Chitinous palynomorphs and palynodebris representing crustacean exoskeleton remains from sediments of the Banda Sea (Indonesia)

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Palynological residues from surface sediments in the Banda Sea (Indonesia) are characterised by the presence of chitinous palynomorph types that can be correlated with exoskeletons of crustaceans, notably calanoid copepods. A series of 27 palynomorph types are described and informally categorised. Also the quantitatively prominent transparent palynodebris and its diffuse degradation products are derived from crustaceans. Selective preservation of the chitinous remains is considered to be related to the effects of high plankton production and high sedimentation rate.

Contents

Introduction

Terrigenous and planktonic organic matter in palynological residues is composed of a range of biomacromolecules of a different nature and a varied resistance to degradation. Notably in vascular plants, one may recognise biomacromolecules that are particularly resistant (lignins, tannins, sporopollenin, cutans, suberans; Tegelaar et al., 1989; Tegelaar, 1990). This also applies to the algaeans, characteristic of various algal categories. Conversely, it is generally recognised that polysaccharides can be rapidly depolymerised and hydrolysed through enzymatic processes (Stout et al., 1988, 1989; Moers, 1989; Moers et al., 1989). Characteristic polysaccharide biomacromolecules, such as cellulose, chitin and various hemicelluloses, are thus considered to have a low preservation potential (Tegelaar et al., 1989; Tegelaar, 1990).

However, despite the relative lability of polysaccharide plant and animal tissues, paradoxically their structurally preserved remains occur throughout the Palaeozoic to Recent palynological record. Such records include well-preserved, rich and diverse associations of presumed chitinous palynomorphs of arthropod, annelid, protist and fungal origin (Traverse, 1988; van Waveren & Visscher, in press). The chemical background for their selective preservation during diagenesis and thermal maturation is unknown. At least part of the records suggest chemical transformation of chitin into more resistant organic macromolecules.

On a global basis, chitin is among the most prominent polysaccharides occurring in nature. Annual production of this nitrogenous polysaccharide has been estimated to correspond to 40.10^{13} g organic carbon, approximately the same as cellulose (Poulicek, 1985). High annual production is notably due to chitin formation by terrestrial and marine arthropods. Exoskeletons of arthropods are composed of a complex of chitin (15-27%) and protein (12-73%), with the rest of the exoskeleton consisting of inorganic and non-amino containing organic compounds (Austin et al., 1981).

Microscopic remains of arthropod exoskeletons may be regularly detected in palynological assemblages of Neogene to (sub-)Recent age. Remains of insects are well-known from terrestrial Quaternary deposits (e.g., van Geel, 1978; Mateus, 1992). Occurrences of arthropod remains in marine sediments, on the other hand, have not yet been comprehensively documented. They are known, however, from deep marine sedimentary settings in the Pacific, Atlantic and Indian Oceans, where unidentified appendages of crustaceans have been illustrated as part of Recent, Quaternary or Pliocene palynomorph associations (e.g., Boulouard & Delauze, 1966; Caratini et al., 1975, 1978; van der Kaars, 1987).

Apart from palynomorphs identified as copepod egg-envelopes (van Waveren, 1992, 1994; van Waveren & Marcus, 1993; van Waveren & Visscher, in press) of which the chemical composition is still unclear, a morphologically wide variety of presumed chitinous fragments of crustacean exoskeletons has been detected during a palynofacies analysis of box-core samples taken in the Banda Sea, Indonesia (van Waveren, 1989; van Waveren & Visscher, in press). As a contribution to the understanding of the fate of chitinous animal tissues in deep sea sedimentary environments, the present paper is a first attempt to describe and classify the crustacean exoskeleton component among both palynomorphs and palynodebris from (sub-)Recent marine sediments.

Material and methods

Material

Samples were collected from box-cores taken along the Seram, Tanimbar and Timor transects of the Banda Sea, during cruise G-5 of the Indonesian-Dutch Snellius-II expedition in 1984-1985 (van Hinte et al., 1986; Situmorang, 1992; van Waveren & Visscher, in press). The samples were taken from the top 7 cm of the sediments in the box-cores.

Sample processing and analysis

The 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 residue was sieved over a 10 μm mesh screen, mounted on a cover glass using a wetting agent (Cellobond), and dried. Elvacite was used as a permanent mounting medium. Analysis of permanent slides included the description and informal categorisation of morphologically characteristic exoskeleton fragments. Identification was achieved by comparison with the features of a copepod subjected to palynological sample preparation techniques and by comparison with literature illustrations (notably Sars, 1903-1918; Scott, 1909). Among the more commonly occurring fragments, 27 palynomorph types and one palynodebris type were distinguished. The types were described and identified with a varying degree of precision (copepod remains, crustacean remains, arthropod remains).

Descriptive terminology

The body of an arthropod consists of many segments (or somites), which may be alike or different and which constitute three primary body divisions (head, thorax and abdomen). Head somites are always fused together; in many arthropods other additional somites may also be fused. Each somite of the simpler arthropods has one or two pairs of jointed appendages. In more specialised arthropods most or all of the posterior appendages are lost. The appendages show a wide range of modification. They function for locomotion, respiration, grasping, mastication, oviposition and as sensory organs. In typical arthropods body parts as well as appendages are encased in a jointed chitinous exoskeleton.

Since exoskeleton remains in palynological residues from the Banda Sea sediments are most frequently derived from crustacean zooplankton, their description was mainly based on the following conventional terminology for copepods (Borradaile & Potts, 1961; Barnes, 1987; Fig. 1):

- **abdomen**: part of the copepod body caudal of the genital somite, including the genital somite;
- **antenna**: first and second appendage on the head of the copepod;
- **appendage**: antennae, mandibles, maxillae, maxillipeds, rami, and swimming feet of the copepod;
- **articulation**: joint between the different segments of the copepod;
- **basipodite**: segment of the swimming foot on which both the endopodite and the exopodite are attached;
- **biramous**: forked;
- **coxa**: segment of the swimming foot between the somite and the basipodite;
- **endopodite**: internal branch of the fork of a biramous appendage;
- **exopodite**: external branch of the fork of a biramous appendage;
- **gnathobasis**: basal lobe of a mandible;
- **implantation**: joint on the appendage where a hair or other process has been attached;

- **head**: conical to round cuticular exoskeleton segment, carrying the eye(s), the mandible, the maxilla, and the antennae;
- **intercoxal plate**: plate positioned between the two coxa of swimming feet;
- **mandible**: third appendage on the head;
- **maxilla**: fourth appendage on the head;
- **maxilliped**: first thoracic appendage;
- **protopodite**: the coxa and the basipodite of a swimming foot;
- **ramus**: single branch of the last biramous somite of the abdomen;
- **rostrum**: dorso-frontal prolongation of the head;
- **somite**: segment between two joints of the cylindrical cuticle enclosing the copepod body;
- **sternite**: ventral side of somite;
- **swimming foot**: second to sixth appendage of the thorax;
- **telson**: abdominal somite carrying the anus;
- **tergite**: dorsal side of the somite;
- **thorax**: part of the copepod situated between the head and the (first abdominal) somite carrying the genital operculum;
- **uniramous**: not forked.

For the description of the swimming feet of copepods the following definitions are used (see Fig. 2):

- **lateral side**: denticulate or convex side;
- **medial side**: concave and/or not ornamented side;
- **proximal articulation**: largest of the articulations;
- **distal articulation**: smallest articulation;
- **implantations**: smaller than the articulations, on the medial and lateral edges of the appendage;
- **length**: defined here as parallel to the medial side;
- **width**: defined here as the maximum width perpendicular to the length.

Denticulate mandible parts are described with the descriptive terminology developed by Jansonius & Craig (1971) for the morphologically related annelid palynomorphs (scolecodonts; see Fig. 3):

- **bight**: concavity of the outside face of a jaw, open to the posterior side;
- **dentary**: series of denticles along the inner dorsal margin; in some forms the dentary is edenticulate;
- **depth**: largest dimension of the inner or outer face of a jaw perpendicularly to the dentary and in the plane going through the dentary, measured from the base of the dentary to the ramal extremity;
- **falcal arch**: concave margin of the falx, may be denticulate or edenticulate;
- **falx**: sickle-shaped extension of the anterior part of the jaw, often forming a hook or a fang;
- **fenestra**: in dorsal view the translucent part approximately corresponding to the myocoelic opening;
- **length**: largest dimension of a jaw parallel to the median axis, between posterior-most and anterior-most points.
- **myocoele**: space inside, and more or less enclosed by, the jaw, usually extending to the tip of the denticles;

- **myocoele opening**: outline of the latero-ventral margin of the jaw faces, enclosing the myocoele.

