Tintinnomorphs from deep-sea sediments of the Banda Sea (Indonesia)

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Preservational circumstances, probably related to high productivity and high sedimentation rates, result in the occurrence of a wide variety of tintinnid palynomorphs in (sub-)Recent sediments of the Banda Sea. These organic (probably chitinous) remains include both loricae and cysts, as well as the stalked pouches in which the cysts were originally encapsulated. Collectively termed 'tintinnomorphs', these palynomorphs are described and classified in an informal scheme that may serve as a key to the recognition of 76 morphologically distinctive types.

Contents

Introduction

The Tintinnida represent a suborder of planktic ciliated protozoans. Modern tintinnids construct an organic test, the lorica, that frequently includes agglutinated foreign matter (Barnes, 1987). Early accounts on the chemical composition of the organic loricae referred to the wall as consisting of chitin or cellulose (see Tappan & Loeblich, 1968). Although some authors have preferred the terms pseudochitinous or chitinoid, in practice, the wall substance is usually denoted as chitin. Optically, modern loricae suggest a broad range in composition; they may be extremely delicate and of a gelatinous or membranous consistency, or they may be relatively firm and resistant. They are resistant to strong acids.

The geological record of organic tintinnid remains is obscure and highly imperfect. Some authors have suggested a relationship between tintinnids and chitinozoans (Reid & John, 1981). The latter represent a distinctive but enigmatic category of Palaeozoic marine palynomorphs (Traverse, 1989), having a highly resistant wall that

is commonly referred to as chitinous or pseudochitinous, despite evidence of the absence of chitin (Voss-Foucart & Jeuniaux, 1972). Alternative to a tintinnid affinity, however, chitinozoans have variously been assigned to a wide range of other protozoans, metazoans or fungi (see, e.g., Traverse, 1989; Cashman, 1990, 1991). Pre-Quaternary records of non-chitinozoan palynomorphs, resembling organic tintinnid loricae are extremely scarce; earliest known occurrences are from the Lower Triassic of Ireland and Israel (Visscher, 1970, 1971; Eshet, 1990) and the Upper Triassic of Sicily (H. Visscher and W.A. Brugman, pers. comm.). Apart from an early account from Jurassic coprolites by Rüst (1885), they have also been encountered in thin sections of Late Jurassic-Early Cretaceous carbonates (Doben, 1963). Eicher (1965) obtained isolated Cretaceous loricae, constructed of arenaceous particles agglutinated in an insoluble organic matrix.

As an alternative to organic loricae, extinct microfossils of probable tintinnid affinity can be characterised by a calcareous nature of the lorica (see review by Loeblich & Tappan, 1968). With an imperfectly known downward range into the Early Palaeozoic (Hermes, 1966; Chennaux, 1968), a wide morphological variation of calcareous loricae, described as calpionellids, is notable in thin sections of pelagic carbonates of Late Jurassic and Early Cretaceous age (e.g., Colom, 1948, 1965; Remane, 1964; Loeblich & Tappan, 1968). Isolated calcareous loricae are less common, but a variety of taxa has been described from the Eocene (Loeblich & Tappan, 1968).

There is little information on tintinnid occurrences in the Neogene. In the Quaternary, however, organic tintinnid remains can be particularly abundant in lake deposits (see review by Frey, 1964). Occurrences of tintinnid remains in modern marine sediments were demonstrated by Reid & John (1978) to represent cysts rather than loricae. Although still inadequately understood with respect to their formation and function, such cysts are long since known from zooplankton research. Already Meunier (1910) defined the category 'Papulifères' to include a wide variety of generally flask-shaped cysts abundantly found in Arctic waters.

During a comprehensive palynofacies analysis of (sub-)Recent marine sediments of the Banda Sea (van Waveren & Visscher, in press), organic tintinnid remains were found as an accessory element of the zooplankton-derived component of palynomorph associations. They show a wide morphological variability and are considered to include both loricae and cysts. Similarly to the preservation of microscopic crustacean remains (exoskeleton fragments, egg-envelopes; van Waveren, 1992, 1994; van Waveren & Marcus, 1993; van Waveren & Visscher, in press), their occurrence may be related to the combined effects of high productivity (Baars et al., 1990) and high sedimentation rates (Ganssen et al., 1989) in the Banda Sea.

In the present paper the tintinnid palynomorphs from the Banda Sea sediments are described, illustrated and classified according to an informal morphological system. At present, the introduction of any formal nomenclature for the palynomorphs would result in a confusing and unnecessary classification scheme within tintinnid systematics. In this respect, it should be realised that: (1) tintinnids show strong polymorphism, especially in tropical and sub-tropical systems (Souto, 1981); (2) intraspecific variability exists in many tintinnid species (Boltovkoy et al., 1990); (3) lorica-cyst relationships among tintinnids still need to be systematically investigated; (4) there can be convergence between the morphology of cysts and loricae (Reid & John,

1978); tintinnid classification is based on the shape of the lorica (Corliss, 1979), but this classification is not broad enough to describe the morphological variation observed in tintinnid palynomorphs; and (5) since cyst formation is a common stage in the life-cycle of many naked or aloricate ciliates (Corliss & Esser, 1974), part of the cysts could also belong to other ciliated protozoans (Reid & John, 1978).

The term 'tintinnomorphs' is here introduced in order to emphasise that palynomorphs resembling tintinnids cannot be always separated into loricae or cysts and may even represent cysts of other protozoans.

Material and methods

Material

Samples were collected from box-cores taken at various depths 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. Microscopic analysis of permanent slides under normal transmitted light included the drawing, description and classification of 76 types of tintinnomorphs.

Descriptive terminology and classification criteria

In principle, a tintinnid may produce three different categories of palynomorphs (Fig. 1):
- a lorica (b);
- a pouch attached to the aboral (basal) side of the lorica (c);
- a cyst encapsulated in the pouch (d).

The produced tintinnomorphs may show the following features (Fig. 2):
- a corolla enclosing a chamber;
- an opening (sometimes with operculum);
- a calyx (a hollow appendix);
- a stem (a massive appendix);
- a horn (calyx plus stem);
- a collar.

The side of the opening is termed oral side, oppositely occurs the aboral side.

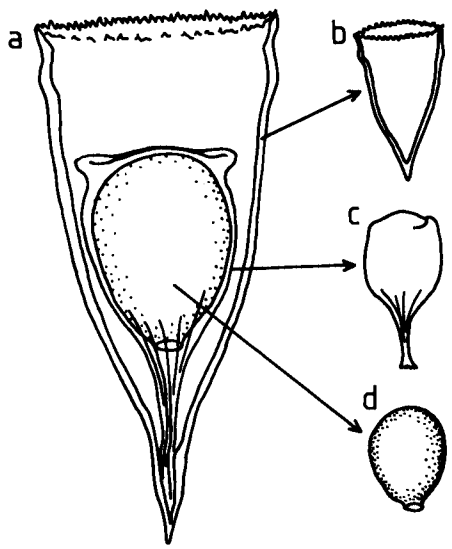


Fig. 1. *Favella serrata* (redrawn from Reid & John, 1978, pl. I,A,B), showing the three possibilities for the nature of tintinnid palynomorphs; a: cyst formation; b: lorica; c: pouch; d: cyst.

Classification criteria are applied in the following order:

(A) Shape of the corolla (Fig. 3). Overall shape is considered to be the primary classification criterion because it is also used for the classification of the modern Tintinnida. The corolla can be spherical (0), elliptical (1), elongated elliptical (2), egg-shaped, aborally blunt (3), egg-shaped, orally blunt (4), hexagonal (5), rectangular (6), asymmetrically rhombic, aborally blunt (7), asymmetrically rhombic, orally blunt (8), triangular (9), and tetragonal (10).

(B) Surface structure (Fig. 4), related to the composition of the wall. The surface can be smooth (0) or ornamented as a result of agglutination (1).

(C) Shape of the calyx (Fig. 5). This criterion constitutes a link between the tubular and the rounded tintinnomorphs. It highlights the continuity in morphology between shapes that a priori do not seem to be related. The calyx can be absent (0),

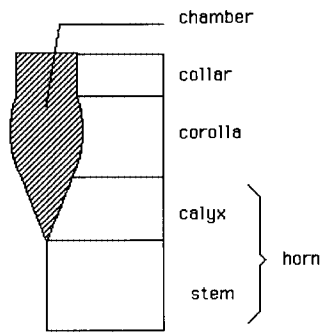


Fig. 2. General tintinnomorph organisation.

