

Review

Turbellarian egg capsule as one type of aquatic palynomorph; reconsideration of Tintinnomorph

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Abstract: Tintinnomorphs have attracted attention in the analysis of aquatic palynomorphs due to their characteristic funnel, bell, pitcher, or cup-shaped morphology, although they have not been predominant in aquatic palynomorph assemblages in comparison with dinoflagellate cysts, microforaminiferal linings and crustacean resting eggs. In this paper, through an examination of the history of tintinnomorph research, the origin of tintinnomorphs becomes clearer. Recent studies of aquatic or non-pollen palynomorphs have revealed that the tintinnomorphs consist of various remains from several types of organisms of different origins, including ciliate lorica, resting cysts, and turbellarian egg capsules. Considering these results, several technical terms for description of turbellarian egg capsules are reassessed. Also, new insight on the origin of acritarchs called *Palaeostomocystis* and *Beringiella* is shown based on comparison of morphological features of modern turbellarian egg capsules. However, the establishment of a species concept for turbellarian egg capsules and their usefulness as paleo-environmental indicators will require further investigation of modern turbellarian egg capsules.

Key words: tintinnomorph, turbellaria, palynomorph, egg capsule, *Palaeostomocystis*, *Beringiella*

Introduction

Holocene to Late Pleistocene sediments contain various microfossils (remains). In the field of micropaleontology, microfossils (remains) composed of organic walls have been collectively called palynomorphs (Travers, 2007). Among them, pollen, fern spores, and dinoflagellate

cysts are attracting attention as powerful indicators for paleoclimatological and paleoenvironmental reconstruction, and basic research on their morphology, chemical composition of their walls, physiology and ecology is actively progressing (e.g. Van Nieuwenhove et al., 2020 for dinoflagellate cysts). On the other hand, palynomorphs (e.g., ciliate cysts, foraminiferal linings,

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Note : In this article, many published studies are introduced and followed together with photo figures and drawings. When we refer these figures in the text, abbreviations with small letters are used like pl. and fig.

resting eggs and body fragments of cladocerans, and coenobia of green algae) have been regarded as minor components in comparison with major pollen, fern spores, and dinoflagellate cysts. If they are dominant, these palynomorphs have been especially noticed. In recent years, interest has been focused on palynomorphs other than pollen, fern spores, and dinoflagellate cysts, and research results, including reviews, have been published one after another (Hartman et al., 2018; Matsuoka and Ishii, 2018; Pieńkowski et al., 2020; Mudie et al. 2021; McCarthy et al., 2021).

On the other hand, these minor palynomorphs are often the remains of dormant cells and have not received much attention from modern biologists. Micropaleontologists have basically endeavored to construct a classification system based on the microfossil morphology. However, at times, these researches are a too focused on morphological information (e.g. van Waveren, 1993), and lose sight of the affinity of the remains. One such example is the study of hystrichospheres related to fossil dinoflagellates (Sarjeant, 1974). Since the dormant cells (cysts) remaining in the sediment and their motile cells (plankton) are morphologically different, a germination experiment was required to establish a correspondence between both. Such new methods were needed for further research developments. Thus, increasing the basic biological information about organic microfossils in sediments that were not fully characterized in previous studies will be useful for future paleoenvironmental and paleoclimate researches.

Recent studies (e.g., Haas, 1994; Hartman et al., 2018; Mudie et al., 2021) have pointed out that fossils called tintinnomorphs by van Waveren (1993), which were grouped as palynomorphs with similar morphology, have different biological affinities. Turbellarian egg capsules are the origin of one of the main types of tintinnomorphs. Therefore, in this study, we will review modern turbellarian egg capsules collected in sediments and propose future research directions from the viewpoint of palynology.

