Distribution of copepod egg-envelopes in sub-Recent sediments from the Banda Sea (Indonesia)

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Waveren, I.M. van. Distribution of copepod egg-envelopes in sub-Recent sediments from the Banda Sea (Indonesia). — Scripta Geol., 105: 53-67, 7 figs., 1 pl., Leiden, August 1994. I.M. van Waveren, Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands.

Key words: Copepoda, sub-Recent, Banda Sea, acritarch, distribution.

Sediment samples from the Banda Sea were clustered according to the percentages of the different morphotypes of copepod egg-envelopes they contained. The clustering indicates a geographically distinct cluster determined by the occurrence of higher percentages of a single type of copepod egg envelope. It may be indicative of the influence of Equatorial Indian Ocean surface water, notably in the southwestern part of the Banda Sea that is not affected by upwelling.

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Introduction

Palynomorphs having a spherical, ellipsoidal, discoidal, or polygonal body which possesses an equatorial line of weakness, along which complete or incomplete rupture tends to occur, have been included by Segroves (1967) in his acritarch subgroup Schizomorphitae. Their biological nature is obscure, although Cretaceous and Tertiary palynomorphs included in *Schizosporis* Cookson & Dettmann, 1959, or morphologically related form-genera, are frequently regarded as prasynophyte algae. Recently, however, palynomorphs corresponding to the diagnosis of schizomorphic acritarchs from sub-Recent sediments could be identified as the envelopes of crustacean (copepod) eggs (van Waveren, 1992; van Waveren & Marcus, 1993; see also McMinn et al., 1992). From surficial sediments of the Banda Sea, Indonesia, twenty distinctive morphotypes of copepod egg-envelopes were described. They constitute a prominent component of the overall palynomorph association (van Waveren, 1993). Elsewhere in the Indonesian waters, similar palynomorphs occur in sediments from the Java Sea (van Waveren, 1989) and the Flores Basin (pers. observ.). Also in



Fig. 1. Upwelling and downwelling in the the Banda Sea (redrawn from Wyrtki, 1957); 0000 = downwelling (February, NW monsoon), xxxx = upwelling (August, SE monsoon).

other parts of the world, they have been detected (usually misidentified or unidentified) in Neogene to Recent sediments from varied marine settings, e.g, in the Arabian Gulf (Caratini et al., 1978), offshore Venezuela (Caratini, et al., 1975), the Gulf of California (Martínez-Hernández & Hernández-Campos, 1991), and the Angola Basin (pers. observ.).

To date, this category of palynomorphs has not been subject of environmental interpretation as no ecological significance could be attributed to occurrences of the morphotypes. Since their zooplanktonic origin has now been firmly established, the present paper is a first attempt to establish a relationship between occurrences in deep-sea sediments and environmental variation.

In general, the Banda Sea represents an area of seasonal upwelling (Fig. 1). In August southeasterly winds blow away the surface water, which is replaced by nutrient rich water from deeper layers. In January nutrient depleted surface water penetrates the Banda Sea by northwesterly winds (Wyrtki, 1957; Zijlstra et al., 1990). The southwestern part of the Banda Sea, on the other hand, is unaffected by seasonal upwelling.

Seasonal variations in nutrient supply result in significant variations of the quantitative composition of the copepod communities that dominate zooplankton biomass in the Banda Sea (Baars et al., 1990). It may be hypothesised, therefore, that geographically determined variations in nutrient regime will influence the composition of the copepod egg-envelope component of palynological associations from surface sediments. Through a quantitative analysis, the present paper concentrates on a comparison of the copepod egg-envelope records from upwelling and non-upwelling areas in the Banda Sea.

Material and methods

A series of 62 samples (Table 1) was collected from box-cores taken along three transects of the Banda Sea, during cruise G-5 of the 1984–1985 Snellius II oceanographic expedition (van Hinte et al., 1986; Situmorang, 1992). The three transects are: (1) the Seram Transect (leg 2), (2) the Tanimbar Transect (leg 4), and (3) the Timor Transect (leg 6). Contrasting water-depths along these transects are determined by morphotectonic configuration (Fig. 2). The Seram Transect is a SW to NE cruise tract, south of Seram to Irian Jaya (Fig. 3), across the Weber Trough, the Gorong Structural High and the Seram Trough. The Tanimbar transect was taken approximately from east to west (Fig. 4), across the Weber Trough, the Tanimbar Structural High and the Tanimbar Trough. The Timor Transect was taken approximately from North to South, East of Timor (Fig. 5), across a variety of morphotectonic units between the South Banda Basin and the Sahul Shelf.