In a scolecodont the anterior side is the side of the falx. The ventral side is the side of the falcal arch and dentary.

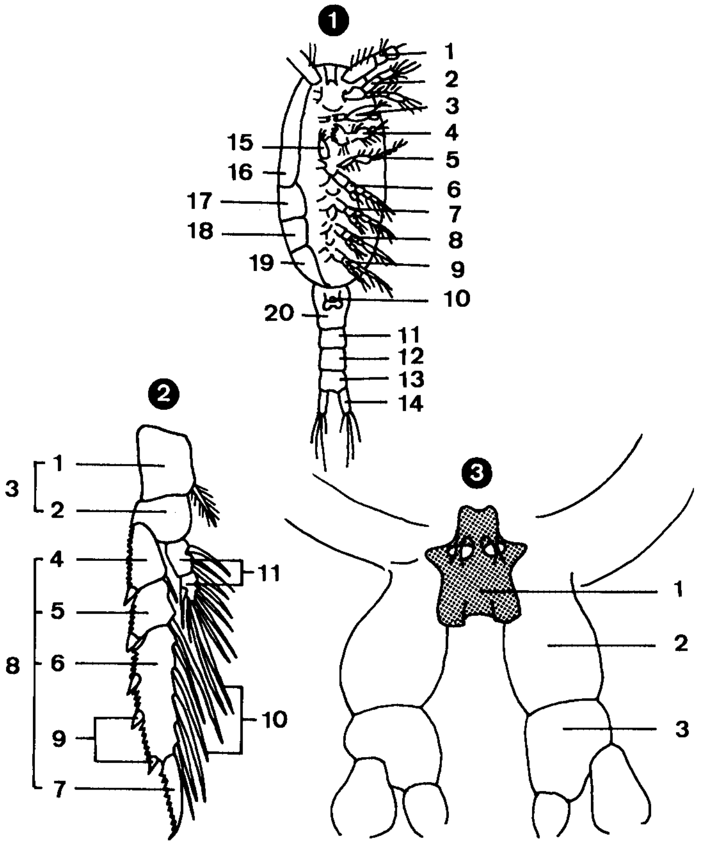

Fig. 1. Copepod descriptive terminology.

1 - Diagrammatic ventral view of *Pseudocalanus* (after Barnes, 1987); 1: 1st antenna; 2nd antenna; 3: mandible; 4: maxilla; 5: maxilliped; 6: 1st swimming foot; 7: 2nd swimming foot; 8: 3rd swiming foot; 9: 4th swimming foot; 10: genital operculum; 11: 2nd abdominal somite; 12: 3rd abdominal somite; 13: anal segment; 14: caudal ramus; 15: 2nd maxilla; 16: head with first somite fused; 17: 2nd thoracic somite; 18: 3rd thoracic somite; 19: 4th and 5th thoracic somites (fused); 20: genital segment (6th thoracic somite and 1st abdominal somite). Note that in *Pseudocalanus* the fifth pair of swimming feet is missing.

2 - Organisation of a calanoid swimming foot of *Candacida norvegica* (redrawn from Sars, 1911). 1: coxa; 2: basipodite; 3: protopodite; 4: 1st segment of the exopodite; 5: 2nd segment of the exopodite; 6: second-most distal segment of the exopodite; 7: most distal segment of the exopodite; 8: exopodite; 9: processes; 10: brushy hairs; 11: endopodite.

3 - Intercoxal plate of a calanoid copepod of the Candaciidae (drawn after a sample made available by M. Kouwelaar); 1: intercoxal plate; 2: coxa; 3: basipodite.

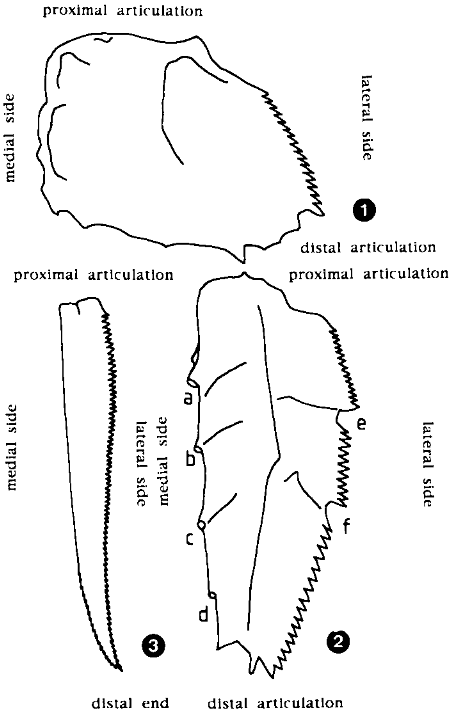

Fig. 2. Copepod appendage descriptive terminology.
1 - First or second segment of the exopodite of a swimming foot.
2 - Second-most distal segment of the exopodite of a swimming foot; a-f: implantations.
3 - Most distal segment of the exopodite of a swimming foot.

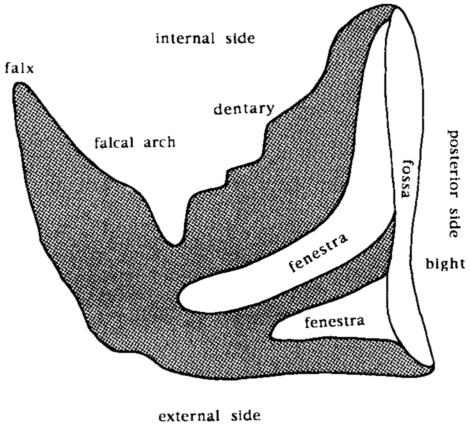

Fig. 3. Scolecodont descriptive terminology (after Jansonius & Craig, 1971).

Palynomorphs originating from copepod exoskeletons

Palynomorph Type 1 (PM 1) (Pl. 2, fig. 3)

Length-width ratio <1. Two main articulations; the upper one is approximately as wide as the lower one. Lateral side with denticulation. Single implantation, half the size of the articulations, situated between the lateral denticulate ornamentation and the lower articulation. Size varying between 100 and 250 µm. Colour generally light brown, occasionally either dark to opaque or transparent.

PM 1 represents the first or the second segment of the exopodite of a swimming foot of a member of the Candaciidae.

Palynomorph Type 2 (PM 2) (Pl. 2, fig. 4)

Length-width ratio between 2 and 4. Two main articulations; the upper one is only a little larger than the lower one. Lateral side ornamented with three different scales of denticulation, each separated by an implantation. Medial side without denticulation and with five implantations. Size strongly varying between 120 and 420 µm. Pigmentation sometimes very strong. Short hairs may occur on the upper surface of the palynomorph. Very rare specimens occur without the lateral denticulation. These are less well preserved as denticulated specimens; they are very thin and transparent.

Although some Candaciidae do not show a lateral denticulation at the second-most distal segment of the exopodite of the swimming feet, it is a characteristic feature of the family (pers. comm. J.C. von Vaupel Klein). PM 2 is the second-most distal segment of the exopodite of swimming feet of a member of the Candaciidae.

Palynomorph Type 3 (PM 3) (Pl. 2, figs. 6, 8-9)

Length-width ratio >5. Single superior articulation. No implantations. Denticulation often occurs on the lateral side. The denticles decrease in size distally. Denticulation is seldom seen on the medial side. Some specimens assignable to this category do not show any denticulation at all. Palynomorphs are bent, faintly sinusoidal or straight; they are widest at the upper half of the appendage. Pigmentation generally darker than in PM 1 and 2. Size varying between 130 and 200 µm.

As denticulation of the lateral side of the terminal spine is a common feature among copepods, PM 3 can only be identified as the most distal exopodite of the swimming foot of a calanoid copepod.

