2 05	-0.68950	-0.70943
Si 02	2.11837	-0.18349
MgO	0.83196	0.25223
Lamellation	-0.79327	-0.74855

in the samples of the Lake District, less marked in the samples of the Long Mountain and the Colwyn Bay area, and lowest in the Holy Cross Mountains samples, in which authigenic sedimentation prevails.

- Anaerobic, calm sedimentary environment (the organic carbon content) : most marked in the Holy Cross Mountains, less marked in the Long Mountain, and inconspicuous in the Lake District and the Colwyn Bay area.

The R-mode factor analysis of all variables (see below) will shown that the *Conochitina* aff. *elegans* form group will increase the variance along the axis determined by the Na/K ratio and the organic carbon content, so that this axis will appear as a separate factor.

Q-mode factor analysis of the *Chitinozoa* form groups : Only twenty samples were considered because the samples of the Lake District and sample F3E of Gotland do not contain *Chitinozoa.* The resulting twenty eigenvalues contain five eigenvalues greater than 1.0000, possessing 98 °/o of the total variance. After a Kaiser Varimax rotation we get five factor with loadings and communalities as shown in tab. 4. Looking at the factor scores (tab. 5), we can interpret the first factor as principally determined by an high abundance of *Conochitina pachycephala* form group specimens in a positive way, the second negatively by *Conochitina* aff. *elegans,* the third positively by *Linochitina erratica,* the fourth negatively by *Ancyrochitina primitiva,* and the fifth positively by *Linochitina cingulata.* This five factors cannot be grouped in a geographic way. Samples taken at the same locality are spread over different factors, excluding provincialism. Only the samples from Scania are characterized by a single factor, namely the *Linochitina erratica* factor. The *Conochitina pachycephala* factor is spread over the *ludensis* zones of Gotland, Homer and the Colwyn Bay area, and over the *nassa* zones of the Holy Cross Mountains and Ludlow. The *Conochitina* aff. *elegans* factor determines the *ludensis* zone of the Long Mountain and the *ludensis* and *nassa* zones of the Holy Cross Mountains. The *Ancyrochitina primitiva* factor characterizes the *nassa* zone of Gotland and Homer. The *Linochitina* factor is spread over the *ludensis* zone of Ludlow and the

Table 4.- Loadings and communalities of the Q-mode analysis on the Chitinozoa distribution

SAMPLE	FACTOR LOADINGS					FINAL COMMU-NALITY
	1	2	3	4	5	
SK 1	-0.06471	0.06887	0.98961	0.09813	0.04324	0.99976
SK 2	-0.07994	0.08622	0.98082	0.09695	0.11685	0.99888
SK 3	-0.10736	0.10546	0.98594	-0.03547	0.05315	0.99881
F1 A	0.99052	-0.02633	-0.11113	-0.03751	-0.04344	0.99748
F1 C	0.99052	-0.02633	-0.11113	-0.03751	-0.04344	0.99747
FX	0.33764	0.22793	-0.17000	-0.83651	-0.15022	0.91717
LU 1	0.28649	-0.13610	0.29284	-0.17851	0.86775	0.97122
LU 4	0.77028	0.05810	-0.32449	-0.34827	-0.30233	0.91470
H 2	0.99052	-0.02633	-0.11113	-0.03751	-0.04344	0.99747
H 6	0.45468	-0.49172	-0.07618	-0.68298	-0.08521	0.92805
H 7	-0.13845	0.08078	-0.01312	-0.98241	0.07917	0.99725
LM 1	-0.23345	-0.95768	-0.05791	0.11690	0.00896	0.98874
LM 4	-0.12803	0.12184	-0.01437	0.15288	0.97098	0.99763
LM 6	0.54779	-0.78068	0.06924	0.18895	0.21511	0.99632
W 1	0.85486	-0.32085	0.05423	-0.33292	0.17564	0.97818
W 3	0.65041	-0.65261	0.10936	-0.04346	0.37026	0.99988
P 4	-0.25008	-0.92057	-0.11750	-0.25167	-0.10878	0.99896
P 9	0.19840	-0.94349	-0.17634	0.09106	-0.12989	0.98391
P10	0.59928	-0.77393	-0.11070	0.11760	-0.06448	0.98835
P13	0.87264	0.03881	0.06787	0.10803	0.46976	0.99997