Sample processing

The samples were taken from the top 7 cm of the sediments in the box–cores. The

Table 1. Box-core numbers, water depth and general lithological description (after van Hinte et al., 1986; Situmorang, 1992).

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Box core	Water depth	Lithology
16	4090	washed out clay with volc. debris. Rabdomina at the top
20	5334	clay with volc, pebbles, at top sand with Rabdominas
22	6023	clay with volc, peoples, at top sand with volc, debris
24	5056	homogeneous and burrowed clay
26	4068	homogeneous clay with scattered foram.
27	3351	clay containing foram, top is clay with volcanic debris and foram.
30	2994	clay, homogeneous, burrows; forams decrease downcore
32	1960	foram ooze, foram clay
33	1723	foram ooze, at top foram clay
35	1091	sandy clay to sandy foram clay; foram ooze at the top
37	505	sand of medium fine size
38	372	sandy clay
43	823	foram nanno-ooze on homogeneous foram clay
49	1349	silty/sandy clay very unconsolidated
52	1967	foram ooze
54	2119	brown foram clay
58	1846	brown foram ooze
60	1564	homogeneous and burrowed foram ooze
61	1402	homogeneous and burrowed foram clay
62	1097	foram clay
63	919	clay with some foram.
65	486	clay with some forams and some volc. glass
66	160	coquina (shell hash) with silty clay pebbles
68	358	biogenic ooze
71	78	bioclastic sand with some volc. glass and clay pebbles
74	141	sand with volc. particles, at the top calcareous sand
76	346	blue stiff clay with some forams, at the surface coarse black sand
78	713	foram sand on burrowed foram sand
81	1077	foram ooze with distinct biotite/glauconite
83	1654	foram with nanno-ooze, top with foram ooze
86	1391	foram sand mixed with clay
88	1023	clay with some foram. and pteropods, foram ooze at the top
90	780	biogenic sand, coarser at the top
91	591	foram sand with dark grains
92	481	clay with peobles on alternating foram ooze and slity clay
94	460	foram sand
95	581	foram ooze of sand size, coarsening upwards
	1070	foram sand, the base is coarser, contains granules and peoples
90	2141	norally salid with his sorted granules and peoples
102	2070	homogeneous cleuwith forem
102	J272 AQA1	clay overlain by sandy clay with yold sand and FU foram
106	6241	clay (ovidised) on silty clay
110	6251	clay on laminated clay
111	5199	homogeneous sandy mud with volc clastics and tuff nellets
121	4059	homogeneous clay with faecal pellets, also some black grains
128	1414	muddy sand with dispersed glass granules
129	1777	homogeneous foram ooze with floating dark volc. (?) grains
130	2772	foram bearing muddy silty clay, dispersed volc, grains
133	2592	foram clay, at the top foram muddy laver
135	1727	foram ooze with a layer of metamorphic gravel
138	1038	clayey foram sand with terrigeneous pebbles
139	1570	foram ooze over foram sand
141	2294	calc. ooze with foram. and burrows
143	2870	clay with planktonic foram.
146	3000	homogeneous calcareous silty clay
148	1951	foram clay with characteristical vertical burrows
150	1832	foram nanno-ooze with burrows
152	1286	brown clay on planktonic foram. clay
157	416	foram ooze on nanno-foram ooze
159	210	foram ooze with shell hash (biogenic sand underneath)
162	90	sand with biomorpha on lamellibranchiata hash



Fig. 2. Sample/depth relation and morphotectonic units along the Seram, Tanimbar and Timor transects.



Fig. 3. Sample location Seram Transect.

samples were dried and dry weight was measured (for each sample c. 5 g of sediment). Calcium carbonate was dissolved with hydrochloric acid (HCl 30%). Silicates were dissolved with hydrofluoric acid (HF 43%). The organic residue was sieved over a 10 µm mesh screen. Following the method of Stockmarr (1971), two tablets containing a known number of exotic spores were added for subsequent assessment of particle concentration. The residue was mounted on a cover glass using a wetting agent (Cellobond), and dried. Elvacite was used as a permanent mounting medium.