Palynomorph Type 4 (PM 4) (Pl. 2, fig. 7)

Single superior articulation. Palynomorphs are bent and have no denticulation. A faint longitudinal lineation can be seen on these palynomorphs.

PM 4 is identified as the distal segment of one of the fifth pair of swimming feet of several possible species of male calanoids.

Palynomorph Type 5 (PM 5) (Pl. 2, fig. 5)

PM 5 is similar to PM 4. It can be differentiated, however, by its spherical proximal articulation.

Because of its similarity to PM 4, PM 5 is also identified as the distal segment of one of the fifth pair of swimming feet of several possible species of male calanoids.

Palynomorph Type 6 (PM 6) (Pl. 2, figs. 4, 6)

Shape approximately pentagonal, elongated perpendicularly to the basal side. The three lower sides slightly concave, the two upper sides slightly convex; the top is truncated. Anterior and posterior sides have different structures. The anterior side has four holes in the upper half of the pentagon, two are perpendicular to the plane of observation and two are parallel to it. These elongate holes are situated symmetrically around the middle line, perpendicular to the base. Some of the palynomorphs of this type can have a hole in the middle part of the lower half, some have a medial constriction. These plates are thicker than most of the other crustacean palynomorphs. Size varying between 50 and 100 µm. Colour generally light greyish brown.

PM 6 is identified as the intercoxal plate between the two coxa of a copepod swimming-foot. The type was recognised in a dissected specimen belonging to the genus *Candacia*.

Palynomorph Type 7 (PM 7) (Pl. 4, fig. 3)

Tubular segment with an ornamentation of densely spaced pigmented hairs. The hairs look like a short mane. The tubular segment is greyish brown, the hairs are darker. Length 180 µm.

PM 7 is a copepod fragment, representing a segment of the antenna of a male *Candacia* at the location were the mane disappears.

Palynomorph Type 8 (PM 8) (Pl. 3, fig. 8)

Elongated transparent double spine. At its base this palynomorph has a transparent shield from which a double spine emerges, c. 8 µm wide and 150 µm long. The shield is larger at the base than at the point where the spines are attached.

Spines corresponding to PM 8 are identified as the rostrum of a calanoid copepod.

Palynomorph Type 9 (PM 9) (Pl. 4, fig. 1)

Series of convex denticles ornamented by a striation converging to the tip. A base line is present, concave at the tooth base. Colour transparent. Size c. 120 µm.

PM 9 is identified as the gnathobasis of the mandible of a copepod.

Palynomorph Type 10 (PM 10) (Pl. 4, fig. 5)

Depth to length ratio c. 1. Falcal arch very reduced. Dentary nearly edenticulate. A large fenestra and a smaller one are present. A small bight can be observed.

Length 95 µm. Colour light to dark brown.

PM 10 includes terminal fragments of the gnathobasis of the mandibles of calanoid copepods.

Palynomorph Type 11 (PM 11) (Pl. 4, fig. 6)

Shape triangular with a right angle at the posterior ventral side. Depth and length approximately equal. The falx is a double hook. The falcal arch is small. No dentary can be seen. A fenestra can be observed from the second hook to the myocoele opening. No bight can be seen. Length 45 µm. Colour light to dark brown.

PM 11 includes terminal fragments of the gnathobasis of the mandibles of the calanoid copepods.

Palynomorph Type 12 (PM 12) (Pl. 4, fig. 8)

Length to depth ratio >1. Falx formed by a slightly curved hook. The falcal arch shows a faint dentation. A dentary exists but without denticles. The fenestra is reduced. The bight is large (1/3 of the length) and is located on the ventral posterior side. Length 60 µm. Colour opaque to brown.

PM 12 includes terminal fragments of the gnathobasis of the mandibles of the calanoid copepods.

Palynomorph Type 13 (PM 13) (Pl. 3, fig. 1)

Palynomorph composed of light brown tissue. Two branches bifurcate approximately half way the tissue. The branches show a variable pattern of bifurcating smaller branches. A 'head' is visible with two less irregular branches. Size varying between 100 to 200 µm.

PM 13 is the sternite of a copepod, caudal of the mouth, at the level of the mandibles.

Palynomorph Type 14 (PM 14) (Pl. 3, figs. 2-3)

Tubular segment. Length/width ratio variable; length varying between 80 and 100 µm, width between 40 and 30 µm. Colour transparent to light brown.

These tubular segments could represent copepod tail segments.

Palynomorphs originating from crustacean exoskeletons

Palynomorph Type 15 (PM 15) (Pl. 3, figs. 9-11)

Elongated and curved palynomorph. Shape can be best described as the shape of an elephant tusk. Capillary channel present in the convex side of the fragments. Length 200-300 µm, width 4 µm at one end to 20 µm at the other end.

These elongated curved palynomorphs could not be identified with certainty through direct comparison. However, a crustacean (probably copepod) affinity is plausible, since their percentages in sediment samples show a correlation coefficient of 0.9 with the percentage of the sum of the copepod exopodite segments. PM 15 is also known from sediments of the Sea of Oman (Caratini et al., 1978, pl. 3, fig. 7).

Palynomorph Type 16 (PM 16) (Pl. 4, fig. 2)

Shape slightly flattened triangular. The external side is the triangle-base. The posterior side is one side of the triangle. The other side is denticulate. No falx or falcal arch can be seen here. The first denticle is underdeveloped, while the second is overdeveloped. The myocoele opening and the posterior side coincide. Here, the outline of the palynomorph nearly coincides with the myocoele, only the denticle-ends are not hollow. A small bight is present on the dorsal side of the posterior margin. Length 60 µm, depth slightly smaller. Colour transparent.

PM 16 could represent the resistant part of an amphipod mandible (see Vonk, 1988, fig. 28).

Palynomorphs originating from arthropod exoskeletons

Palynomorph Type 17 (PM 17) (Pl. 4, fig. 7; Fig. 4: 1)

Fossa and posterior side coincide. Sickle-shaped, with a slightly flaring handle. Mean size 60 µm. Colour opaque.

PM 17 is considered to represent mandible remains of arthropods (? crustaceans).

Palynomorph Type 18 (PM 18) (Fig. 4: 2)

Fossa and posterior side coincide. Feather-shaped, slightly curved at the tip. There is a small constriction between the handle and the feather. Mean size 60 µm. Colour opaque.

PM 18 is considered to represent mandible remains of arthropods (? crustaceans).

Palynomorph Type 19 (PM 19) (Fig. 4: 3)

Similar shape as PM 18, but with a denticle of 10 µm rooted just above the constriction, positioned on the side towards which the feather is curved. Mean size 60 µm. Colour opaque.

PM 19 is considered to represent mandible remains of arthropods (? crustaceans).

Palynomorph Type 20 (PM 20) (Fig. 4: 4)

Similar shape as Type 19, but the denticle is reduced to 4 µm and positioned at 1/3 of the distance between the constriction and the tip of the palynomorph. The tip of the palynomorph and the denticle diverge. The handle is flaring. Mean size 60 µm. Colour opaque.

PM 20 is considered to represent mandible remains of arthropods (? crustaceans).