Table 5.- Factor scores of the Q-mode factor analysis on the distribution of the Chitinozoa form groups

CHITINOZOA FORM GROUPS	FACTOR SCORES				
	1	2	3	4	5
Conochitina aff elegans	-0.45157	-2.35353	-0.33814	0.26595	-0.28602
Conochitina pachycephala	2.45141	-0.06516	-0.27503	-0.09283	-0.10752
Linochitina cingulata	-0.25052	0.22882	-0.27867	0.44703	2.38588
Linochitina erratica	-0.07072	0.13267	2.41640	0.45553	-0.19300
Sphaerochitina lycoperdoides	-0.39833	0.82128	-0.48067	-0.50602	-0.47308
Ancyrochitina primitiva	-0.44475	0.04613	0.09827	-2.21379	0.02486
Ancyrochitina ancyrea	-0.33582	0.62809	-0.58360	0.77314	-0.81660
Ancyrochitina cf diabolus	-0.49870	0.56170	-0.55837	0.87101	-0.53451

nassa zone of the Long Mountain. Going from the *nassa* zone towards the *ludensis* zone, we can detect the following trends :

(1) In Gotland and Homer : grom *Ancyrochitina primitiva* to *Conochitina pachycephala* factor.

(2) In Ludlow : from *Conochitina pachycephala* to *Linochitina cingulata* factor.

(3) In the Long Mountains : from *Linochitina erratica* and *Linochitina cingulata* factors to *Conochitina* aff. *elegans* factor.

(4) Scania and the Holy Cross Mountains : remain stable and are determined by a single factor, respectively the *Linochitina erratica* factor and the *Conochitina* aff. *elegans* factor, except for one sample of the *nassa* zone of the Holy Cross Mountains (P13), which seems to be influenced by the *Conochitina pachycephala* factor.

The identical transitions in Homer and Gotland are remarkable. Looking at the regional geologic context, we see that both regions are characterized by a transition from a calcareous-rich sedimentation to a structurized reef building. The *Ancyrochitina primitiva* factor thus seems to correspond with a fore reef biotope and the *Conochitina pachycephala* with a reef biotope.

R-mode factor analysis of all variables : All 21 variables were submitted to an R-mode factor analysis towards the 25 samples. From the 21 resulting eigenvalues, only 4 are greater than 2.000 and contain 60 °/o cumulative variances. The Kaiser Varimax rotation gave loadings and communalities as indicated in tab. 6. The low communalities of the *Ancyrochitina ancyrea, Ancyrochitina* cfr. *diabolus* form groups and of the physical variables, lamellation and time, point to the restricted importance of these variables in the resulting factors. Seven eigenvalues are greater than 1.0000, with a cumulative variance of 93 °/o, six are greater than 1.5000, with a cumulative variance of 76 °/o, and four, as mentioned above, are greater than 2.0000, with a cumulative variance of 60 °/o. The information relevant to the environmental interpretation contained in the seven largest eigenvalues is analogous to the information contained in the four largest eigenvalues. By retaining seven factors we see that the first four factors are further split in "single variable" factors. The lamellation and time variables, which cannot be interpreted in the factors, give an important contribution to the variance. A R-mode factor analysis without these variables gives four factors with 63 °/o cumulative variance or six factors with 79 °/o cumulative variance. The samples from the Lake District also influence disproportionally the variance because of their lack of *Chitinozoa.* Without these samples an R-mode factor analysis results in four factors with 66 °/o cumulative variance or six factors with 80 °/o cumulative variance.

Returning to tab. 6 and 7, we see that two factors are controlled by physico-chemical variables and the two others by biological variables. The occurrence of specimens belonging to the genus *Conochitina* is determined by the physico-chemical factors, while the occurrence of the other genera is determined by the biological factors. The two physico-chemical factors represent bottom conditions ; hence a benthonic habitat can be concluded for the genus *Conochitina.* The genera *Sphaerochitina, Ancyrochitina* and *Linochitina,* the occurrence of which is independent