Sample analysis

For each of the 62 samples 200 copepod egg-envelopes were counted, using normal transmitted light microscopy. The percentages of the 20 different morphotypes described by van Waveren (1992) were calculated (Table 2). These morphotypes include:

- 1. psilate morphotype;
- 2. pillared morphotype;
- 3. scabrate morphotype;
- 4. scabro-granulate morphotype;
- 5. scabro-spined morphotype;
- 6. scabro-annulate morphotype;

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- 7. cerebro-spined morphotype;
- 8. dendro-cerebrate morphotype;
- 9. palmate morphotype (Pl. 1, figs. 1, 3);
- 10. palmo-tectate morphotype;
- 11. alveo-reticulate morphotype;
- 12. septo-tectate morphotype (Pl. 1, figs. 2, 4);
- 13. murate morphotype;
- 14. columnar tecto-scabrate morphotype;
- 15. rugulate morphotype;
- 16. rugulo-palmate morphotype;
- 17. cerebrate morphotype;
- 18. pigmented aureolate morphotype;
- 19. pigmented dendrate morphotype;
- 20. pigmented verruco-spine morphotype.

Cluster analysis

In order to compare the composition of the copepod egg-envelopes in the different samples from the three transects, a Q-mode cluster analysis was performed by using BIOPAT, Program System for Biological Pattern Analysis (Hogeweg & Hesper, 1972; updated version 1984; see also Hogeweg, 1976). The analysis clustered the sam-



Fig. 4. Sample location Tanimbar Transect.



Fig. 5. Sample location Timor Transect.

ples (objects) as a function of the percentages of the 20 different morphotypes (properties). The applied clustering method is a non-supervised detection method, particularly useful for revealing the dominating pattern of a data set. The generated groups are validated by a label: a property not included in the clustering. The label for the present clustering is a geographical label.

The similarities between the samples are calculated using the city bloc distance (mean character difference). This similarity measure is expressed in the following way:

$$\mathbf{S}(\mathbf{A},\mathbf{B}) = \sum_{i=1}^{n} |\mathbf{P}_i \mathbf{a} - \mathbf{P}_i \mathbf{b}|$$

where S(a,b) is the similarity measure between a and b, *n* is the amount of prop-

Table 2. Percentages of morphotypes of copepod egg-envelopes recognised in palynological associations from sediments in the Banda Sea. Morphotypes 1-20 are listed vertically, sample (box-core) numbers are listed horizontally.