1. Modern Platyhelminthes

1-1 Taxonomy of Turbellaria (flatworms)

Traditionally, the phylum Platyhelminthes was divided into four classes: Turbellaria, Monogenea, Trematoda,

and Cestoda. However, as a result of molecular phylogenetic studies, it has become clear that Turbellaria is a paraphyletic group. Therefore, it is not maintained as a class and has been dismantled. According to Ruggiero et al. (2015), the Platyhelminthes are classified into two subphyla and four classes. Turbellaria has been subdivided into subphylum Catenulidea, class Catenulida (e.g., *Stenostomum saliensae*, *Catenula lemnae*) and subphylum Rhabditophora (class Macrostromorpha (Polycladidea, e.g., *Pseudoceros bimarginatus*, *Pseudoceros scintillates*), class Polycladidea (e.g., *Notoplana humilis*), and class Neoophora (e.g., *Coniochaeta hoffmannii*). Although Monogenea (e.g., *Hexostoma thynni*), Trematoda (e.g., *Paradeontacylix grandispinus*), and Cestoda (e.g., *Taenia saginata*) have been confirmed to be cohesive as taxa, they are now positioned as infraclasses within class Neoophora. Since most of the taxa producing egg capsules, such as the families Umagillidae, Dalyelliidae and Typhloplanidae, were formerly classified into the Turbellaria, it may be preferential to keep the term “Turbellaria”, which is not used as a formal taxonomic name anymore. In this article, we propose to use “turbellaria” and focus only on the reconsideration of tintinnomorphs, some of which are considered to be produced by turbellarians (Table 1).

1-2. Turbellarian egg capsules in plankton samples

Lohmann (1910) introduced two morphologically different organisms as "Geschwänzte Cyste" in the plankton collected by Vanhöffen (1897, p. 287, taf. 6, fig. 5) at Karajak Fjord on the west coast of Greenland; Lohmann (1910) explained that they are the same two types described by Kräfte (1906) as follows (Translated from the German description; Fig. 1):

“1. Spindle-shaped egg forma a (Kräfte 1906, fig. 7a, b = Lohmann 1910, fig. 15 a, b) (reproduced in Fig. 1A).

as "The bluish green to brownish shell is slender and spindle-shaped and ends on both sides in a thin thread of the same color about 1/3 of the length of the whole organism, one of which occasionally shows an adhesive disc-shaped thickening, which makes the eggs likely to stick. Especially since only empty casings were found floating freely, which were either still provided with both end threads, had split open at the side (fig. 7a) or in which a small cover with a cut surface inclined to the longitudinal axis had jumped off (fig. 7b). In the large

Table 1 List of turbellarian species that produce egg capsules. There are many publications dealing with turbellarian egg capsules collected from sediment; however, most of them do not mention species names.