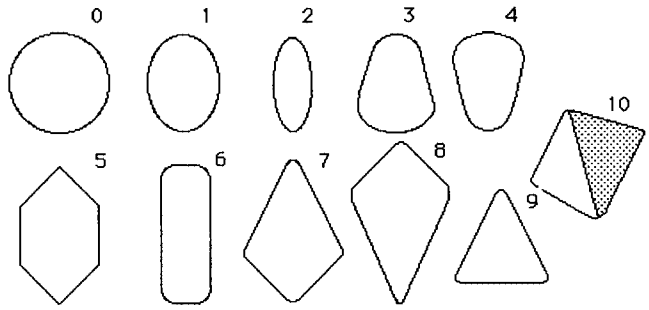


Fig. 3. Corolla shape; 0: spherical; 1: elliptical; 2: elongated elliptical; 3: egg-shaped, aborally blunt; 4: egg-shaped, orally blunt; 5: hexagonal; 6: rectangular; 7: asymmetrically rhombic, aborally blunt; 8: asymmetrically rhombic, orally blunt; 9: triangular; 10: tetragonal.

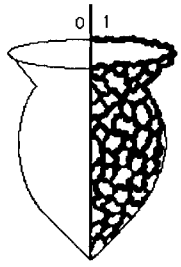


Fig. 4. Wall structure; 0: smooth; 1: ornamented.

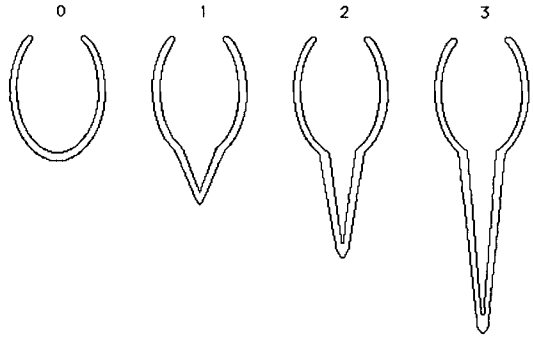


Fig. 5. Shape of the calyx; 0: calyx absent; 1: short triangular; 2: elongated triangular; 3: elongated tubular.

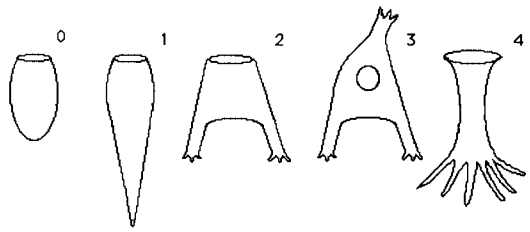


Fig. 6. Number of stems; 0: stem absent; 1: single stem; 2: two stems; 3: three stems; 4: more than three stems.

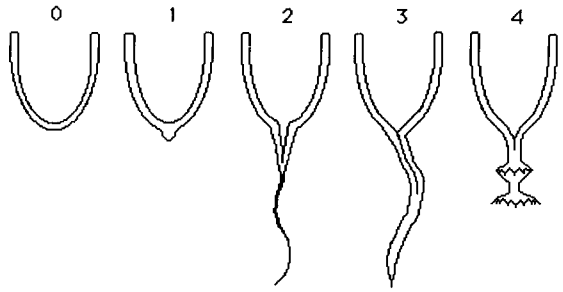


Fig. 7. Type of stems; 0: stem absent; 1: nodular; 2: flagellar; 3: tailed; 4: rooted.

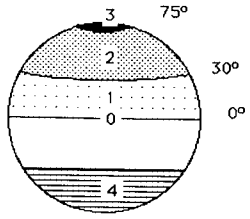


Fig. 8. Opening positions defined in terms of 'latitude': 0: 'equatorial' at 0°; 1: 'large', between 0° and 30°; 2: 'medium', between 30° and 75°; 3: 'small', superior to 75°; 4: inferior to equatorial.

short-triangular (all sides of equal length) (1), elongated triangular (2), or tubular (3).

(D) Presence and number of stems (Fig. 6). The tintinnomorph can have no stem (0), a single stem (1), two stems (2), three stems (3), or more stems (4).

(E) Type of stems (Fig. 7). In tintinnid loricae and cysts the stem may have various shapes. Also the thin-walled pouch encapsulating the cyst is attached to the aboral bottom of the lorica by a stem with a root-like structure. Tintinnomorph stems can be absent (0), nodular (1), flagellar (2), tailed (3), or rooted (4).

(F) A lower rank in the classification is given to the position (size) of the opening (Fig. 8). The position of the opening is defined in terms of 'latitude': 'equatorial' at 0° (0); 0° to 30° 'large' (1); between 30° and 75° 'medium' (2); superior to 75° 'small' (3); and inferior to equatorial (4).

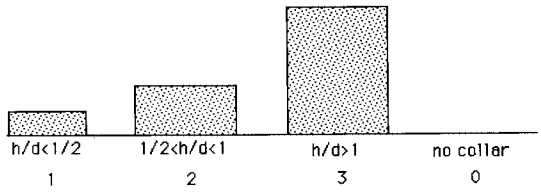


Fig. 9. Collar elongation defined by the ratio between its height and its diameter (h/d); 0: collar absent; 1: 'short'; 2: 'middle'; 3: 'long'.

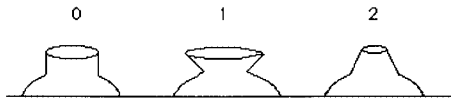


Fig. 10. Collar shape determined by the sides of the collar in cross-section; 0: parallel; 1: diverging; 2: converging).

Fig. 11. Opening ornamentation; 0: absent; 1: annulate; 2: irregularly torn; 3: striate.

(G) Properties of the collar, such as collar elongation (Fig. 9), are also given a low rank in classification. The collar elongation is characterised by the ratio between its height and its diameter (h/d). This ratio can be < 0.5 'short' (1); between 0.5 and 1 'middle' (2), and >1 'long' (3). The collar can also be absent (0).

(H) Collar shape (Fig. 10). The shape is determined by the sides of the collar in cross-section. Sides can be parallel (0), diverging (1), or converging (2).

(I) Collar ornamentation (Fig. 11). Ornamentation can be absent (0), annulate (1), irregularly torn (2), or striate (3).

The thickness of the wall is not used as a classification criterion here because loricae walls increase in thickness during life (Souto, 1981). Also size and colour are not taken into consideration. Flagellar to tailed types can reach a total length of 700 µm, but the length of their calyx and corolla together varies between 60 µm and 200 µm; rooted types have a smaller size of c. 200 µm. The colours of the tintinnomorphs varies from hyaline to ochre-brown. The rooted types in particular, combine a thin wall with a light colour, while the other types generally have thicker walls and a darker colour.

Descriptive coding

In the following key to the identification of tintinnomorph types a letter coding has been applied to denote the various shape categories (initial four to five letters).

Also the presence or absence of wall ornamentation is indicated by one or two added letters. A number is than added to identify different types within each letter-code category, recognised on the basis of classification criteria of lower rank. Each of the observed types is illustrated on Figures 12 to 17.

Letter coding is as follows:

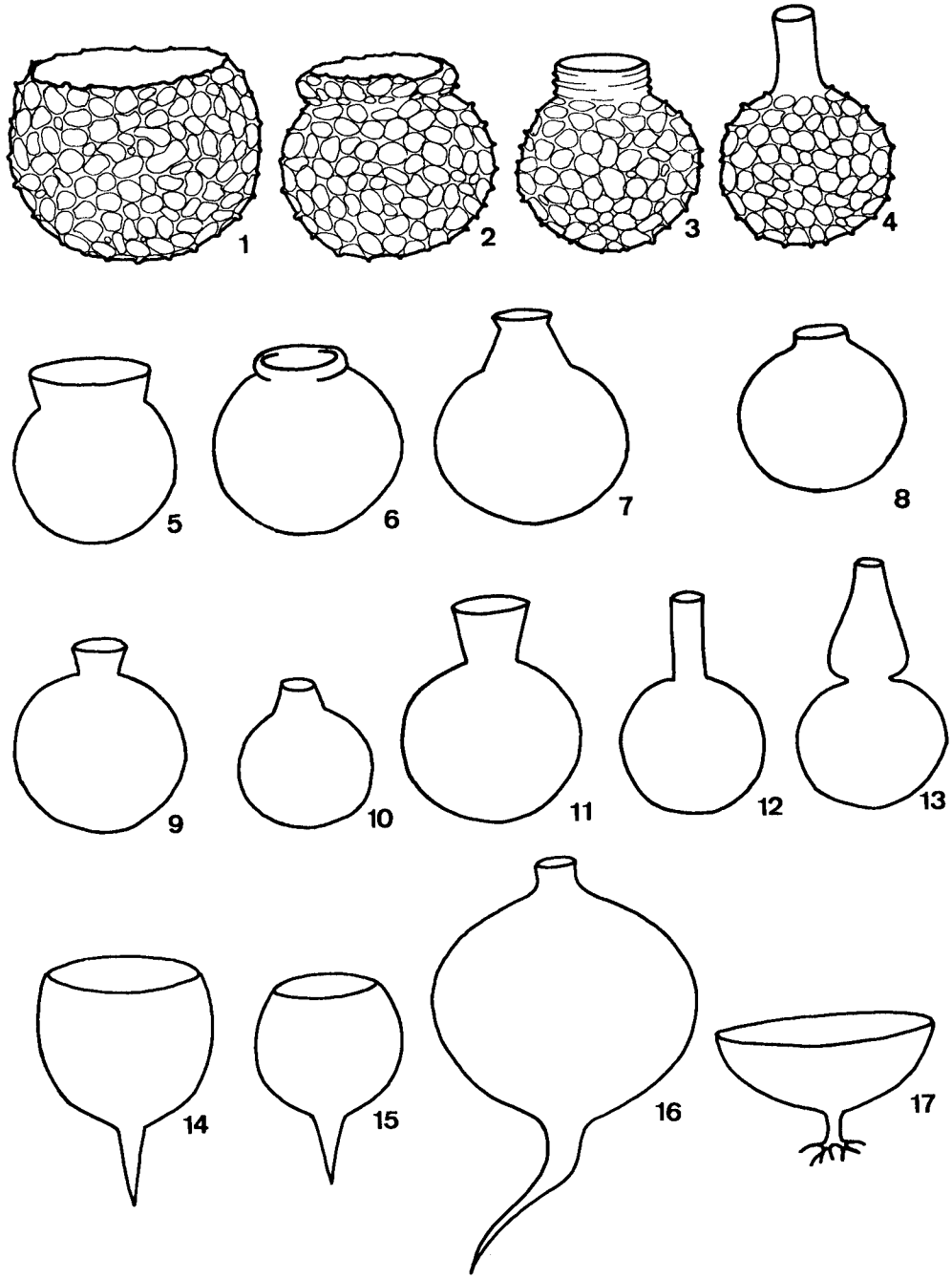
SPHER - spherical
ELLIP - elliptical
ELEL - elongated elliptical
ESAB - egg-shaped, aborally blunt
ESOB - egg-shaped, orally blunt
HEXA - hexagonal
RECT - rectangular
ARAB - asymmetrically rhombic, aborally blunt
AROB - asymmetrically rhombic, orally blunt
TRIA - triangular
TETRA - tetragonal
O - ornamentation present
NO - no ornamentation

Example: **ESOBNO-4** indicates the fourth type (4) recognised within the category of tintinnomorphs characterised by an egg-shaped orally blunt (**ESOB**) shape and a not-ornamented (**NO**) wall.

Key to the identification of tintinnomorph types

- spherical types: (**SPHER**)
  - ornamented: (**SPHERO**)
    - without calyx, without stem
      - opening large
        - no collar: **SPHERO-1** (Fig. 12: 1)
        - short collar, annular, no collar ornamentation: **SPHERO-2** (Fig. 12: 2)
      - opening medium
        - short collar, parallel, striate ornamentation: **SPHERO-3** (Fig. 12: 3)
      - opening small
        - long collar, parallel, no collar ornamentation: **SPHERO-4** (Fig. 12: 4)
    - with short triangular calyx, without stem, opening large: **SPHERO-5** (Fig. 17: 4)
  - not ornamented: (**SPHERNO**)

Fig. 12. Spherical ornamented (SPHERO) and not ornamented (SPHERNO) tintinnomorph types from the Banda Sea; 1: SPHERO-1 (sample Sn-250); 2: SPHERO-2 (sample Sn-250); 3:SPHERO-3 (sample Sn-415); 4: SPHERO-4 (sample Sn-415); 5: SPHERNO-1 (sample Sn-191); 6: SPHERNO-2 (sample Sn-253); 7: SPHERNO-3 (sample Sn-327); 8: SPHERNO-4 (sample Sn-259); 9: SPHERNO-5 (sample Sn-229); 10: SPHERNO-6 (sample Sn-316); 11: SPHERNO-7 (sample Sn-333); 12:SPHERNO-8 (sample Sn-250); 13: SPHERNO9 (sample Sn-258); 14: SPHERNO-10 (sample Sn-154); 15: SPHERNO-11 (sample Sn-258); 16: SPHERNO-12 (sample Sn-168); 17: SPHERNO-13 (sample Sn-398).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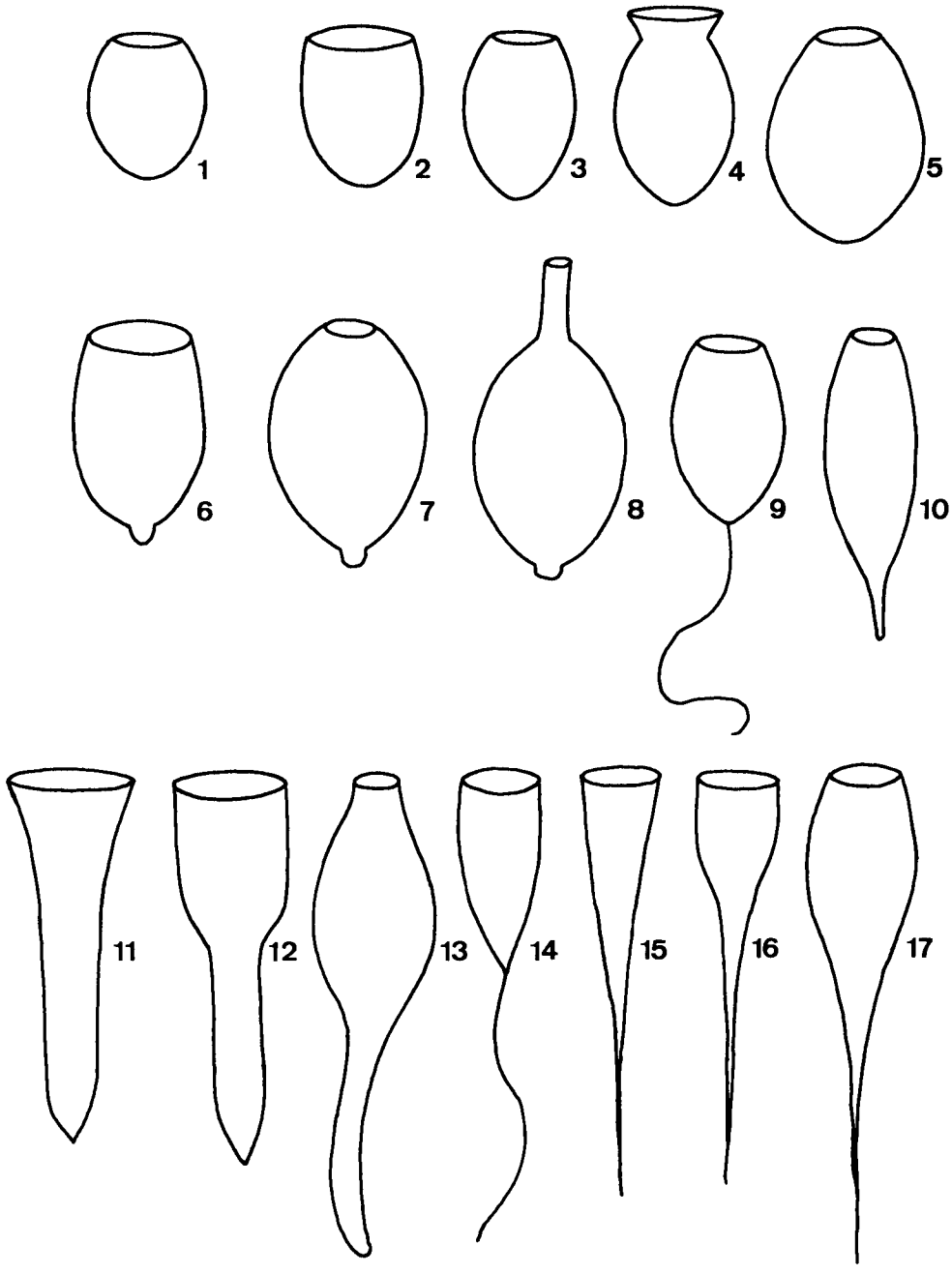
- without calyx, without stem
  - opening medium
    - short collar
      - diverging, no collar ornamentation: **SPHERNO-1** (Fig. 12: 5)
      - parallel-sided, annular collar: **SPHERNO-2** (Fig. 12: 6)
    - middle collar, converging with small diverging rim around the opening, no collar ornamentation: **SPHERNO-3** (Fig. 12: 7)
  - opening small
    - short collar
      - parallel, no collar ornamentation: **SPHERNO-4** (Fig. 12: 8)
    - middle collar
      - diverging, no collar ornamentation: **SPHERNO-5** (Fig. 12: 9)
      - converging, no collar ornamentation: **SPHERNO-6** (Fig. 12: 10)
    - long collar
      - diverging, no collar ornamentation: **SPHERNO-7** (Fig. 12: 11)
      - parallel, no collar ornamentation: **SPHERNO-8** (Fig. 12: 12)
      - diverging/converging, no collar ornamentation: **SPHERNO-9** (Fig.12: 13)
  - with elongated calyx, without stem
    - opening large, no collar: **SPHERNO-10** (Fig. 12: 14)
    - opening medium, no collar: **SPHERNO-11** (Fig. 12: 15)
  - with calyx, with stem
    - tailed stem, opening small, middle collar, parallel sided, without collar ornamentation: **SPHERNO-12** (Fig. 12: 16)
    - rooted stem, opening equatorial, no collar: **SPHERNO-13** (Fig. 12: 17)
- elliptical types: (**ELLIP**)
  - ornamented: (**ELLIPO**)
    - without calyx, without stem, medium, short collar, straight, no collar ornamentation but arched openings in the region from 0 µm to 30 µm: **ELLIPO-1** (Fig. 17: 2)
  - not ornamented: (**ELLIPNO**)
    - without calyx, without stem, medium opening, no collar: **ELLIPNO-1** (Fig. 13: 1)
- elongated elliptical types: (**ELEL**)
  - not ornamented: (**ELELNO**)
    - without calyx, without stem
      - opening equatorial, no collar: **ELELNO-1** (Fig. 13: 2)
      - opening medium
        - no collar: **ELELNO-2** (Fig. 13: 3; Plate 1, fig. 3)