	16	20	22	24	26	27	30	32	33	35	37	38	43	49	52	54	58	60	61	62	
1 2	17.4	7.0	-	3.3	1.8	3.2	12.5	8.1	5.1	3.5	3.5	2.2	5.6	-	10.5	-	8.1	-	12.0	17.6	
3	6.4	7.5	4.7	4.9	22.5.	5.3	4.3	3.3	2.8	3.5	3.5	3.3	3.6	6.5	3.7	4.9	6.7	17.5	1.6	5.4	
5	0.6	1.0	3.1	0.5	9.9	-	-	-	-	24.8	24.5	-	0.4	5.5 2.0	-	-	-	0.9	0.5	0.6	
78	0.3	1.6	1.5	3.8	1.0	2.1	1.8	9.5	л. 1.В	5.8	- 5,8	-	5.6	4.5	3.1	4.4 4.9	1.9 0.5	1.5	0.5	6.1	
9 10	15.5 3.5	8.6	4.7	15.4	3.7	35.7	34.4	25.8	23.6	-	24.5	11.1	19.9 0.4	4.5	13.0 4.3	9.3 2.7	15.3 3.8	6.6 2.1	6.0 3.3	6.1 1.8	
11 12	_ 14.5	14.5	7.3	 23.0	2.4 24.1	8.5	1.4	4.8	12.5	_ 24.5	_ 18.8	5.0 49.7	 23.1	_ 20.5	26.5	4.4 28.6	2.4 13.9	2.1 14.7	2.2 23.5	2.4 3.0	
13 14	34.8 1.6	39.8	42.3	28.6	14.5 5.1	18.0 3.8	18.6	23.9 7.8	17.6	26.6	24.5 9.4	26.8	21.9 3.4	25.5 4.5	29.6 3,7	36.8	33.9 2.9	37.9 3.0	35.0 4.9	4 - 3.6	
15 16	-	17.2	10.9	-	2.9	2.5	0.7	0.9	0.1	0.6	0.6	0.5	6.0	0.5	-	-	0.9	2	-	Ξ	
17 18	1.3	1.0	0.8	-	0.8	0.7	0.3	0.9	- 1.4	0.6	0.6	-	0.4	1.0	-	4.4	0.9	- 0.9	Ξ	1.2	
19 20	1.0 2.2	-	4.7	2.2 2.2	0.5 1.3	0.7	0.3	2.4 0.5	2.3 1.4	1.2	1.1	0.5	4.4 4.4	2.5 2.5	2.5 2.5	-	4.3 4.3	4.5 5.4	6.5 1.6	5.4	
	63	65	66	68	71	74	76	78	81	83	86	88	90	91	92	94	95	97	98	99	102
1	6.2	10.6	2.8	-	0.8	-	-	-	0.4	0_4	-	3 0	2 1	0.7	2 5	2 4	-	-	-	0_4	-
3	4.9	2.3	3.3	3.7	4.6	2 -	6.6	1.7	7.1	7.1	1.6	5.4	ã.9	16.3	9.3	3.7	4.6	2 -	6.6	1.7	7.1
5	0.4	0.5	Ξ	0.6	0.8	-	-	1.2	0.8	0.4	1.2	-	2.3	2.3	0.5	0.8	0.5	-	0.6	-	4.5
78	4.0	1.1	0.5	1.8	3.9	-	6.6	4.1	0.8	2.9	-	1.5	-	3.1	-	0.4	1.5	-	0.6	0.4	1.9
9 10	6.2	10.6	7.2	8.6	3.1	2 -	13.3	18.3	24.5	21.4	18.0	13.4	23.2	12.3	17.7	15.5	32.6	18.2 3.0	12.9	14.4	25.7
11 12	1.8	1.7	0.5	0.6		-	16.6	11.8	0.5	23.9	2.4	11.9	2.3 9.3	0.7	13.4	15.5	28.6	12.1	11.6 22.7	0.9 43.7	
13 14	29.9 3.1	20.7	13.4	40.7	55.0	6 -	46.6	49.7 5.3	33.8	32.8 3.3	46.0	43.3 5.9	39.5	35.4 5.4	38.3	40.2	14.8	14.2	15.9 4.3	18.9	28.8 5.1
15 16	Ξ	-	0.5	-	6.2	-	Ξ	Ξ	Ξ	1.2	-	-	-	-1	2.9	-	-	-	Ξ	-	-
17 18	0.9	-	-	0.6	2.4	-	-	1.7 4.7	2.6 2.1	0.4	0.4	-	-	1.5 0.8	1.9 0.9	0.8	2.5 2.5	3.0	0.6 1.8	0.4 2.7	1.3
19 20	4.9 4.0	1.7 0.5	1.1 0.5	3.7 5.5	2.3 5.4	-	3.3 3.3	0.6 4.7	4.7 1.3	3.8 0.4	2.8 2.0	5.9	-	1.5 2.3	6.7 4.8	10.3 2.0	4.6 1.5	6.0	11.6	7.2 0.4	6.4
	104	106	110	111	121	128	129	130	133	135	138	139	141	143	146	148	150	152	157	159	162
1 2	2.4	-	1.в	1.5	-	-	-	_	1.6	-	-	-	-	-	2.7	-	1.2	-	-	-	-
3	9.0	21.3	7.8	1.4	7.5	-	2.2	6.5	4.1	5 -	15.5	-	-	-	8.1	B.9	3.5	9.0	3.7	17.7	4.3
5	1.9	-	0.5	0.5	-	-	69.6 0.7	-	0.8	-	-	- 0.9	0.9	-	-	0.8	1.2	- 1.3	3.7	Ξ	2
7 8	3.2	0.1	4.6	-	5.2	-	0.7	Ξ	0.8	-	1.1	3.8	0.9	3.5	4.0	2.4	2.3	1.2	1.2	Ξ	4.3
9 10	34.3	30.5	41.0	49.1	53.0	71.4	2.9	21.3	48.8	-	23.3	56.2	39.5 6.1	42.1	37.8 1.8	46.0	56.5	41.0 8.3	23.4 3.7	26.7	13.0
11 12	2.6 22.5	8.3	0.4	0.5	1.5 8.2	7.1	2	Ξ	8.9	25.0	1.1	1.9	6.1	- 8.8	6.3	22.6		8.3	1.2 3.7	2.2	8.7
13 14	12.2 1.9	31.5 2.7	12.4	17.3	7.5 3.0	21.4	1.5	31.1 13.1	19.5 4.9	25.0	11.0 26.6	13.3 7.6	32.4	17.5	22.5 8.1	1.6 5.6	15.3 5.9	18.6 5.1	39.5 11.1	31.1 6.7	39.1 21.7
15 16	-	-	0.9	1.4	-	-	2.9	1.6	-	Ξ	-	0.9	0.9	-	0.9	-	· -	-	1.2	2	÷
17 18	1.2 3.2	2.8 3.7	1.4	0.5	2.2 5.2	-	1.5	3.2 4.9	3.2	-	3.3 1.1	1.9	2.6	-	- 1.8	1.6 1.6	1.2 3.5	1.3 1.3	2.5 2.5	2.2	-
19 20	3.2 0.6	3.7	1.8 1.8	1.4 1.4	3.7	_	2.2	8.2	2.4 1.6	-	3.3	4.8	2.6	8.8	5.4	3.2	2.3	3.8 0.6	2.5 1.2	11.1	-