Palynomorph Type 21 (PM 21) (Fig. 4: 5)

Fossa and posterior side coincide. No constriction. Reduced denticle, positioned

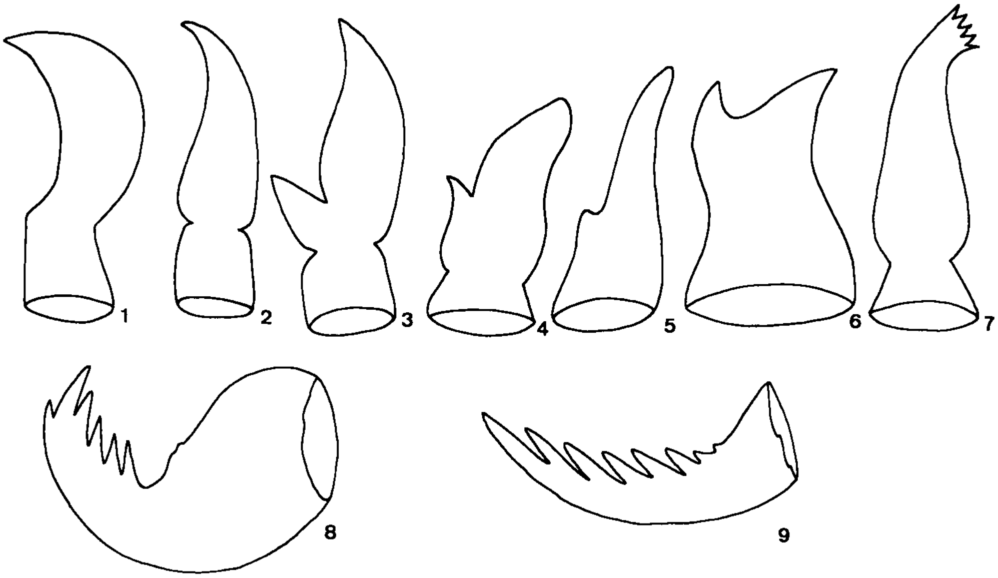

Fig. 4. Palynomorph types representing opaque arthropod mandible remains. 1: PM 17; 2: PM 18; 3: PM 19; 4: PM 20; 5: PM 21; 6: PM 22; 7: PM 23; 8: PM 24; 9: PM 25.

at 1/3 of the whole palynomorph. Fossa and posterior side coincide. Size varying between 40 and 80 µm. Colour opaque.

PM 21 is considered to represent mandible remains of arthropods (? crustaceans).

Palynomorph Type 22 (PM 22) (Fig. 4: 6)

Overall shape resembles that of PM 21, but the palynomorph is relatively wide and the denticle is much more pronounced and positioned next to the tip of the palynomorph. Size varying between 40 and 80 µm. Colour opaque.

PM 22 is considered to represent mandible remains of arthropods (? crustaceans).

Palynomorph Type 23 (PM 23) (Fig. 4: 7)

Overall shape resembles that of PM 18, but the tip is finely denticulate and the handle is strongly flaring. Mean size 60 µm. Colour opaque.

PM 23 is considered to represent mandible remains of arthropods (? crustaceans).

Palynomorph Type 24 (PM 24) (Fig. 4: 8)

Fossa and posterior side coincide. Denticulate falx. Denticles are of irregular length (1 to 4 µm). The dentary is edenticulate. Size varying between 40 and 80 µm. Colour opaque.

PM 24 is considered to represent mandible remains of arthropods (? crustaceans).

Palynomorph Type 25 (PM 25) (Fig. 4: 9)

Fossa and posterior side coincide. Acute denticles decreasing in size from the falx (6 µm) to the dentary. Size varying between 40 and 80 µm. Colour opaque.

A palynomorph resembling PM 25, but with only three denticles including the falx was identified by van Geel et al. (1989) as the mandibles of species of the insect genus *Sialis* (alder fly). Similarly it is here suggested that PM 25 might represent the remains of an insect mandible. Yet, a crustacean affinity cannot be completely ruled out.

Palynomorph Type 26 (PM 26) (Plate 4: 4)

Elongated fragments with acute denticulation. The denticles are loosely spaced. PM 26 represent unidentified arthropod remains.

Palynomorph Type 27 (PM 27) (Pl. 3, fig. 7)

Elongated bifurcated fragments. PM 27 represent unidentified arthropod remains.

Palynodebris originating from crustacean exoskeletons

Palynodebris Type 1 (PD 1) (Pl. 1, figs. 3-7; Fig. 5: 1-8)

Organic debris consisting of fragmented transparent tissue of varying shape and size. Tissue structureless. Larger fragments (60 to 100 µm) have the shape of an elongated hexagon, of which one side can be shorter than the other; elongated pentagonal shapes were also found. Larger fragments often folded along the longer axis; this axis can be bent. The folded tissues are sometimes found connected in rows of two or three elements. Often fragments can be found with grey to opaque inclusions; such fragments show also evidence of local thinning or disintegration of the tissue.

Identification of PD 1 in terms of a crustacean affinity has been experimentally supported. A copepod was subjected to the acid treatment applied in sample preparation for palynological analysis. The exoskeleton of this copepod appeared to be acid resistant. After acid treatment, particularly the dorsal somites still showed a clear delineation. The remains are frequently constituted of elongated transparent tissues, folded along the longer axis. Thus there is a direct correlation between at least the larger fraction of PD 1 and the dorsal somites of crustacean exoskeletons. Since the smaller fraction of the particles displays identical optical properties, the majority of transparent palynodebris may be considered to have a crustacean (possibly even copepod) origin.

Discussion

The description of organic remains of chitinous crustacean exoskeletons from marine deposits have attracted little attention. Yet, the regular occurrence of palynomorphs representing remains of crustacean exoskeletons have earlier been detected

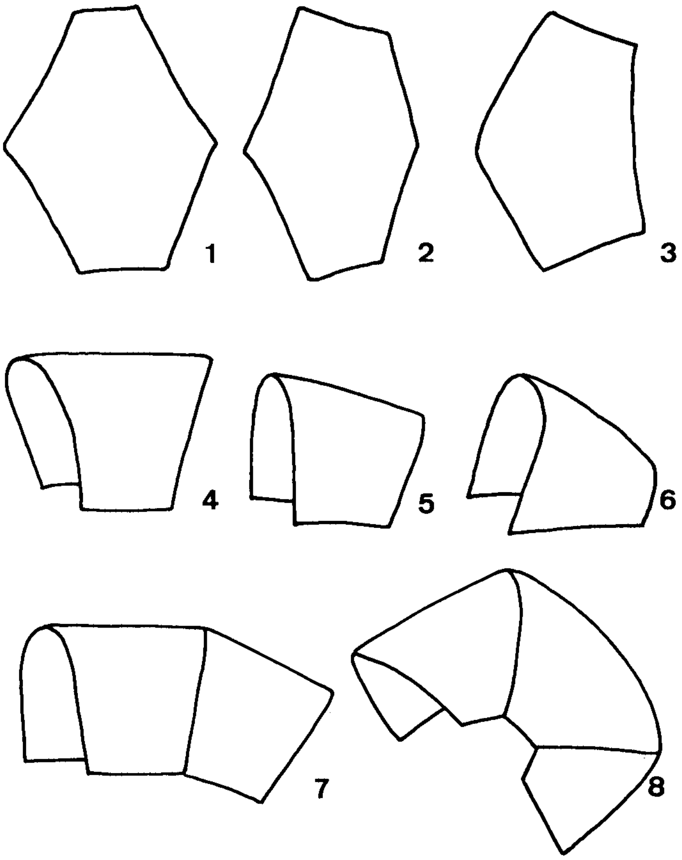

Fig. 5. Shape variation within PD 1. 1: hexagonal; 2: hexagonal with one shorter side; 3: pentagonal; 4: hexagonal, folded; 5: hexagonal with a shorter side, folded; 6: pentagonal, folded; 7: two attached dorsal somites; 8: three attached dorsal somites.

in Neogene to Recent palynological assemblages from a variety of sedimentary settings, ranging from coastal-brackish (Mateus, 1992) to deep-sea (Boulouard & Delauze, 1966; Caratini et al., 1975, 1978; van der Kaars, 1987) environments. The large number of distinctive palynomorph types found in the Banda Sea emphasises the variety of exoskeleton remains that may contribute to the composition of palynomorph associations in young deep-sea sediments.

More importantly, the present paper demonstrates that also the palynodebris component of palynological residues from young sediments may partly originate from crustacean exoskeletons. An assessment of the overall palynodebris composition in the Banda Sea (van Waveren & Visscher, in press)) suggests that in addition to about 72% palynodebris of terrigenous origin, about 28% of the debris corresponds to PD 1. Also from a quantitative point of view, therefore, the possibility of the presence of a significant crustacean-derived component should be taken into consideration when attempting to identify the origin of organic carbon in young marine sediments.