Species	Order: Family	Morphology (Shape of egg capsule)
<i>Oametra arbora</i> (Ozaki, 1932)	Marcus, 1949	ovoidal with slender stalk
<i>Provostea indicus</i> (Schultz, 1851)	Graff, 1882	elongatedly ovoidal with short stalk
<i>Castrella pinguis</i> (Silliman, 1884)	Fuhrmann, 1884	subspherical with filament
<i>Anoploleum nanosia</i> Schneider, 1858		
<i>Anoploleum tichopi</i> Beck, 1925		
<i>Syndesmis echinorana</i> Meisner, 1923		
<i>Syndesmis franciscana</i> (Lohman, 1946)	Marcus, 1949	
<i>Anoploleum kymuanae</i> Shinn, 1983		
<i>Wahlia pulchella</i> Kozloff and Shinn, 1987		
<i>Syndesmis deandersoni</i> Stunkard and Corliss, 1951		
<i>Syndesmis collingwoodi</i> (Hertel, Dlezynski and Uebelaker, 1990)	Jondelius, 1996	Oval to diamond-shaped, posterior end with a short stalk that bears long filaments
<i>Syndesmis rubida</i> Kozloff and Westervelt, 1990		Ovoidal to shortly ellipsoidal with long stalk
<i>Syndesmis albida</i> Kozloff and Westervelt, 1990		ovoidal to subspherical with long filamentous stalk, 68-160 µm x 56-120 µm
<i>Syndesmis ovalinae</i> (Marcus, 1968)	Hertel and Duszynski, 1991	elongate with long filamentous stalk
<i>Microdalyellia amigera</i> (Schmidt, 1862)	Geyssior, 1938	ovoidal with long filamentous stalk
<i>Geyssioria virgillifera</i> (Platnickow, 1906)	Ruebush and Hayes, 1939	truncated pyramid, wide pylome
<i>Strongylosoma nadiatum</i> (Miller OF, 1773)	Orsted, 1844	spherical, wide pylome
<i>Mesosoma lingua</i> (Abladgaard, 1789)	O. Schmidt, 1848	spherical, radial operculum suture
<i>Gyroris hemaphysodius</i> Ehrenberg, 1831		Roundly cup-shaped (I-A, B) and cup-shaped (I-C, D) with stalk furnishing attachment apparatus, wide pylome
Neorhabdocoela unknown		spherical with short stalk
<i>Urosoma oprimae</i> (Graff, 1882)	Westblad, 1955	oval or suboval cocoons which are thin-walled and contain several subspherical ovoidal egg capsules. Each egg capsule has sealing zone in the shell. 219 (150-290) x 170 (100-260) nm
<i>Gyroris hemaphysodius</i> Ehrenberg, 1831		ovoidal to ellipsoidal, yellowish brown, large pylome
<i>Syndesmis pataconiza</i> Bruges and Ivanov, 2010		ovoidal with very long filamentous stalk
<i>Microsotomum lineare</i> (O. F. Muller, 1773)	Orsted, 1843	Yellowish, spherical (200-250 nm)
<i>Plagiostomum tenanti</i> Ford and Du Plessis, 1874		Dark yellowish, ovoidal with stalk
<i>Dugesia gonocophala</i> Duges, 1850		black to brownish orange, spherical (2000 nm) egg capsule
<i>Stenostomum</i> sp.		single egg capsule, no stalk
<i>Microdalyellia</i> sp.		many egg capsules in animal tissue, no stalk
<i>Dalyellia</i> sp.		single egg capsule, no filament
<i>Geyssioria</i> sp.		ovoidal with operculum suture
<i>Typhloplanina viridana</i> (Abladgaard, 1789)	Orsted, 1843	yellowish orange to reddish brown, spherical with operculum suture, 144 – 330 µm
<i>Strongylosoma nadiatum</i> (O.F. Muller, 1773)	Orsted, 1844	spherical, reddish brown, no stalk, 155-185nm
<i>Rynchonostoma rostratum</i> (O.F. Muller, 1773)	Orsted, 1844	spherical to ellipsoidal, yellowish brown, no stalk, 200 nm
<i>Rhishanella truncata</i> (O. Schmidt, 1858)	Voigt, 1892	Elongatedly ovoidal, 160 nm
<i>Mesosoma productum</i> (O. Schmidt, 1848)	O. Schmidt, 1888	egg, ovoidal, yellowish to reddish brown, 270-360 nm
<i>Mesosoma lingua</i> (Abladgaard, 1789)	O. Schmidt, 1848	egg, spherical, brown
<i>Bathronostoma persanatum</i> (O. Schmidt, 1848)	Braun, 1885	usually one and rarely two-to three egg capsules involving one or rarely two eggs
<i>Gyroris hemaphysodius</i> Ehrenberg, 1831		subspherical, yellowish orange, short stalk, 350 nm
<i>Ophidocystis (Polycystis) goetzei</i> Bresslau, 1906		ovoidal to ellipsoidal (165x120nm)
<i>Geyssioria garuda</i> Van Steenkiste, Van Mulken and Artois, 2012		egg-shell with sinuate outline
<i>Geyssioria oshoae</i> Van Steenkiste, Van Mulken and Artois, 2012		ovoidal to rhomboidal (180nm)
<i>Geyssioria stokesi</i> Van Steenkiste, Van Mulken and Artois, 2012		elongate egg capsule with stout stalk bearing basal attachment, large pylome bearing irregular suture of operculum
<i>Tennocephala colombiensis</i> Garcés, Puerta, Tabares, Lenis and Velásquez, 2013		yellowish brown, subspherical with very long filamentous stalk
<i>Syndesmis aethiopharynx</i> Westervelt & Kozloff, 1990		brownish, ovoidal with long filamentous stalk
<i>Syndesmis omlenki</i> Brusa, Montes, Marcotequi and Martorelli, 2017		brownish, ovoidal with long filamentous stalk
<i>Syndesmis selkani</i> Brusa, Montes, Marcotequi and Martorelli, 2017		ovoidal with long filamentous stalk (125 µm long and 85 µm wide), wide pylome with operculum bearing irregular suture
<i>Syndesmis karalikaikina</i> Monneus, Vanhove and Artois, 2019		ovoid, brownish
<i>Geyssioria</i> sp.		Large, spherical egg capsule with filamentous stalk, 2000 nm
<i>Gracila amocephala</i> (Woodworth, 1987)	Ball, 1974	not clear
<i>Itaipisa novacalantica</i> Diez, Schockaert, Reygel and Artois, 2021		not clear
<i>Reinhardtynchus pacificus</i> Diez, Schockaert, Reygel and Artois, 2021		not clear
<i>Galapagella cubensis</i> Diez, Schockaert, Reygel and Artois, 2021		not clear
<i>Stimplocystis asymmetrica</i> Diez, Schockaert, Reygel and Artois, 2021		not clear