Fig. 13. Elliptical, not ornamented (ELLIPNO) and elongated elliptical, not ornamented (ELELNO) tintinnomorph types from the Banda Sea: 1: ELLIPNO-1 (sample Sn-247); 2: ELELNO-1 (sample Sn-211); 3: ELELNO-2 (sample Sn-196); 4: ELELNO-3 (sample Sn-201); 5: ELELNO-4 (sample Sn-258); 6: ELELNO-5 (sample Sn-161); 7: ELELNO-6 (sample Sn-325); 8: ELELNO-7 (sample Sn-335); 9: ELELNO-8 (sample Sn-244); 10: ELELNO-9 (sample Sn-196); 11: ELELNO-10 (sample Sn-152); 12: ELELNO-11 (sample Sn-196); 13: ELELNO-12 (sample Sn-196); 14:ELELNO-13 (sample Sn-226); 15: ELELNO-14 (sample Sn-320); 16: ELELNO-15 (sample Sn-320); 17:ELELNO-16 (sample Sn-156).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- small collar, diverging, no collar ornamentation: **ELELNO-3** (Fig. 13: 4)
- opening small, no collar: **ELELNO-4** (Fig. 13: 5)

- without calyx, with stem
  - nodded
    - opening medium, no collar: **ELELNO-5** (Fig. 13: 6)
    - opening small
      - no collar: **ELELNO-6** (Fig. 13: 7)
      - long collar, parallel, no collar ornamentation: **ELELNO-7** (Fig. 13: 8)
  - flagellate, opening medium to small, no collar: **ELELNO-8** (Fig. 13: 9)

-with calyx, without stem
- with an elongated triangular calyx, opening small: **ELELNO-9** (Fig. 13: 10; Plate 1, fig. 6)
- with a tubular calyx
  - opening inferior to equatorial, no collar: **ELELNO-10** (Fig. 13: 11; Plate 1, fig. 9)
  - opening equatorial, no collar: **ELELNO-11** (Fig. 13: 12; Plate 1, fig. 10)
  - opening small, middle collar, converging: **ELELNO-12** (Fig. 13: 13; Plate 1, fig. 7)

-with calyx, with stem
- small triangular calyx, flagellate stem, opening large, no collar: **ELELNO-13**(Fig. 13: 14)
- elongated triangular calyx, tailed stem, no collar
  - opening inferior to equatorial: **ELELNO-14** (Fig. 13: 15; Plate 1, fig. 11)
  - opening equatorial: **ELELNO-15** (Fig. 13: 16; Plate 1, fig. 12)
  - opening medium: **ELELNO-16** (Fig. 13: 17; Plate 1, fig. 13)

- egg-shaped, aborally blunt types: (**ESAB**)
  - ornamented: (**ESABO**)
    - without calyx, without stem
      - opening large, middle collar, converging sides with striate ornamentation: **ESABO-1** (Fig.14: 1; Plate 1, fig. 1)
    - without calyx, with stem
      - opening medium, diverging collar, no collar ornamentation: **ESABO-2** (Fig. 14: 2; Plate 1, fig. 2)
  - not ornamented: (**ESABNO**)
    - without calyx, without stem
      - opening large, no collar: **ESABNO-1** (Fig. 14: 3)
      - opening small, long parallel-sided collar, no collar ornamentation: **ESABNO-2** (Fig.14: 4)

-without calyx, with stem
- tailed stem, opening small, at 2/3 of the tintinnomorph a zone of diverging and converging exists, the opening is placed asymmetrically: **ESABNO-3** (Fig. 14: 5)