erties, P_i a is the value of the *i*-th property for sample a, and P_i b is the value of the *i*-th property for value b.

The clustering is agglomerative. Because the structure in the data set was expected to be weak due to the variety of factors it can reflect, Ward's (1963) clustering criterion was needed because of its strong filtering capacities (Hogeweg, 1976; Hogeweg & Hesper, 1981). This criterion minimises the sum of the square centroid as objects are being agglomerated. The protocol of the clustering is the dendrogram.



Fig. 6. Dendrogram showing clustering of Banda Sea samples according to percentages of 20 morphotypes of copepod egg-envelopes.





- (1) Northern Weber Trough (samples 16 to 35)
- (2) Gorong Structural High (samples 36 to 40)
- (3) Seram Trough (samples 42 to 54)
- (4) Irian Jaya Slope (samples 58 to 68)
- (5) Central Weber Deep (samples 97 to 111)
- (6) Tanimbar Structural High (samples 88 to 95)
- (7) Tanimbar Trough and Arafura Shelf (samples 71 to 86)
- (8) South Banda Basin to Timor Structural High (samples 121 to 135)
- (9) Timor Trough (samples 138 to 150)
- (10) Sahul Slope and Shelf (samples 152 to 162)

Results

Clustering

The dendrogram (Fig. 6) indicates a partition in two major categories of samples: (1) Cluster 1, composed of samples 27, 30, 95, 110, 111, 121, 128, 129, 133, 139, 141, 143, 146, 148, 150, and 152; and (2) Cluster 2, composed of all other samples.

The clustering was determined by relatively high percentages of copepod egg envelopes from morphotype 9.

The cluster analysis indicates that most samples from Cluster 1 are located along the Timor Transect. Thus, although samples 130, 135, 138, 148, 157, 159 and 162 from the Timor Transect belong to Cluster 2, part of the samples from this transect is characterised by a copepod egg-envelope content that is distinctily different from the overall composition elsewhere in the Banda Sea.

Abundance

In order to visualise the regional variations in composition and to analyse whether abundance and composition are related, the mean abundance of morphotype 9 in the different parts of the three transects (Fig. 7) is plotted together with the sum of all other morphotypes. Concentrations of copepod egg-envelopes (number per gram of dry sediment, calculated according to the method of Stockmarr, 1971) indicates that sediments from the Central Weber Trough (area 5) and the northern and central parts of the Timor Transect (areas 8 and 9) have relatively high abundances of morphotype 9.

Discussion

Quantitative composition and abundances of organic sedimentary particles are influenced by sedimentation rate (van Waveren, in prep.). High sedimentation rates may enhance the preservation potential of chemically labile organic matter constituents. In contrast to crustacean exoskeleton fragments, however, the general compositional characters of the studied copepod egg-envelope associations cannot be related to different sedimentation rates that have been estimated for individual parts of the Banda Sea (Ganssen et al., 1989; van de Paverd & Bjørklund, 1989). Consequently, geographical patterns in the quantitative distribution of copepod egg-envelopes are likely to reflect distribution patterns of source-communities of copepod species.