Classification followed by Turbellarian
 WoRMS (World Register of Marine Species)
<http://www.marinespecies.org/turbellarians/index.php>
 and
 INPN (Inventaire National du Patrimoine Naturel)
https://inpn.mnhn.fr/espece/cd_nom/543104/tab/taxo?lg=en

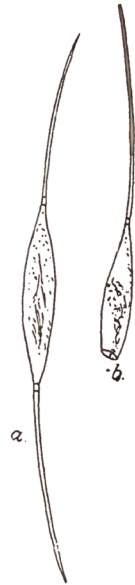


Fig. 15. Spindle egg, forma a, (After Kräfft)
a) egg with a lid-like tip, b) egg cracked at the side



Fig. 16. Spindle egg, forma b, (After Kräfft)
a) Larger and , b) smaller specimen, the shell is
at one pole cracked open like a lid.

Fig. 1 Turbellarian egg capsules in plankton sample collected by Vanhöffen (1897) as cysts possessing a tail (A from fig. 15 and B from fig. 16 in Lohmann, 1910).

"spindle egg" there is no indication of the seam along which the lid comes off. The length was about 1 mm, the thickness 60 μm . Probably Kräfft rightly considered these as trematode eggs and they were found in the plankton of the North Sea off the Elbe and Weser estuaries."

"2. Spindle-shaped egg forma b (Kräfft 1906, fig. 7c, d = Lohmann 1910, fig. 16a, b) (Fig. 1B).

as "Like the previous shape, but more rounded and with a seam running in an oblique direction; Adhesive threads with a clearly defined adhesive disc (not shown on the drawing). Length 200–300 μm , thickness 100–170 μm ". It is inferred that the Spindle forma a of fig. 7a seems to be a pre-hatching egg capsule with filaments on both sides, fig. 7b seems to be a post-hatching egg capsule losing an operculum, and Fig. 7c, d are post-hatching egg capsules with different morphologies.

Although Kräfft (1906) suggested these were eggs of trematoda, they seem to be classified as the Rhabdoceola (turbellaria) rather than Trematoda, because these organisms illustrated have greenish to brownish wall of egg capsules possessing a stalk as explained later. Some Trmatoda species like *Cardicola orientalis* has crescent-shaped eggs and Monogenean *Vallisiopsis contorta* has fusiform eggs with long filaments at both ends and a non-pigmented and nearly transparent wall (Japan Fisheries

Resource Conservation Association, 2015). These morphologies are different from typical turbellarian egg capsules. Therefore, these spindle forms may be identical to Neorhabdoceles (turbellaria) not Trematoda.