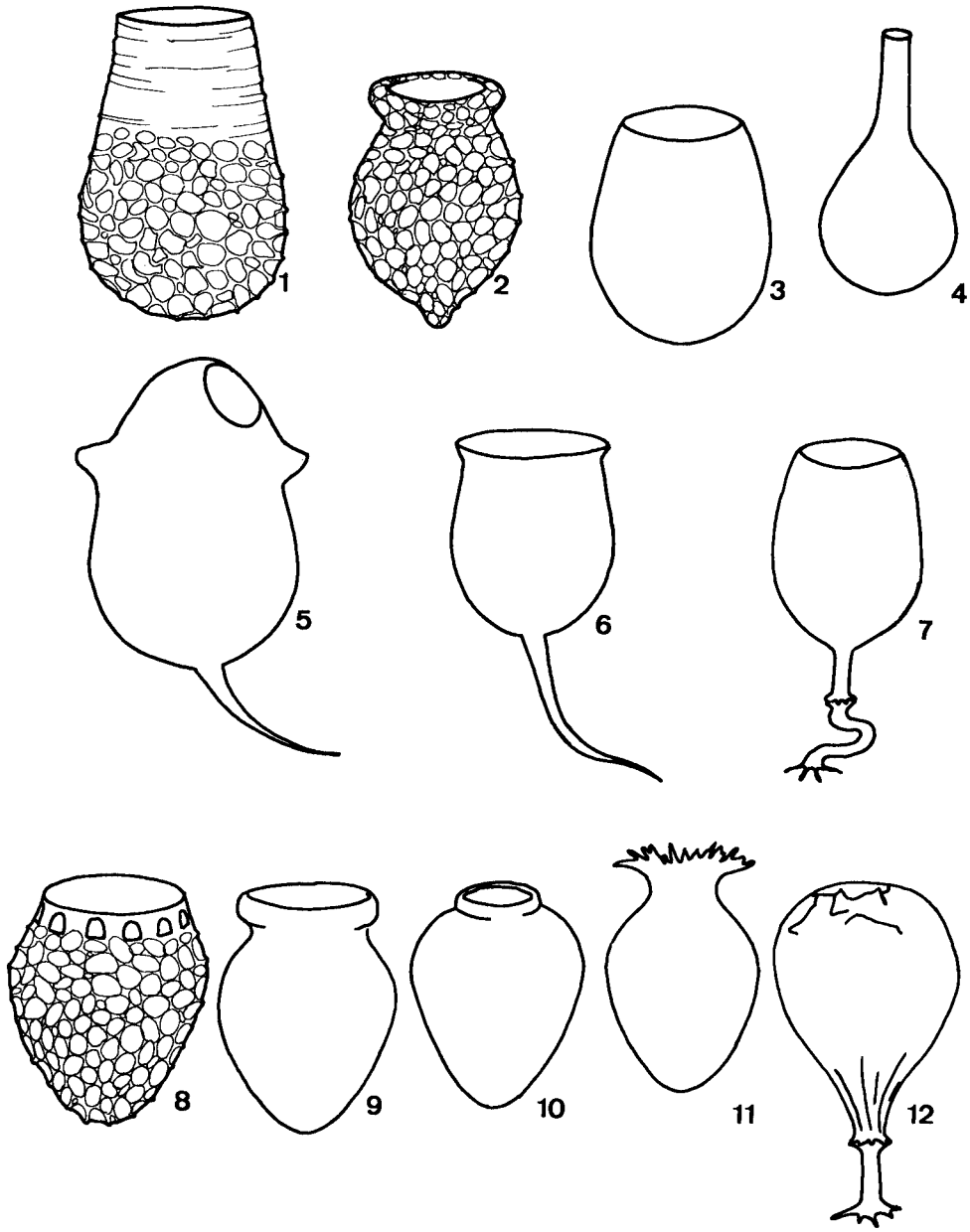
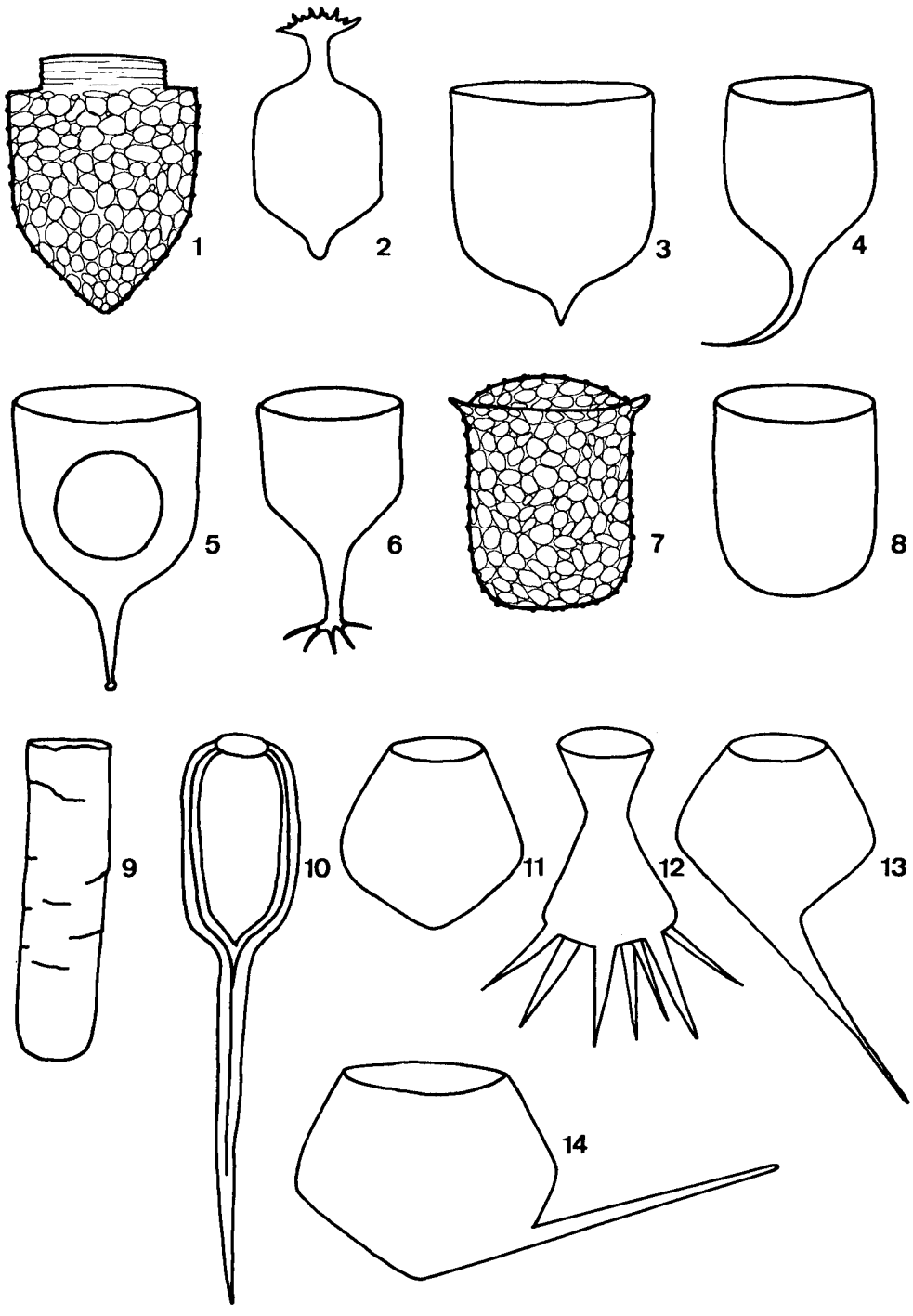


Fig. 14. Egg-shaped, aborally blunt, ornamented (ESABO) and not ornamented (ESABNO), egg-shaped, orally blunt, ornamented (ESOBO) and not ornamented (ESOBNO) tintinnomorph types from the Banda Sea; 1: ESABO-1 (sample Sn-243); 2: ESABO-2 (sample Sn-236); 3:ESABNO-1 (sample Sn-153); 4: ESABNO-2 (sample Sn-230); 5: ESABNO-3 (sample Sn-390); 6: ESABNO-5 (sample Sn-173); 7: ESABNO-6 (sample Sn-169 A); 8: ESOBO-1 (sample Sn-241); 9: ESOBNO-1 (sample Sn-237); 10: ESOBNO-2 (sample Sn-220); 11: ESOBO-3 (sample Sn-373); 12: ESOBNO-4 (sample Sn-248).

- same as **ESABNO-3**, but without opening: **ESABNO-4** (Fig. 17: 1)
- tailed stem, opening large, short collar, diverging, no collar ornamentation: **ESABNO-5** (Fig.14: 6)
- rooted stem, opening medium, no collar: **ESABNO-6** (Fig. 14: 7)

- egg-shaped, orally blunt types: (**ESOB**)
  - ornamented: (**ESOBO**)
    -without calyx, without stem, opening medium, arched openings in the region from 30 µm to 75 µm: **ESOBO-1** (Fig. 14: 8)
  - not ornamented: (**ESOBNO**)
    - without calyx, without stem
      - opening medium:
        - small collar, parallel, annulate: **ESOBNO**-1 (Fig. 14: 9)
        - middle collar
          - parallel, lacy: **ESOBNO-2** (Fig. 14: 10)
          - diverging, no collar ornamentation: **ESOBNO-3** (Fig. 14: 11)
    -with short triangular calyx, with rooted stem, opening medium to small, opening irregular: **ESOBNO-4** (Fig. 14: 12; Plate 1, fig. 3)
- hexagonal types: (**HEXA**)
  - ornamented: (**HEXAO**)
    - without calyx, without stem, opening large, small collar, parallel-sided with striate ornamentation: **HEXAO-1** (Fig. 15: 1)
  - not ornamented: (**HEXANO**)
    - without calyx, with stem
      - nodded, opening small, long parallel collar, with a lacy ornamentation: **HEXANO-1** (Fig.15: 2)
    - with small calyx, without stem
      - opening large, no collar: **HEXANO-2** (Fig. 15: 3)
    - with calyx, with stem
      - small calyx
        - tailed, opening large to equatorial, no collar: **HEXANO-3** (Fig. 15: 4)
      - elongated calyx
        - nodded stem, opening large to equatorial, no collar: **HEXANO-4** (Fig. 15: 5)
        Remark: probably cyst present inside a lorica
        - rooted, opening large to equatorial, no collar: **HEXANO-5** (Fig. 15: 6)
- rectangular types: (**RECT**)
  - ornamented: (**RECTO**)
    -without calyx, without stem
      - opening equatorial to large, short collar

Fig. 15. Hexagonal ornamented (HEXAO) and not ornamented (HEXANO), rectangular ornamented (RECTO) and not ornamented (RECTNO), and asymmetricallly rhombic, aborally blunt, not ornamented (ARABNO) tintinnomorph types from the Banda Sea; 1: HEXAO-1 (sample Sn-250); 2: HEXANO-1 (sample Sn-201); 3: HEXANO-2 (sample Sn-253); 4: HEXANO-3 (sample Sn-253); 5: HEXANO-4 (sample Sn-324); 6: HEXANO-5 (sample Sn-249); 7: RECTO-1 (sample Sn-250); 8: RECTNO-1 (sample Sn-258); 9: RECTNO-2 (sample Sn-152); 10: RECTNO-3 (sample Sn-261); 11: ARABNO-1 (sample Sn-261); 12: ARABNO-3 (sample Sn-152); 13: ARABNO-2 (sample Sn-320); 14: ARABNO-4 (sample Sn-335).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- diverging collar: **RECTO-1** (Fig. 15: 7)
Remark: operculum observed
- annular collar, two rows of large openings present below the collar, the lower row has smaller openings than the upper one: **RECTO-2** (Fig. 17: 3)