Table 6.- Loadings and communalities of the R-mode factor analysis

VARIABLE	FACTOR LOADINGS 1	2	3	4	FINAL COMMU-NALITY
Chitinozoa Density	-0.04702	0.07160	0.17153	0.82261	0.71345
Chitinozoa Diversity	-0.19641	0.24512	0.59483	0.40620	0.61749
Chitizonoa Preservation	-0.55092	-0.71373	-0.17535	-0.23817	0.90040
Scolecodonta Density	0.20533	-0.06193	0.73047	-0.21557	0.62606
C. aff elegans	-0.39642	0.67707	-0.01900	-0.13083	0.63305
C. pachycephala	0.57935	0.15527	-0.07639	-0.34416	0.48404
L. cinguata	-0.06032	-0.09711	-0.11172	0.59013	0.37380
L. erratica	-0.03361	0.08487	-0.08698	0.75411	0.58458
S. lycoperdoides	0.17603	-0.06001	0.86948	0.02851	0.79140
A. primitiva	-0.04802	0.07983	0.84978	0.02532	0.73145
A. ancyrea	-0.08133	0.03051	0.33519	0.23592	0.17556
A. cf diabolus	-0.14346	-0.13674	-0.09641	0.43820	0.24060
CO_2	0.94745	0.00347	0.03067	-0.01242	0.89877
Organic Carbon	-0.39942	0.77451	-0.10540	0.08896	0.77843
Na/K	-0.29729	-0.69895	-0.06109	0.11020	0.59279
Fe II/ Fe III	-0.34266	-0.48663	-0.20760	0.10063	0.40745
$P_2 O_5$	-0.78746	0.22175	-0.09906	0.07156	0.68421
$Si O_2$	-0.93871	-0.01870	-0.04053	0.01283	0.88334
M gO	-0.73908	-0.18855	-0.06622	0.28288	0.66619
Time	0.17882	0.51754	-0.12401	-0.02301	0.31573
Lamellation	-0.30887	-0.32521	-0.27833	0.48163	0.51059

of bottom conditions, are possibly planktonic. The characteristics of the four factors are :

(1) Factor 1 : a high CO_2 content, a low SiO_2 content and the presence of *Conochitina pachycephala* form groups specimens.

(2) Factor 2 : a high organic carbon content, low Na/K and Fe^{II}/Fe^{III} ratios, and the presence of *Conochitina* aff. *elegans* form group specimens.

(3) Factor 3 : a high diversity of *Chitinozoa*, the presence of *Scolecodonta* and of specimens belonging to the *Sphaerochitina lycoperdoides* and *Ancyrochitina primitiva* form groups.

(4) Factor 4 : a high density of *Chitinozoa* and the presence of specimens belonging to the *Linochitina erratica* and *Linochitina cingulata* form groups.

INTERPRETATION

Biotopes : The four factors of the R-mode factor analysis can be interpreted as biotopes. Factors 1 and 2 represent benthonic biotopes and factor 3 and 4 pelagic biotopes. The first factor corresponds to a biotope situated in an infralittoral, turbulent and oxydizing environment, in which preferentially *Conochitina pachycephala* form group specimens develop. The second factor corresponds to a circalittoral, calm and reducing environment, in which preferentially *Conochitina* aff. *elegans* form group specimens grow. The two pelagic biotopes (factor 3 and 4) can be distinguished, the first by a high Chitinozoa diversity, the second by a high Chitinozoa density. The contrast between high taxonomic diversity and high biologic density can be interpreted as the result of a stable trophic regime in the former case, and an unstable one, but with a higher nutrient supply, in the latter case (Valentine, 1973). In the light of this interpretation *Scolecodonta* and *Sphaerochitina lycoperdoides* and *Ancyrochitina primitiva* form group specimens seem to prefer a stable trophic regime, while *Linochitina erratica* and *Linochitina cingulata* form group specimens seemingly prefer a higher nutrient supply in a less stable trophic regime.