2. Study history of turbellarian egg capsules as fossils preserved in sediments

2-1 Freshwater sediments

Brownish funnel-, bell-, pitcher-, and cup-shaped palynomorphs have occasionally been observed during pollen analysis studies carried out mainly in Holocene sediments due to their high durability, but have been recorded as "problematica" due to their unknown identity (e. g., Erdtman, 1922; Nilsson, 1952). Many of them were records from freshwater sediments, but did not receive much attention because they were low in concentration compared to pollen, fern and fungal spores (e.g., Faegri and Iversen, 1989).

Harmsworth (1968) found the presence of Neorhabdoceles (Platyhelminthes) egg capsules in sediment cores collected at Blelham Tarn, England, and suggested them to belong to two types: a *Gyratrix* type: a dark-colored and wine glass-shaped body with or without striation and bearing stalk, and a *Microdalyellia*

type: dark-colored, U-shaped body, and spherical body much lighter in color. Interestingly, Harmsworth (1968) described that egg capsules are composed of orthopolyphenols and are initially white (de Beauchamp, 1961), but they rapidly turned black when transformed into quinone, and *Neorhabdoceles* egg capsules were composed of the body capsule and the operculum.

The oldest occurrence of fossil turbellarian egg capsules (*Gyratrix* type) was reported in the Middle Pleistocene (ca. 250×10^3 yBP) freshwater sediments of Lake Biwako, central Japan by Kadota (1973).

Pennak (1978) illustrated two morphologically different egg capsules: one is spherical and larger (planarian cocoon), and the other is ellipsoidal with an operculum and a slender stalk (*Gyratrix* sp.), and both have basal attachments at the end of stalks. Pennak (1978) also mentioned that the cocoons (egg capsules) are initially light-colored when recently deposited, but soon become dark brown or blackish. While introducing the methods of Quaternary palynology, Warner (1990) explained non-pollen palynomorphs with funnel, bell, pitcher, and cup-shaped morphologies as *Neorhabdoceles* (flatworm) egg capsules: *Gyratrix* type with a slender stalk, *Microdalyellia* type, and spherical-shaped type.

Haas (1996) named *Neorhabdoceles* oocytes (turbellarian egg capsules) in gyttja sediments of the freshwater lake "Wallisellen-Langachermoos" in Switzerland according to their morphological characteristics in the process of studying them from a paleoecological point of view. Haas (1996) identified the following species: *Microdalyellia amigrea* (Type 1A–E), *Gieysztorina virgulifera*, *Strongylostoma radiatum* (Type 1A–B), *Mesostoma lingua* Type, *Gyratrix hermaphroditus* Ecotype 1A *Gieysztorina virgulifera* D, and *Neorhabdoceles* Unknown Type A. Gelorini et al. (2011) described non-pollen palynomorphs conserved in East African lake sediments to contribute to future paleoenvironmental studies. As microscopic zoological remains, Gelorini et al. (2011) recorded egg capsules identified as *Gyratrix hermaphroditus* and *Microdalyellia amigrea* of *Neorhabdoceles* (turbellaria). However different morphotypes within these species were observed, and these morphotypes were regarded as not different species. Thus, the study of turbellarian egg capsules preserved in sediments was initially focused on the Holocene freshwater sediments.

2-2 Marine sediments

Bujak (1984) discovered palynomorphs of dark-colored and U-shaped body without filaments from the Late Pleistocene sediments of the Bering Sea, treated them as microplankton incertae sedis, and described *Beringiella fritilla* as a new genus and species in Acritarcha. This species was subsequently transferred to the genus *Palaeostomocystis* by Roncaglia (2004), and then *Beringiella* was identified as a junior synonym of the genus *Palaeostomocystis*. The genus *Palaeostomocystis* was erected by Deflandre (1937) with the type species of *Palaeostomocystis reticulatum* from the Cretaceous in France. However, we need more careful consideration of this taxonomic change, as we discuss later.