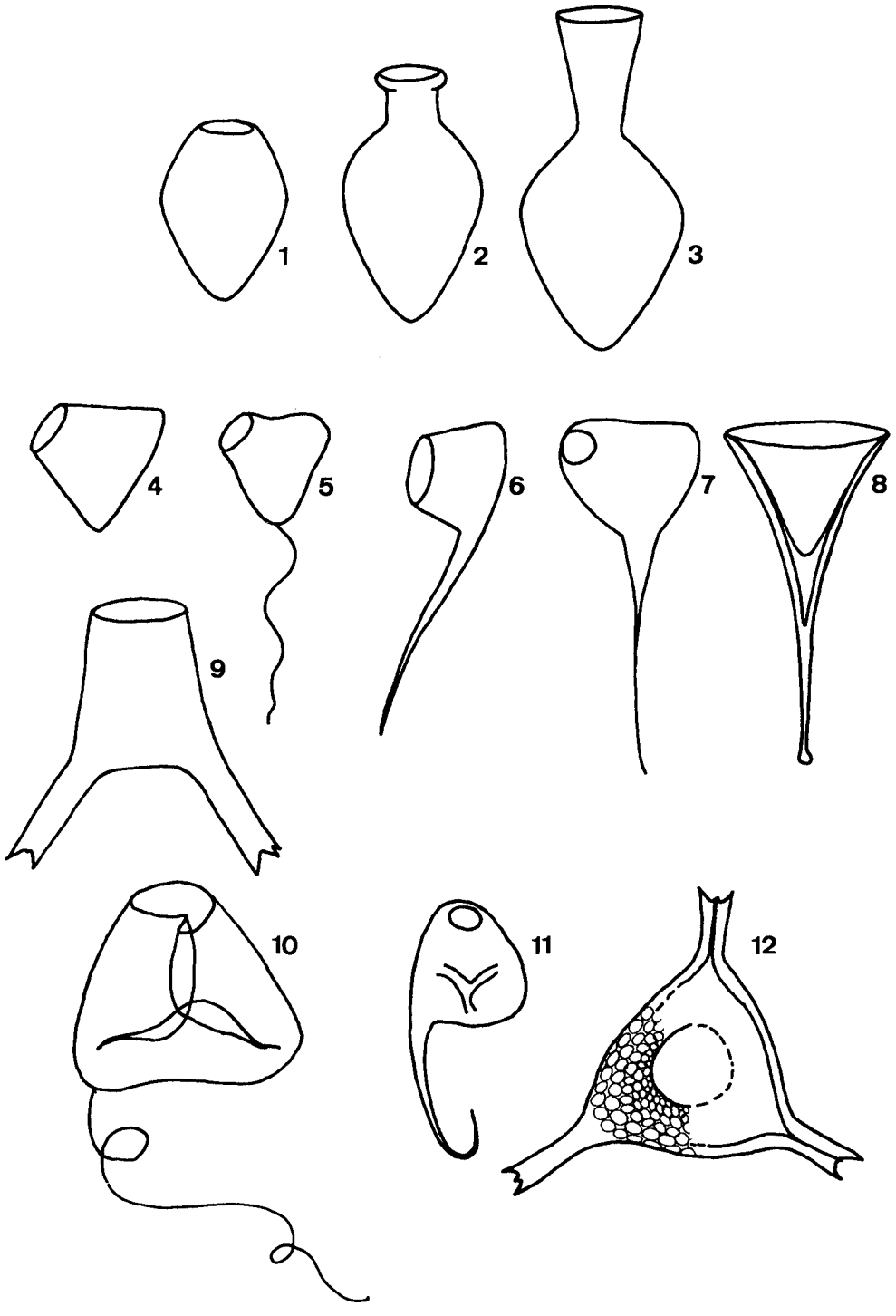
- not ornamented: (**RECTNO**)
- without calyx, without stem
- opening equatorial
- no collar: **RECTNO-1** (Fig. 15: 8)
- no collar, corolla elongated with length/width ratio >4: **RECTNO-2** (Fig. 15: 9; Plate 1, fig. 8)
- with small calyx, tailed stem, no collar, double wall: **RECTNO-3** (Fig. 15: 10)

- asymmetrically rhombic, aborally blunt types: (**ARAB**)
- not ornamented: (**ARABNO**)
-without calyx, without stem
- opening medium to large, no collar: **ARABNO-1** (Fig. 15: 11)
- without calyx, with stem
- with a single tail-like stem placed asymmetrically, opening medium to large, no collar: **ARABNO-2** (Fig. 15: 13)
- with more than three tail-like stems, opening medium, middle to long diverging collar, no collar ornamentation: **ARABNO-3** (Fig. 15: 12; Plate 1, fig. 4)
- with small calyx, with tailed type of stem
- opening medium, no collar: **ARABNO-4** (Fig. 15: 14)

- asymmetrically rhombic, orally blunt types: (**AROB**)
- not ornamented: (**AROBNO**)
- without calyx, without stem
- opening small
- no collar: **AROBNO-1** (Fig. 16: 1)
- middle collar, parallel, annulate: **AROBNO-2** (Fig. 16: 2)
- long collar, diverging, no collar ornamentation: **AROBNO-3** (Fig. 16: 3)

- triangular types: (**TRIA**)
Remark: for the triangular types, the horn(s) and the opening are always placed at the corner of the triangular shape.
- not ornamented: (**TRIANO**)
- without calyx, without stem
- opening small, no collar: **TRIANO-1** (Fig. 16: 4)
- without calyx, with stem
- flagellar tail, opening medium: **TRIANO-2** (Fig. 16: 5)

Fig. 16. Asymmetrically rhombic, orally blunt, not ornamented (AROBNO), triangular not ornamented (TRIANO), tetragonal ornamented (TETRAO) and not ornamented (TETRANO) tintinnomorph types from the Banda Sea; 1: AROBNO-1 (sample Sn-244); 2: AROBNO-2 (sample Sn-261); 3: AROBNO-3 (sample Sn-419); 4: TRIANO-1 (sample Sn-370); 5: TRIANO-2 (sample Sn-261); 6: TRIANO-3 (sample Sn-425); 7: TRIANO-4 (sample Sn-392); 8: TRIANO-5 (sample Sn-253); 9: TRIANO-6 (sample Sn-346); 10: TETRANO-1 (sample Sn-253); 11: TETRANO-2 (sample Sn-253); 12: TETRAO-1 (sample Sn-300).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- with calyx, with stem
  - opening large, no collar, asymmetrical position of tail: **TRIANO-3** (Fig. 16: 6)
  - opening small: **TRIANO-4** (Fig. 16: 7)
  - opening equatorial, no collar, nodded tail-type stem: **TRIANO-5** (Fig. 16: 8)
- without calyx, with two tailed to rooted types of stem, opening medium to large, no collar: **TRIANO-6** (Fig. 16: 9)

- tetragonal types: (**TETRA**)

Remark: for the tetragonal types, the horn(s) and the opening are always placed at the corner of the triangular shape.

- ornamented: (**TETRAO**)
  - without calyx, with three rooted stems, medium to small opening, no collar, wall ornamented with alveoles decreasing in size towards the opening: **TETRAO-1** (Fig.16: 12)
- not ornamented: (**TETRANO**)
  - without calyx, with flagellar stem, opening medium, no collar: **TETRANO-1** (Fig. 16: 10)
  - with small calyx and tail-type stem, opening small, at one corner, no collar: **TETRANO-2** (Fig.16: 11).

Discussion

Reid & John (1978) suggested that among organic tintinnid remains only the cysts are resistant to degradation in the sediments. However, according to the present author, their study demonstrates that *Favella serrata* could well produce three different categories of palynomorphs: a lorica, a pouch attached to the aboral side of the lorica, and a cyst encapsulated in the pouch (see Fig. 1, redrawn from Reid & John, 1978, plate I, A, B). It is here considered that the tintinnomorph association found in the Banda Sea sediments certainly includes two types of tintinnid remains (loricae and cysts), while there are some indications that also the third type (pouches) are possibly present. However, it should be realised that convincing discrimination between loricae and cysts is hampered by the probability of their frequent morphological convergence (Reid & John, 1978). Yet, in general terms, horned and ornamented tintinnomorphs may tentatively be considered to represent probable loricae, whereas flask-shaped types may be regarded as probable cysts. Rooted tintinnomorphs may partly represent the rooted pouches, partly sessile non-tintinnid ciliates.