In the Banda Sea, most associations of copepod egg-envelopes from sediment samples from the Seram and Tanimbar Transects are dominated by Morphotypes 12 and 13 (see Table 2, see van Waveren, 1992). These transects cover areas influenced by seasonal upwelling. It may be assumed, therefore, that in the Banda Sea a dominance of morphotypes 12 and 13 could well be regarded as a reflection of upwelling conditions. During the upwelling season, copepod communities are dominated by the species *Calanoides philippinensis* and *Rhincalanus nasutus* (Baars et al., 1990). Further research is needed to determine whether these characteristic upwelling species produce egg-envelopes corresponding to these morphotypes.

In marked contrast to the Seram and Tanimbar Transects, along the Timor Transect at least part of the associations of copepod egg-envelopes is dominated by Morphotypes 9. The latter transect is situated outside the area with upwelling. There is no quantitative information on the composition of copepod communities. However, quantitative analysis of planktonic foraminifera recovered in the Banda Sea during oligotrophic conditions indicates a contrasting zooplankton composition along the Timor Transect (Troelstra & Kroon, 1989; Troelstra et al., 1989). The different community composition of planktonic foraminifera in this area is considered to be the effect of input of relatively eutrophic Equatorial Indian Ocean surface water. Similarly, therefore, the observed quantitative prominence of copepod egg-envelopes of Morphotype 9 is likely to be indicative of the influence of Indian Ocean waters in the southwestern part of the Banda Sea.

It is noteworthy that samples 95, 104, 110, 111 from the Central Weber Trough (Tanimbar Transect, area 5) and samples 27 and 30 from the Northern Weber Trough (Seram Transect, area 1) are also characterised by a high percentage of Morphotype 9; the dominance of this category, however, is less prominent than in samples from the Timor Transect. This implies that Indian Ocean surface water may still influence the nutrient regime in the central and even the northern part of the Banda Sea. A similar pattern was observed for the pteropod distribution by Schalk (1990). He describes an east-west differentiation for the size and species composition of pteropods from the euphotic zone of the Banda Sea during the southeastern monsoon. The eastern pteropod association is related to a mixed imported Pacific and local fauna, while the western association is a Java/Banda Sea fauna with Indian influence.

It should be realised that part of the samples of the Timor Transect are not characterised by the dominance of Morphotype 9. Most of these samples originate from either shallow areas (Sahul Shelf) or sites under the lee of Timor and neighbouring islands. It is here suggested that local oceanographic conditions may cause that these locations are less influenced by Equatorial Indian Ocean water.

Conclusion

In the Banda Sea there is every indication that the quantitative composition of copepod egg-envelope associations in surface sediments reflects geographical variations in the nutrient regime of the euphotic zone. Morphotype 9 may be indicative of the influence of Equatorial Indian Ocean surface water in areas not affected by upwelling, while the other morphotypes, morphotypes 12 and 13 in particular, reflect an upwellings regime, characterised by seasonally alternating oligotrophic and eutrophic conditions.

Acknowledgements

Research has been carried out as part of the Snellius-II Expedition, organised by the Indonesian Institute of Science (LIPI) and the Netherlands Council of Oceanic Research (NRZ). Much gratitude is due to Professor J.E. van Hinte and collaborators (Geomarine Centre, Free University, Amsterdam) for making available box-core samples from the Banda Sea. Cluster analysis was made possible through the kind support by Professor P. Hogeweg of the Theoretical Biology Group, Utrecht University. Constructive comments on the manuscript were given by J. van Ooyen, A.J.T. Romein and H. Visscher. The investigations were supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), listed under number W-57-258. Publication of the Netherlands Research School of Sedimentary Geology.

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Manucript received 16 February 1993.

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Plate 1

Examples of morphotypes of copepod egg-envelopes determining the cluster analysis.

1. Morphotype 9 (palmate morphotype), × 700. 2. Morphotype 12 (septo-tectate morphotype), × 900. 3. Detail of the wall structure of the palmate morphotype, × 1800. 4. Detail of the wall structure of the septo-tectate morphotype, × 9000.