Funnel, bell, pitcher, and cup-shaped palynomorphs also occur in modern marine sediments apart from plankton, and many of them have been classified as tintinnid cysts and loricae (Reid and John 1978, 1983; van Waveren, 1994; Mudie et al., 2010; 2011; Pieńkowski et al., 2011; 2013). van Waveren (1994) morphologically characterized these funnel, bell, pitcher, and cup-shaped palynomorphs other than tintinnid, based on the case where *Favella serrata* contained a resting cyst in a lorica shown by Reid and John (1978). van Waveren (1994) named them "tintinnomorphs" and classified them into 76 morphotypes and reported their occurrences in deep-sea sediments from the Banda Sea, Indonesia. Thereafter, many researches followed the concept of tintinnomorphs. Among them, Matsuoka (1994, plate II, fig. 9) illustrated a cup-shaped palynomorph furnished with a filament from surface sediments of Aso Bay, West Japan as indeterminate, slightly similar to Cretaceous acritarch *Domasiella* erected by Eisenack (1969).

Cup-shaped palynomorphs (Head 2007, fig. 121, m) occurred in the Eemian Interglacial (Late Pleistocene) sediments collected in the Baltic Sea and were identified as tintinnid lorica by Head (2007). da Silva et al. (2017) reported the production of tintinnomorphs in Holocene sediments collected from the Coastal Plain of Santa Catarina, southern Brazil. Matsuoka et al. (2017) and Matsuoka and Ishii (2018) followed the classification of palynomorphs proposed by van Waveren (1994) and introduced the funnel, bell, pitcher, and cup-shaped palynomorphs called tintinnomorphs as tintinnid (Ciliata). In contrast, Mudie et al. (2020, 2021) recognized that tintinnomorphs also contain

egg capsules of turbellarians that are taxonomically different from ciliate, and emphasized that caution should be exercised in environmental assessment based on these palynomorphs. Thus, the taxonomic position of tintinnomorphs is now in confusion.

3. Modern turbellarian egg capsules

There are two types of turbellarian eggs, dormant (resting) and subitaneous (temporal). Dormant eggs spend their time in a non-adaptive environment in egg capsules and are released through the operculum when the environment becomes favorable.

Hoang et al. (2013) called these two different types “D egg” and “S egg”. Empty egg capsules produced by D eggs will be preserved in sediments and remain as fossils (e.g., Harmsworth 1968 as *Neorhabdocoele* (?) egg capsules). According to video images <https://www.youtube.com/watch?v=sefdjfBmkko>, a single egg capsule together with stylet is observed in *Gyratrix hermaphroditus* Rhrenberg, 1831. This egg capsule is brownish in color, elongated ovoidal in shape and has a slender transparent stalk (filament-like). In another video image of *G. hermaphroditus* <https://www.youtube.com/watch?v=0eesPpts8UQ>, the egg capsule is yellowish brown in color, and elongated ovoidal in shape and at a position one-fourth from the top an operculum suture can be seen. Additionally, a rather stout stalk with a bulge can be observed. The last shot of these images, which is probably after spawning, shows a wider aperture with operculum suture and basal attachment at the posterior end of the stalk. Therefore, this egg capsule seems to be free from a turbellarian body. Egg capsules are one of the reproductive organs of turbellarians belonging to Neorhabdocoela. The egg capsule is an organ in which a part of the vagina swells like a bag and stores fertilized eggs there. Egg capsules contain one or more turbellarians. In addition, on the surface of egg capsules, there are sticky substances secreted and a stalk (or filament) for adhering to other substances after spawning from cement glands (Okugawa in Ueno, 2010). Larger stalks attaching to the basal substance are sometimes hollow (Shinn 1985).