In the following paragraphs a comparison is given between the categories of the plexus of forms from the Banda Sea sediments and the existing classification systems of loricae (Tappan & Loeblich, 1968). In addition, comparison with the information on tintinnid cysts (Reid & John, 1978, 1981) is provided.

Loricae of the family Codonellidae Kent, 1881 are described (Tappan & Loeblich, 1968) as reticulate to agglutinating cup-shaped; they may have a collar and a constricted throat; they can be pointed or have an aboral horn. SPHERO-1, SPHERO-2, SPHERO-6, ESABO-2 and RECTO-1 show these features. SPHERNO-10, SPHERNO-

11 are cup-shaped with an aboral horn but they are not reticulate or agglutinating.

Loricae of the family Codonellopsidae Kofoid & Campbell, 1929 are described (Tappan & Loeblich, 1968) as pot-shaped with a rounded to apiculate aboral end; they may be agglutinating or reticulate; the hyaline collar may have spiral to annular ridges. SPHERO-4, SPHERO-5, ESABO-1, HEXAO-1 have a hyaline collar with or without annular ridges, some are rounded, others are apiculate. These types probably are agglutinating.

Loricae of the family Dictyocystidae Kent, 1881 are bowl-shaped and they are surmounted by arched frames or windows (Tappan & Loeblich, 1968). ESOBO-1, SPHERO-3 and RECTO-2 show the arched framed windows of this family, but the shape is not clearly that of a bowl.

Loricae of the family Ptychoclylididae Kofoid & Campbell, 1929 are bell-shaped with an elongated bowl, the oral rim can be denticulate (Tappan & Loeblich, 1968). HEXANO-2 and HEXANO-4 match this description.

The description of the loricae of the Ptychoclynididae by Tappan & Loeblich (1968) is insufficient since a species of the genus *Favella* (Reid & John, 1978) assigned to the Ptychoclynididae has an aboral horn while this family was defined without this feature. Assuming that the identification of *Favella* in Reid & John (1978) and the assignment of this genus to the Ptychoclynididae are correct, the loricae of the Ptychoclynididae should be described as 'bell-shaped loricae with an elongated bowl, the oral rim can be denticulate and can have an aboral horn'. According to this emended diagnosis, HEXANO-3 and ESABNO-5 may also be placed in the Ptychoclynididae. As ESABNO-3 resembles ESABNO-5 it could belong to this family as well.

According to Tappan & Loeblich (1968) loricae of the Xystonellidae Kofoid & Campbell, 1929 have an elongated, chalice-shaped lorica, an elongated aboral pedicel, and a reticulate wall. Although many of the types observed in the sediments of the Banda Sea have an elongated chalice-shaped form and an elongated aboral pedicel, none is reticulate. Nevertheless, in Reid & John (1978) a species of the genus *Parafavella* belonging to the Xystonellidae was drawn without reticulum. Assuming that both the identification by Reid & John (1978) and an assignment of the genus to the Xystonellidae are correct, the diagnosis of the family should become 'elongated chalice-shaped loricae with an elongated aboral pedicel, and with a smooth or reticulate wall'. Following this diagnosis, the tintinnomorph types ELELNO-9, -10, -11, -12, -13, -14, -15 and -16, as well as RECTNO-2 and -3 would belong to the Xystonellidae. RECTNO-3, however, seems to be a remnant of a cyst, as it has a double wall.

Loricae of the family Tintinnidae Clarapède & Lachmann, 1858 are elongate, flaring orally with an open or closed aboral end (Tappan & Loeblich, 1968). ELELNO-3 with its flaring collar and elongated shape, can be placed in this family.

The lorica of *Pacilina arctica* has a rhombic shape and possesses a tubular calyx (Reid & John, 1981). It resembles ARABNO-2 which has an elongated calyx placed asymmetrically. ARABNO-2 may thus have the features of a tintinnid lorica, possibly of a species of *Pacilina*. ARABNO-4 is very similar to ARABNO-2, except that its horn is in an even more asymmetrical position than in ARABNO-2.

HEXANO-4 is likely to represent a lorica with an enclosed cyst. In their illustration of *Parafavella denticulata*, Reid & John (1978) depicted a similar lorica with a circular cyst in it. In the Banda Sea material, this phenomenon was several times observed.

In Reid & John (1978), the cyst of *Leprotintinnus pellucidus* (Cleve) was illustrated with a small aboral appendix, which is observed in our ELELNO-5, -6, -7, and HEXANO-1. Reid & John (1981) described the cyst type P with an elongated, well differentiated neck. SPHERNO-3, -7, -8, -9, ELELNO-7, ESABNO-2, AROBNO-2, -3, and HEXANO-1 also have that particular feature. The sub-spherical shape of cyst type M, extending into a small neck (Reid & John, 1981) can be seen in SPHERNO-4, -5, and -6. The more elongated cyst type T (Reid & John, 1981) can be seen in ELELNO-2, -4 and in AROBNO-1.

The horned and flagellar types SPHERNO-12, ELELNO-8, TRIANO-3, TRIANO-4, TETRANO-1, and TETRANO-2 are believed to fit in the shape variation observed for tintinnid cysts. On the other hand, the types SPHERNO-1, SPHERNO-2, ELELNO-1, ESABNO-1, ELLIPNO-1, ESOBNO-2, ESOBNO-3, ARABNO-1, and TRIANO-1 have few characteristic features and could be the remains of either tintinnids or other protozoans.

Types characterised by rooted stems (SPHERNO-13, ESOBNO-4, HEXANO-5) could be the remains of sessile life stages of non-tintinnid ciliates. On the other hand, the cyst of *Favella serrata* is encapsulated in a pouch that is rooted in the basal part of the lorica (Reid & John, 1978; see Fig. 1) and resembles tintinnomorphs characterised by the presence of roots.

The identification of specimens with two (TRIANO-6), three (TETRANO-3) and more horns (ARABNO-3) is problematic. TRIANO-6 could be interpreted as a 'twin' form. Twins occur in the tintinnomorphs with an elongated corolla and horn (ELELNO-category; see Fig. 17-5) and the spherical, ornamented types (SPHERO-category; see Fig. 17-4), but in these cases the loricae are fixed at their openings, resulting in fusiform or elongated ornate palynomorphs, respectively. In the TRIANO-category, where the horn is not located aborally, twin formation could result in a shape like TRIANO-6. Type TETRANO-3 with its three horns and its ornamentation decreasing in size towards the opening, is very distinct from all other tintinnomorphs. Considering that different tintinnid families are characterised by a reticulum and that cysts are suspended in the lorica, a shape like TETRANO-3 could represent the cyst of a tintinnid.

Type ARABNO-3 has a long diverging collar and a rhombic shape. These features are characteristic for the tintinnid cysts of the ARABNO-category. The large number of aboral horns, however, is unusual. Reid & John (1981) described a cyst type Q with thick, stick-like spines with a length of at least half the diameter of the chamber. These spines are distributed regularly over the cyst; in ARABNO-3, however, the spines are confined to the aboral side of the cyst.

ARABNO-3 is of particular interest with respect to the discussion on the affinity of the chitinozoans. Morphologically, the type (Plate 1, fig. 4) is fully comparable with well-preserved translucent chitinozoans from the Palaeozoic (Jenkins, 1970).