The possibility of a quantitative prominence of exoskeleton material is further supported by the presence of degradation products of PD 1. Apart from palynodebris and palynomorphs, also amorphous organic material represents an important constituent of the organic matter associations in the Banda Sea. Brown or greyish/transparent diffuse aggregates frequently dominate the palynological residues. Also the organic fraction <10 μm, sieved away during sample processing, mainly consists of amorphous material. Notably in the Timor transect diffuse aggregates are predominantly of the greyish/transparent type. These aggregates show an optical affinity to degraded greyish/transparent particles that may still be categorised as PD 1.

Although the palynodebris and many of the palynomorph types could not yet be identified below the level of crustaceans, the present author believes that by far the greatest part of the crustacean exoskeleton remains originate from planktonic copepods. In the Banda Sea and adjacent seas in the Indo-Malayan/Australian region, copepod communities largely dominate the zooplankton biomass (Baars et al., 1990; Arinardi et al., 1990; Othman et al., 1990). Species diversity is principally determined by representatives of the suborder Calanoida. A number of the palynomorph types encountered can be correlated with exoskeletons of calanoid species, specifically with representatives of the family Candaciidae.

In order to explain the preservation potential of a variety of animal and fungal palynomorphs, claims with respect to their chitinous nature (Traverse, 1989) need to be verified by thorough investigation of both fossil and modern material. However, among such palynomorphs, remains of arthropod skeletons are likely to be partially composed of chitin. In general, the chitin content of modern deep-sea sediments is reported to be very low (Poulicek et al., 1986). Rapid decomposition of chitin is notably due to the activity of (aerobic) chitinoclastic bacteria (ZoBell & Rittenberg, 1938; Campbell & Williams, 1951; Seki & Taga, 1963; Seki, 1966). Although rates of bacterial decomposition may drastically decline with decreasing water temperature (Seki, 1966), chitinoclastic bacteria remain active under deep-sea conditions (Kim & ZoBell, 1972). Occurrences of well-preserved chitinous palynomorphs in sediments of the Banda Sea, therefore, needs to be ascribed to external physical and chemical factors that may enhance chitin preservability.

It has been demonstrated that the burial rate and the degree of organic matter preservation in marine sediments are positively correlated with sedimentation rate (Berner, 1989; Betts & Holland, 1991). In accordance with the results of a comprehensive palynofacies analysis (see van Waveren & Visscher, in press), it is suggested that mass-occurrence of crustacean exoskeleton remains in sediments from the Banda Sea is related to the combined effects of (1) high plankton productivity caused by seasonal upwelling (Schalk, 1987; Gieskes et al., 1988; Baars et al., 1990) and (2) high sedimentation rate (Ganssen et al., 1989; Situmorang, 1992).

Conclusions

Environmental conditions that are conducive to the preservation remains of chitinous crustacean skeletons in young sediments prevail in the Banda Sea. In palynological residues these remains include a variety of palynomorph types, as well as quantitatively prominent transparent palynodebris and its diffuse degradation products. Selective preservation of the chitinous remains is considered to be related to the effects of high plankton production and high sedimentation rate.

Acknowledgements

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References

Arinardi, O.H., M.A. Baars, & Oosterhuis, S.S., 1990. Grazing in tropical copepods, measured by gut fluorescence, in relation to seasonal upwelling in the Banda Sea (Indonesia). — Netherl. J. Sea Res., 25, 4: 545-560.

Austin, P.R., C.J. Brine, J.E. Castle & J.P. Zikakis, 1981. Chitin: new facets of research. — Science, 212: 749-753.

Baars, M.A., A.B. Sutumo, S.S. Oosterhuis & O.H. Arinardi, 1990. Zooplankton abundance in the eastern Banda Sea and northern Arafura Sea during and after upwelling season, August 1984 and February 1985. — Netherl. J. Sea Res., 25, 4: 527-543.

Barnes, R.D., 1987. Invertebrate zoology (5th edition). — Sauder College Publish., Philadelphia: 1-893.

Berner, R.A., 1989. Biogeochemical cycles of carbon and sulfur and their effect on atmospheric oxygen over Phanerozoic time. — Palaeogeogr., Palaeoclimatol., Palaeoecol. (Global Planet. Change Sect.), 75: 97-122.

Betts, J.N., & H.D. Holland, 1991. The oxygen content of ocean bottom waters, the burial efficiency of organic carbon, and the regulation of atmospheric oxygen. — Palaeogeogr., Palaeoclimatol., Palaeoecol. (Global. Planet. Change Sect.), 97: 5-18.

Borradaile, L.A., & F.A. Potts, 1961. The Invertebrata. — Univ. Press, Cambridge: 1-820.

Boulouard, C., & H. Delauze, 1966. Analyse palynoplanctologique de sédiments prélevés par le bathyscape 'Archimède' dans la Fosse du Japon. — Marine Geol., 4: 461-466.

Campbell, L.L., & O.B. Williams, 1951. A study of chitin-decomposing micro-organisms of marine origin. — J. Gen. Microbiol., 5: 894-905.

Caratini, C., J. Bellet, & C. Tissot, 1975. Étude microscopique de la matière organique: palynologie et palynofaciès. In: Géochimie Organique des Sédiments Marins Profonds, Orgon II, Atlantique Nord-Est Brésil. — C.N.R.S., Paris: 157-203.

Caratini, C., J. Bellet, & C. Tissot, 1978. Étude microscopique de la matière organique: palynologie et palynofaciès. In: Géochimie Organique des Sédiments Marins Profonds, Orgon IV, Golf d'Aden, Mer d'Oman. — C.N.R.S., Paris: 265-307.

Ganssen, G., S.R. Troelstra, B. Faber, W.A. van der Kaars, & M. Situmorang, 1989. Late Quaternary palaeo-oceanography of the Banda Sea, eastern Indonesian piston cores (Snellius-II Expedition, cruise G5). — Netherl. J. Sea Res., 24, 4: 491-494.

Geel, B. van, 1978. A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. — Rev. Palaeobot. Palynol., 25: 1-120.

Gieskes, W.W.C., G.W. Kraay, A. Nontji, D. Setiapermana, & A.B. Sutumo, 1988. Monsoonal alternation of a mixed and a layered structure in the phytoplankton of the euphotic zone of the Banda Sea (Indonesia); a mathematical analysis of algal pigment fingerprints. — Netherl. J. Sea Res., 22, 2: 123-137.

Hinte, J.E. van, & Shipboard Party, 1986. Theme I, Geology and Geophysics of the Banda Arc and adjacent Areas. The Snellius-II Expedition Report. — R. Netherl. Acad. Arts Sc.-Indon. Inst. Sc.: 1-79.

Jansonius, J., & J.H. Craig, 1971. Scolecodonts: 1. Descriptive terminology and revision of systematic nomenclature; 2. Lectotypes, new names for homonyms, index of species. — Bull. Can. Petrol. Geol., 19, 1: 251-302.

Kaars, W.A. van der, 1987. Neogene palynology of Deap Sea Drilling Project site 603 on the lower continental rise, northwestern Atlantic. — Init. Repts. DSDP, 92: 783-788.

Kim, J., & C.E. ZoBell, 1972. Agarase, amylase, cellulase and chitinase activity at deap-sea pressure. — J. Oceanogr. Soc. Japan., 28: 131-141.

Mateus, J.E., 1992. Holocene and present-day ecosystems of the Carvalhal Region, Southwest Portugal. — Doctor's Thesis, Univ. Utrecht: 1-184.

Moers, M.E.C., 1989. Occurrence and fate of carbohydrates in Recent and ancient sediments from different environments of deposition. — Doctor's Thesis, Univ. Technology, Delft: 1-195.

Moers, M.E.C., J.J. Boon, J.W. de Leeuw, M. Baas, & P.A. Schenck, 1989. carbohydrate speciation and Py-MS mapping of peat samples from a subtropical open marsh environment. — Geochim. Cosmochim. Acta, 53: 2011-2021.

Othman, B.H.R., J.G. Greenwood, & P.C. Rothlisberg, 1990. The copepod fauna of the Gulf of Carpentaria, and its Indo-West Pacific affinities. — Netherl. J. Sea Res., 25, 4: 561-572.

Poulicek, M., 1985. Importance of chitin in the biogeochemical cycling of heavy metals in oceanic environment. — SCOPE Belgium, Proc. 'Metal Cycling in the Environment': 153-165.