Shinn (1983, 1993) described the behavior of the turbellarian egg capsules as follows. Most of the umagillids that parasitize sea urchins for example,

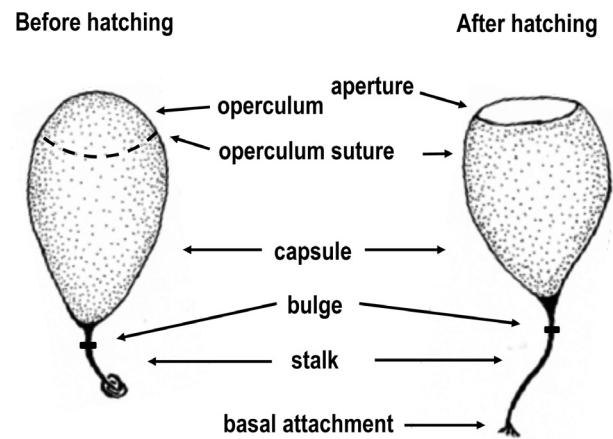


Fig. 2 Descriptive terms for turbellarian egg capsules. Drawing of *Syndesmis hermaphroditus* reported by <https://www.youtube.com/watch?v=0eesPpts8UQ>. A, Egg capsule with operculum stored in the body before hatching. B, Egg capsule without operculum preserved in sediment after hatching. Note a basal attachment at the end of the stalk.

Syndisyrix franciscanus Leham, 1946 have one or several egg capsules and are released into the intestine of sea urchins, and then expelled to seawater together with the feces. Embryos are mature in the egg capsules, dormant in the sea urchins, exposed to intestinal juice after being released into the intestine of sea urchins to induce hatching, and hatch when released into seawater. At the hatching, a part of the egg capsule is split to release embryos. After hatching, the empty egg capsules are preserved in sediments. Also, the interesting photos shown by Zapata and Varela (1981) and <http://dorsetmicroscopy.blogspot.com/2014/07/budding-or-not.html> may suggest that at the hatching, egg capsules attach to suitable particles such as foraminifers.

3-1 Morphology of modern egg capsules

Turbellarian egg capsules consist of mainly three parts: capsule, stalk and basal attachment parts. At one-third of the capsule from the top, an operculum is formed, as indicated by a circular suture at the spawning (Fig. 2). Most of fossilized turbellarian egg capsules extracted from sediments miss the operculum and form an opening which is called an ‘aperture’. Some turbellarian capsules do not have a stalk nor a basal attachment. Based on

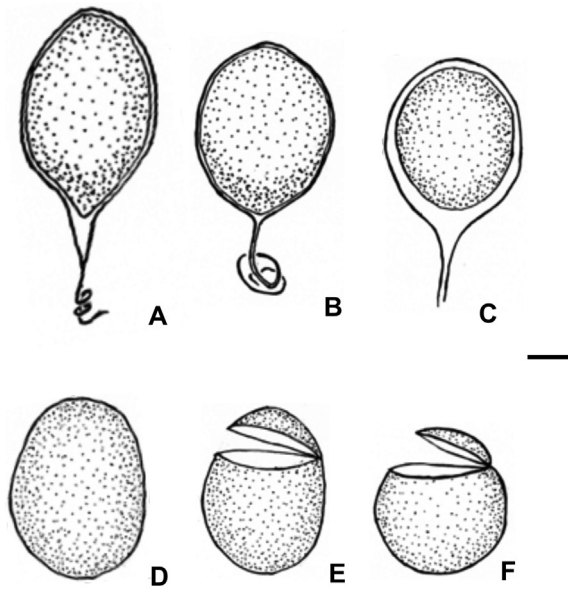


Fig. 3 Six basic morphological types observed in modern turbellarian egg capsules.

A, B, and C, Egg capsules with stalks. D, E, and F, Egg capsules without stalks. A & D, ellipsoidal type. B & E, subspherical to ovoidal type. C & F, spherical type.