Concluding remarks

The discovery of a wide variety of tintinnomorphs in (sub-)Recent sediments of the Banda Sea suggests that in marine depositional settings the preservation potential of the probably chitinous remains of tintinnids may become enhanced under the influence of specific external physical and chemical conditions. In time, therefore, records of

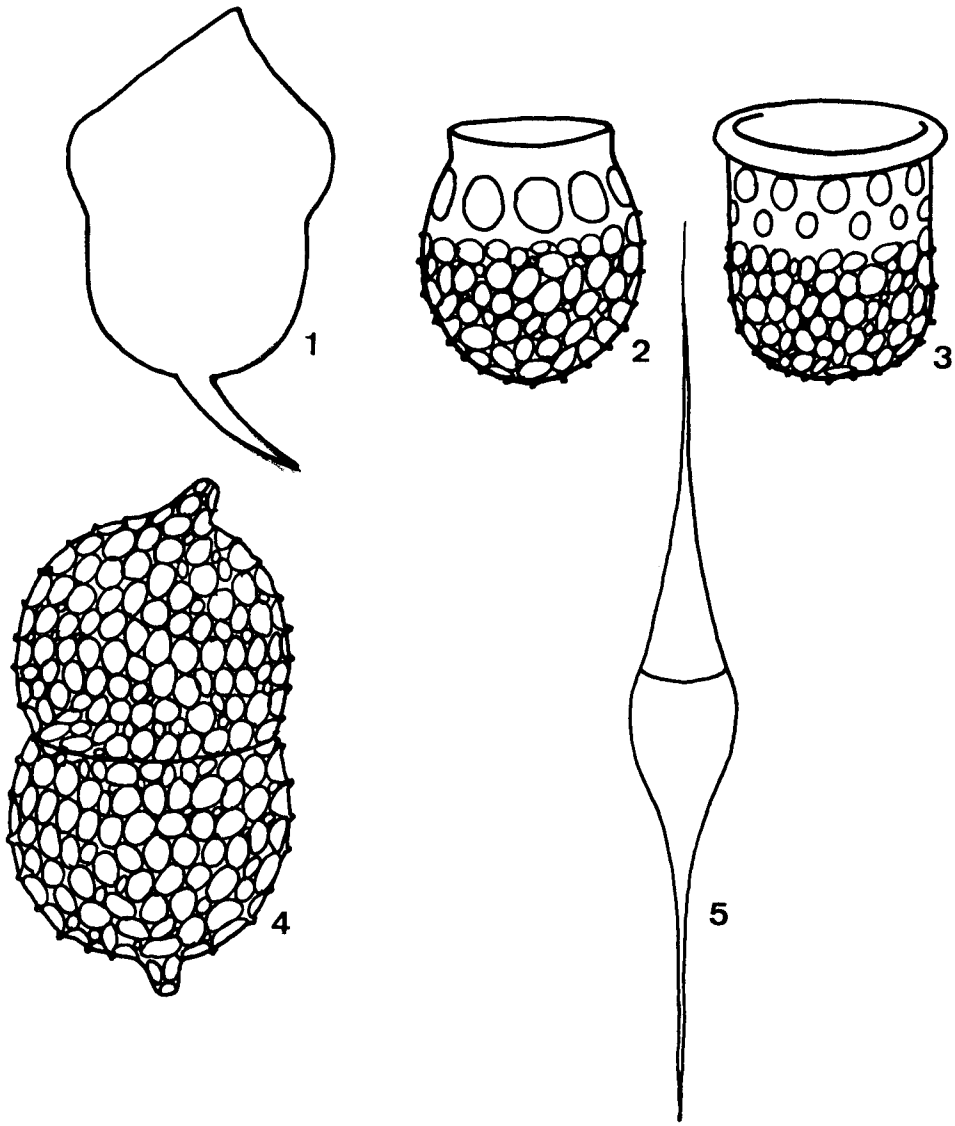

Fig. 17. Egg-shaped, aborally blunt, not ornamented (ESABNO), spherical ornamented (SPHERO), elliptical ornamented (ELLIPO) and elongated elliptical not ornamented (ELELNO), and rectangular ornamented (RECTO) tintinnomorph types from the Banda Sea; 1: ESABNO-4 (sample Sn-169a); 2: ELLIPO-1 (sample Sn-369); 3: RECTO-2 (sample Sn-394); 4: SPHERO-5, two specimens forming twin (sample Sn-422); 5: ELELNO-14 (upper specimen) and ELELNO-16 (lower specimen), forming twin (sample Sn-241).

tintinnomorphs may be of use for marine palaeoecological research. It is hoped that the present informal descriptive scheme will stimulate palynologists to further document the presence of different types of tintinnomorphs in marine sediments.

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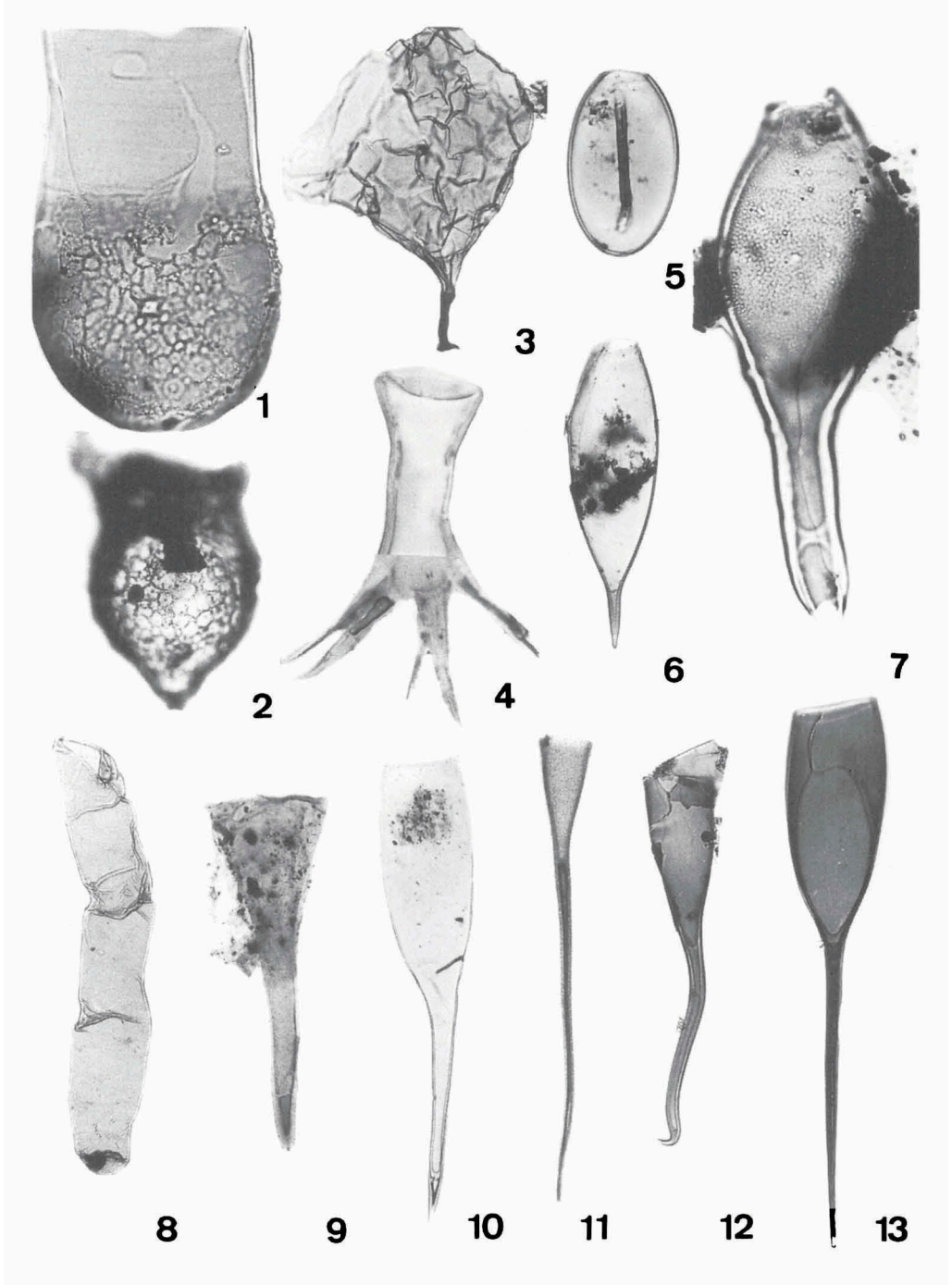
Plate 1

Photomicrographs of selected tintinnomorph types from the Banda Sea; 1: ESABO-1 (slide Sn-243), × 500; 2: ESABO-2 (slide Sn-236), × 500; 3: ESOBNO-4 (slide Sn-248), × 250; 4:ARABNO-3 (slide Sn-152), × 500; 5: ELELNO-2 (slide Sn-196), × 500; 6: ELELNO-9 (slide Sn-196), × 500; 7: ELELNO-12 (slide Sn-196), × 500; 8: RECTNO-2 (slide Sn-152), × 250; 9:ELELNO-10 (slide Sn-152), × 250; 10: ELELNO-11 (slide Sn-196), × 250; 11: ELELNO-14 (slide Sn-233), × 250; 12: ELELNO-15 (slide Sn-233), × 250; 13: ELELNO-16 (slide Sn-156), × 250.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