Table 7.- Factor scores of the R-mode factor analysis

SAMPLE	FACTOR SCORES			
	1	2	3	4
SK 1	0.26893	0.04418	-0.44055	2.43564
SK 2	-0.18390	0.19432	-0.38135	1.72305
SK 3	-0.10125	0.36772	0.15517	1.06650
T 1	-0.98667	-1.28199	-0.60847	-0.75944
T 3	-0.99424	-1.37114	-0.60356	-0.74427
T 7	-0.90036	-1.15007	-0.53809	-1.06598
T 9	-0.98019	-1.62368	-0.74109	-0.83019
F1 A	2.24445	-0.08694	-0.92809	-0.62788
F1 C	2.24544	0.01585	-0.88153	-0.63486
F3 E	1.96801	0.06948	-0.86163	-0.32590
FX	0.98775	-0.15965	2.93155	-0.64351
LU 1	1.07140	0.02143	0.43276	0.78539
LU 4	-0.15206	0.10225	1.66885	0.86523
H 2	0.65670	-0.04537	-0.62722	-0.98233
H 6	0.02477	-0.19682	1.58630	-0.73505
H 7	-0.12906	-0.55196	2.03007	-0.26929
LM 1	-0.67257	0.29442	-0.30569	0.69349
LM 4	-0.16025	-1.06798	-0.63662	1.97230
LM 6	-0.58244	0.04803	0.08856	0.75038
W 1	-0.42861	-0.34660	0.14665	-0.50492
W 3	-0.66830	-0.38842	-0.08499	-0.02367
P 4	-1.18069	2.64660	-0.14303	-0.70465
P 9	-0.59194	1.64777	-0.41782	-0.94933
P10	-0.61250	2.02337	-0.44641	-0.38094
P13	-0.04258	0.79518	-0.39376	-0.11078

Transgression and regression : Going from the *nassa* zone towards the *ludensis* zone we can deduce following trends :

(1) In Gotland and Shropshire we notice the replacement of the pelagic biotope, corresponding to factor 3 from the R-mode factor analysis, by an infralittoral biotope, corresponding to factor 1.

(2) The pelagic biotope, corresponding to factor 4 and characterizing the Scania and Long Mountain samples, shows a diminishing specificity with time : the factor scores of factor 4 decrease in Scania and the Long Mountain going from the *nassa* to the *ludensis* zones.

(3) The Colwyn Bay area, the Holy Cross Mountains of Poland and the Lake District remain stable with respect to time.

The replacement of the pelagic biotope by an infralittoral biotope in Gotland and Shropshire points to a regression during the *ludensis* zone. This regression did only have a minor influence on the sedimentary environment in the other localities. The Polish Holy Cross Mountains were situated in the deeper, reducing parts of the shelfsea, remaining deep enough during the *ludensis* zone regression to keep sedimentary conditions calm and reducing. The Lake District received a strong detritic supply from the Eocaledonian mountain chain, formed by the collision between the Laurentia and Baltica plates, and the *ludensis* zone regression hardly changed this situation. In Scania and the Long Mountain the *ludensis* regression resulted in a decreasing specificity of the pelagic biotope. The pelagic, offshore biotope (factor 4) is characterized by the dominance of *Linochitina* specimens. We can interpret an increase in *Linochitina* specimens going upward in the stratigraphic column in a certain locality as reflecting a transgressive phase, while a decrease of *Linochitina* specimens should point to a regressive phase.

CONCLUSIONS

One of the first problems arising in a paleoecological study is the objective representation of the paleoenvironment, against which the distribution of the biologic taxa will be checked. Parameters based on chemical analyses have the advantage of being numeric and expressed in the same scale for all lithologies. The study shows especially the CO_2 and organic carbon contents and the Na/K ratio to be usefull. The CO_2 content obiously represents carbonate sedimentation, the organic carbon content a reducing environment and the Na/K ratio the relative importance of detritic versus uthigenic sedimentation.

The *Chitinozoa* associations of the regions considered do not seem to be influenced by biogeographic differences. A Q-mode factor analysis showed the distribution of *Chitinozoa* to be controlled by five factors, representing ecological but not geographic groupings. The regions studied possibly form one biogeographic province separated from a possible Laurentia and Gondwana province. Only sampling extended to the corresponding plates can confirm this. The R-mode factor analysis showed that the distribution of the *Conochitina* species is controlled by two chemical factors reflecting bottom conditions, pointing to a benthonic habitat. The distribution of the other genera is controlled by two biological factors and independent of the sedimentary environment, from which we conclude a planktonic habitat. The factor scores of the R-mode factor analysis indicate that an increase of *Linochitina* specimens in the stratigraphic column corresponds to a transgression and a decrease to a regression.

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