Poulicek, M., R. Machiroux, & C. Toussaint, 1986. Chitin diagenesis in deep-water sediments. In: R. Muzzarelli, C. Jeuniaux & G.W. Gooday (eds). Chitin in nature and technology. — Plenum Press, New York: 523-530.

Sars, G.O., 1903-1918. An account of the Crustacea of Norway, 5-6. — Bergen Museum, Bergen: 449 pp., 230 pls, suppl. pls 1-45 (5); 225 pp., 118 pls.

Schalk, P.H., 1987. Monsoon related changes in zooplankton biomass in the eastern Banda Sea and Aru Basin. — Biol. Oceanography, 5: 1-12.

Scott, A., 1909. The Copepoda from the Siboga expedition, 1. Free-swimming, littoral, and semi-parasitic Copepoda. — Siboga Expedition Monogr., 29a: 1-323.

Seki, H., 1966. Microbiological studies on the decomposition of chitin in marine environment. X. Decomposition of chitin in marine sediments. — J. Oceanogr. Soc. Japan, 21: 265-269.

Seki, H., & Taga, 1963. Microbiological studies on the decomposition of chitin in marine environment, 3. Aerobic decomposition of chitin by the isolated chitinoclastic bacteria. — J. Oceanogr. Soc. Japan, 19: 35-38.

Situmorang, M., 1992. Sedimentology and marine geology of the Banda Arc, Eastern Indonesia. — Geol. Ultraiectina, 84: 1-191 (Doctor's Thesis, Univ. Utrecht).

Stout, S.A., J.J. Boon, & W. Spackman, 1988. Molecular aspects of the peatification and early coalification of angiosperm and gymnosperm woods. — Geochim. Cosmochim. Acta, 52: 405-414.

Stout, S.A., W. Spackman, J.J. Boon, P.G. Kistemaker, & D.F. Bensley, 1989. Correlations between the microscopic and chemical changes in wood during peatification and early coalification: a canonical variant study. — Int. J. Coal Geol., 13: 41-64.

Tegelaar, E.W., 1990. Resistant biomacromolecules in morphologically characterized constituents of kerogen: a key to the relationship between biomass and fossil fuel. — Doctor's Thesis, Univ. Utrecht: 1-191.

Tegelaar, E.W., J.W. de Leeuw, S. Derenne, & C. Largeau, 1989. A reappraisal of kerogen formation. — Geochim. Cosmochim. Acta, 53: 3103-3106.

Traverse, A., 1988. Paleopalynology. — Unwin Hyman, Boston, Mass.: 1-600.

Vonk R., 1988. Amsterdam expeditions to the West Indian Islands, Report 55. *Psammonelita uncinata* n. sp. (Crustacea, Amphipoda, Melitidae) from infralittoral sand interstices of Curaçao. — Stygologia, 4-2: 166-176.

Waveren, I.M. van, 1989. Palynofacies analysis of surface sediments from the northeastern Banda Sea (Indonesia). — Netherl. J. Sea Res., 24: 501-509.

Waveren, I.M. van, 1992. Morphology of probable planktonic crustacean eggs from the Holocene of the Banda Sea (Indonesia). In: M.J. Head & J.H. Wrenn (eds). Neogene and Quaternary Dinoflagellate Cysts. — A.A.S.P. Foundation, Dallas, Texas: 89-120.

Waveren, I.M. van, 1994. Distribution of copepod egg-envelopes in sub-Recent sediments from the Banda Sea. — Scripta Geol., 105: 53-67, 1 pl.

Waveren, I.M. van, & N.H. Marcus, 1993. Morphology of recent copepod egg envelopes and their implication for acritarch affinity. In: S.G. Molineux & K.J. Dorning (eds.). Contribution to acritarch and chitinozoan research. — Spec. Papers Palaeont., 48: 111-125.

Waveren, I.M. van, & H. Visscher, in press. Analysis of the composition and selective preservation of organic matter in surficial deep-sea sediments from a high-productivity area (Banda Sea, Indonesia). — submitted to Palaeogeogr., Palaeoclimatol., Palaeoecol.

ZoBell, C.E., & S.C. Rittenberg, 1938. The occurrence and characteristics of chitinoclastic bacteria in the sea. — J. Bacteriol., 35: 275-287.

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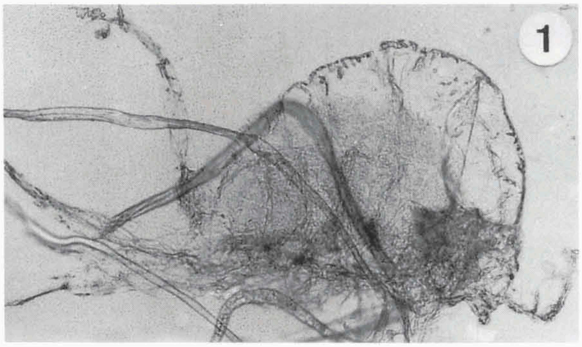
Plate 1

1. Specimen of *Pseudocalanus elongatus* (Boeck), after palynological treatment; slide COP-2; × 100.
2. Former picture, redrawn with emphasis on the dorsal somite delineation.
3. PD 1; three attached fragments, medially folded; sample SN-379; × 400.
4. PD 1; two attached fragments, medially folded; sample SN-379; × 400.
5. PD 1; fragment curled inwards; sample SN-379; × 800.
6. PD 1; hexagonal fragment; sample SN-379; × 400.
7. PD 1; pentagonal fragment, medially folded; sample SN-379; × 400.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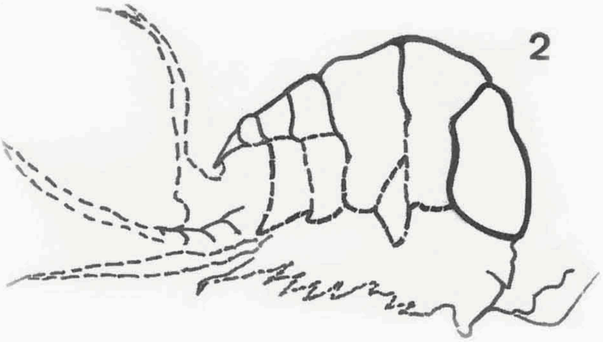
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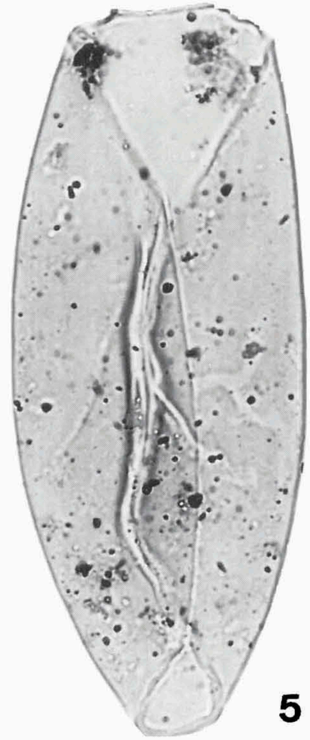
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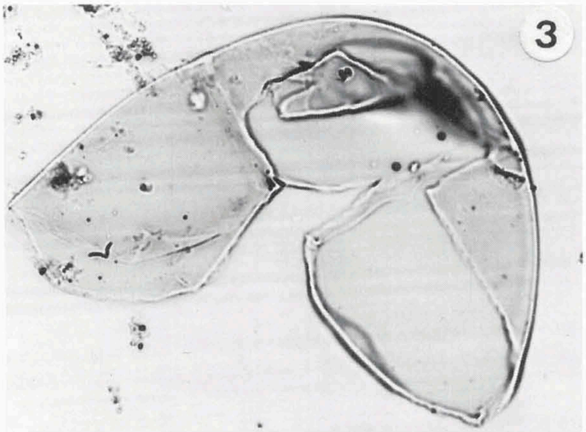
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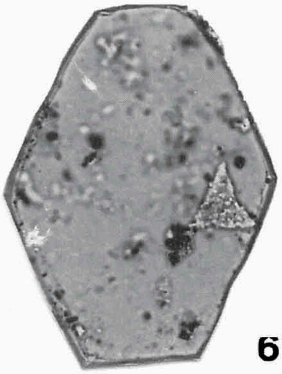
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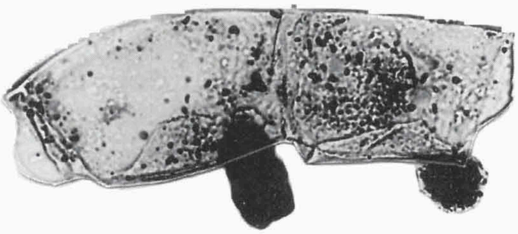

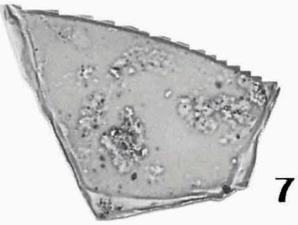
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Plate 2

1. Appendages of *Pseudocalanus elongatus* (Boeck), after palynological treatment; slide COP-2; × 100.
2. Former picture, redrawn with emphasis on the segmentation and shape of the terminal foot.
3. PM 1; copepod exopodite segment; sample SN-240; × 400.
4. PM 2; copepod exopodite segment; sample SN-240; × 400.
5. PM 5; copepod exopodite segment; sample SN-240; × 400.
6. PM 3; copepod exopodite segment; sample SN-240; × 400.
7. PM 4; copepod exopodite segment; sample SN-240; × 400.
8. PM 3; copepod exopodite segment; sample SN-240; × 400.
9. PM 3; copepod exopodite segment; sample SN-240; × 400.

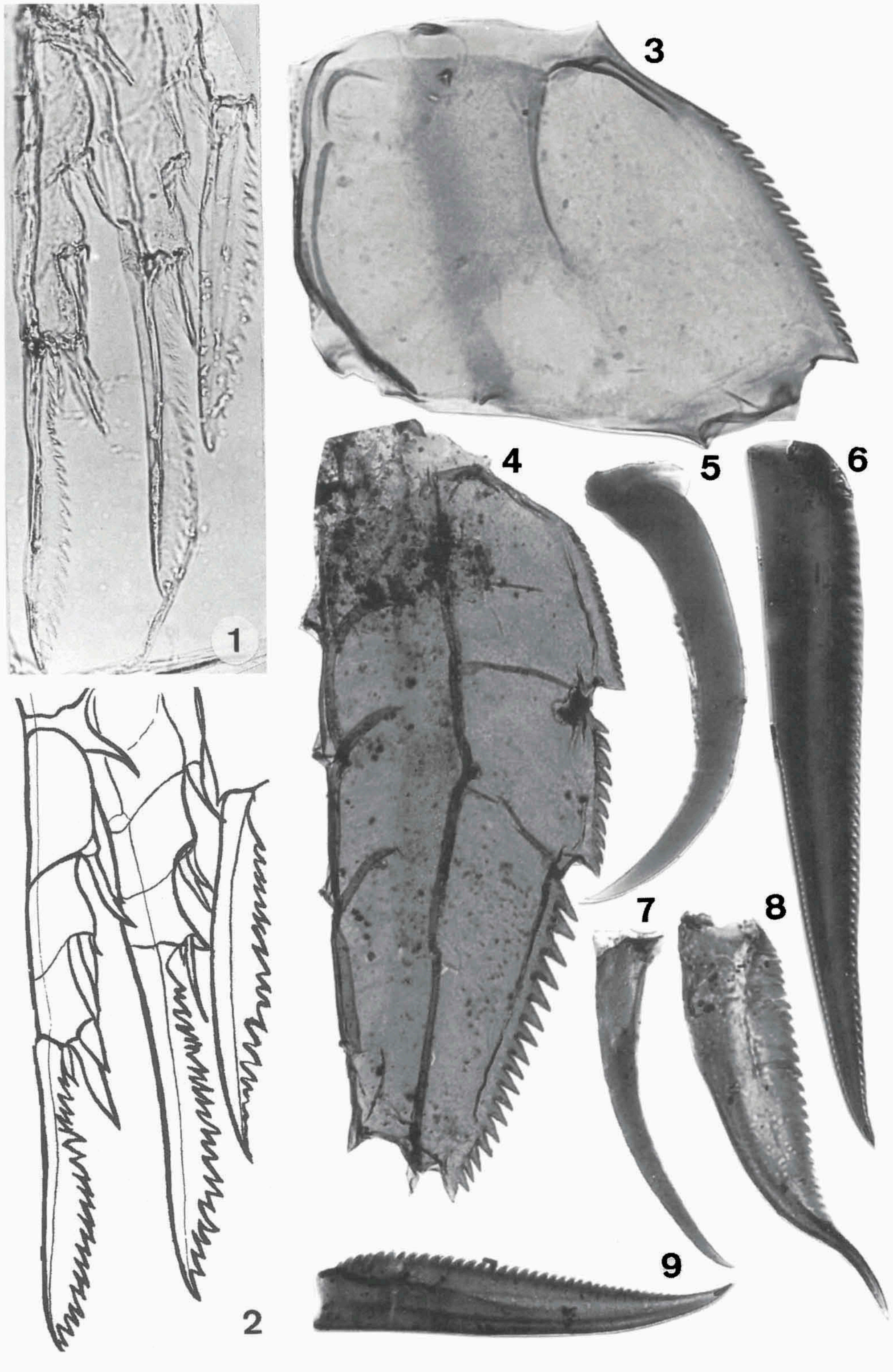
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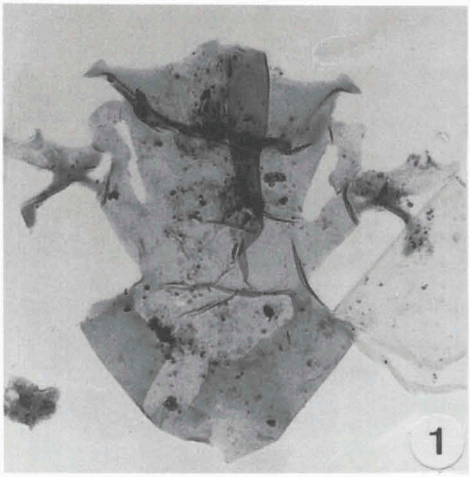
Plate 3

1. PM 13; copepod sternite; slide SN-192; × 400.
2. PM 14; copepod tail fragment; slide SN-192; × 400.
3. PM 14; copepod tail fragment; slide SN-192; × 400.
4. PM 6; copepod intercoxal plate, front side; slide SN-196; × 800.
5. PM 6; copepod intercoxal plate, back side; slide SN-196; × 800.
6. PM 6; copepod intercoxal plate, front side; slide SN-196; × 800.
7. PM 27; unidentified arthropod fragment; slide SN-169, × 400.
8. PM 8; copepod rostral spine; slide SN-196; × 800.
9. PM 15; elongated curved crustacean palynomorph; slide SN-44; × 400.
10. PM 15; elongated curved crustacean palynomorph; × 500 (SEM).
11. PM 15; elongated curved crustacean palynomorph; slide SN-188; × 800.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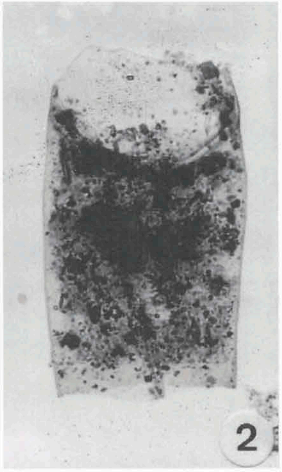
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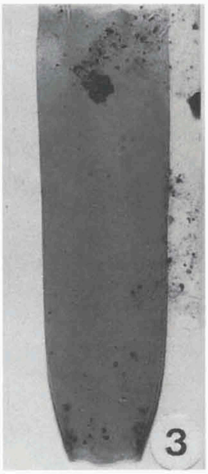
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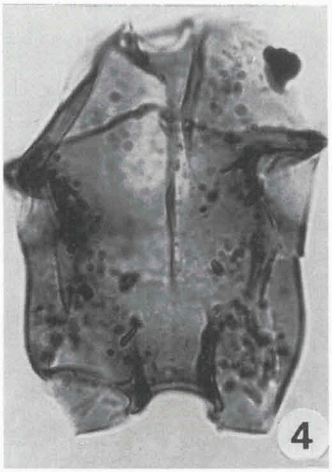
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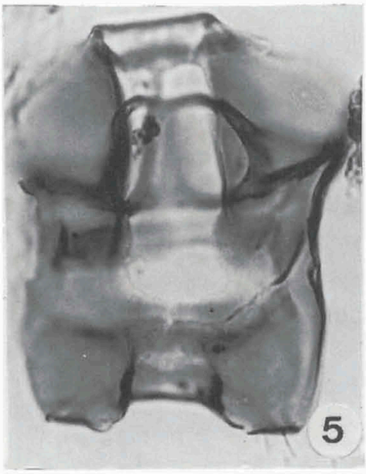
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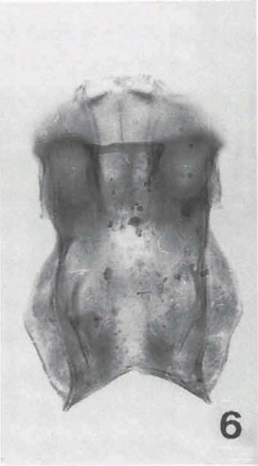
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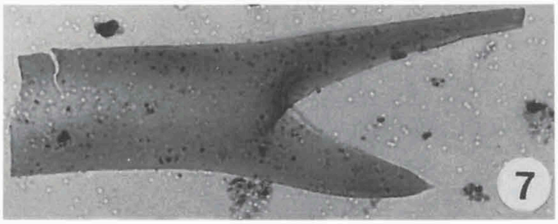
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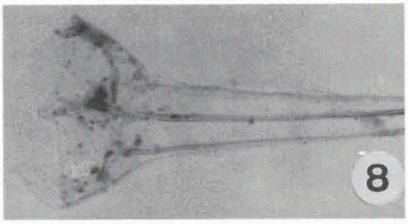
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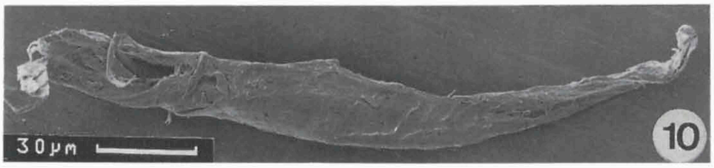
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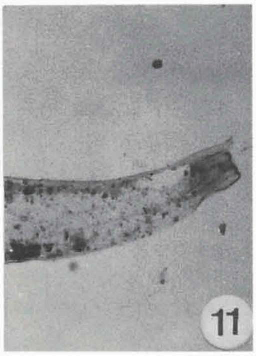
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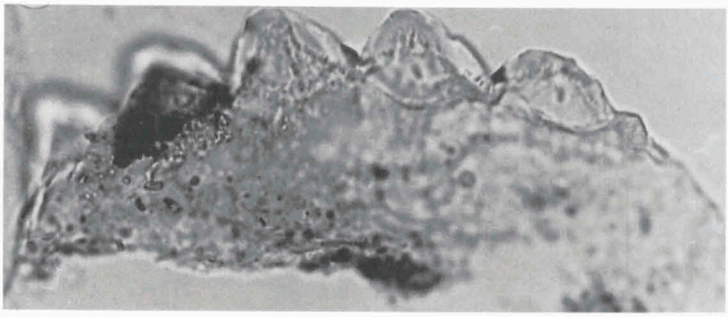
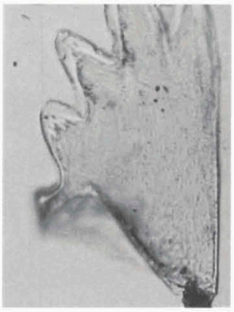
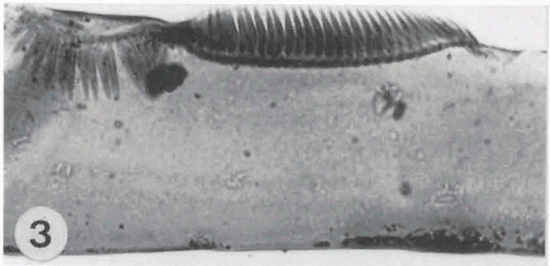
Plate 4

1. PM 9; copepod mandible gnathobasis; slide SN-244; × 800.
2. PM 16; amphipod mandible remain; slide SN-240; × 800.
3. PM 7; copepod antenna remain; slide SN-168; × 500.
4. PM 26; unidentified arthropod fragment; slide SN-168; × 800.
5. PM 10; copepod mandible gnathobasis; slide SN-233; × 400.
6. PM 11; copepod mandible gnathobasis; slide SN-196; × 400.
7. PM 17; arthropod mandible remain; slide SN-120; × 1000.
8. PM 12; copepod mandible gnathobasis; slide SN-233; × 400.







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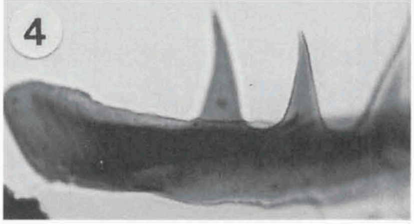

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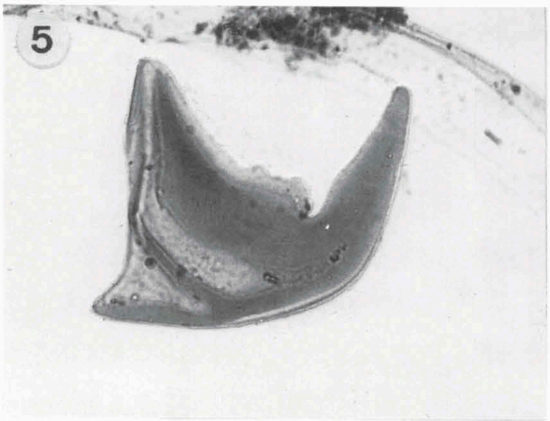

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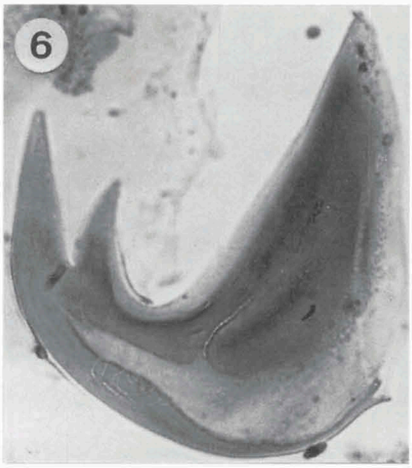

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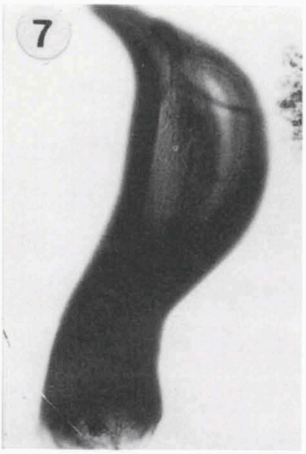

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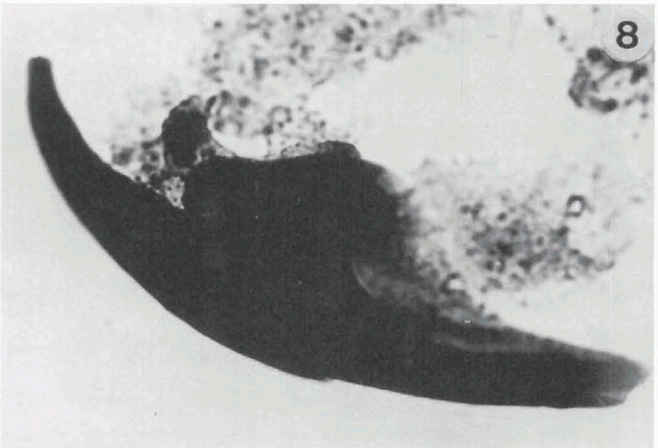

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