A, drawing of *Wahlia pulchella* egg capsule illustrated by Kozloff and Shinn (1987, fig. 2). B, drawing of *Syndesmis dendrastrorum* egg capsule illustrated by Shinn (1988, fig. 2). C, drawing from *Syndesmis evelinae* illustrated by Hertel and Duzynski (1991, fig. 1). D, drawing from *Gieysztoria* sp. from Yamazaki (2020, frontispiece 4 C). E, *Castrella truncata* illustrated by Uchida et al. (1965, fig. 59A). F, drawing from *Strongylostoma ratiatum* illustrated by Okugawa in Ueno (2010, fig. 12–28 F)

these morphological features, modern turbellarian capsules are grouped as follows (Fig. 3);

1. Stalk Group

- 1.1. Ellipsoidal type e.g., *Gyatrix hermaphroditus* (Gelorini et al., 2011) (Fig. 3A)
- 1.2. Cup-shaped type e.g., *Wahlia pulchella* (Kozloff and Shinn, 1987) (Fig. 3B)
- 1.3. Spherical type e.g., *Syndesmis dendrastrorum* (Shinn, 1988) (Fig. 3C)

2. Non-Stalk Group

- 2-1 Ellipsoidal/cup-shaped type e.g., *Gieysztoria* sp. (Yamazaki, 2020) (Fig. 3D, E)

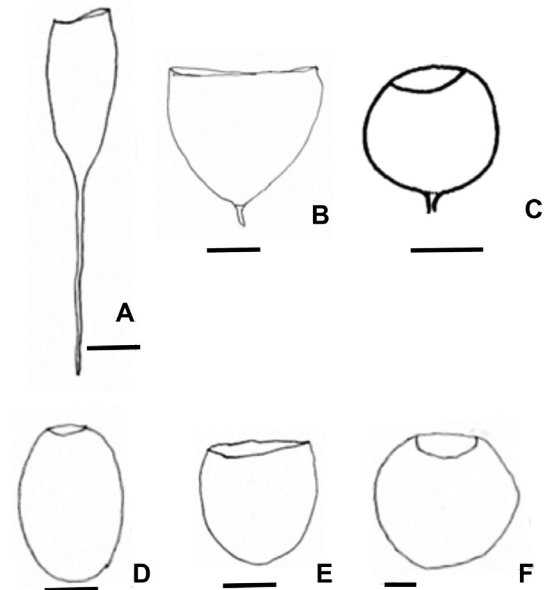


Fig. 4 Six basic morphological types of turbellarian egg capsules preserved in sediments.

A, B, and C, Egg capsules with stalks; D, E, and F, Egg capsules without stalks. A and D, ellipsoidal type. B and E, subspherical to ovoidal type. C and F, spherical type.

A, modified from ELENNO-16 of van Waveren (1994, pl. 1, fig. 13). B, modified from T 1221 of Gelorini et al. (2010, plate VIII, T.1221). C, modified from Haas (1996, fig. 1 (p), Neorhabdocoela Unknown – Type A).

- 2-2 Spherical type e.g., *Bothromesostoma personatum* (Okugawa in Ueno, 2010) (Fig. 3F)

Most turbellarian egg capsules have a smooth surface; however, a few have an ornamented wall, such as the waving striations in *Anoplodium hymanae* Shinn, 1983 (Shinn 1985) (Fig. 4).

3-2 Morphology of turbellarian egg capsules preserved in sediments

A few researchers have produced schematic illustrations of turbellarian eggs as introduced above (Lohmann, 1910; Harmsworth, 1968; Haas, 1996) and of some tintinnomorphs (van Waveren, 1994). In

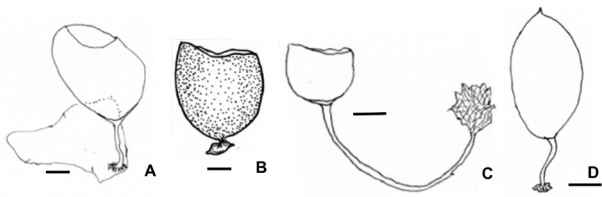


Fig. 5 Possible candidate for fossil turbellarian egg capsules possessing stalk with basal attachment. A-C, turbellarian egg capsules found in modern sediments. A, drawing from Roncaglia and Kuijpers (2006, fig. 3e). B, drawing from Pieńkowski et al., (2011, fig. 5i). C, drawing from Matsuoka (1994, pl. II, fig. 9). D, *Domasiella discophora* (Acritarcha) described by Cookson and Eisenack (1962, pl. 7, fig. 18), which was probably shown upside down and with no aperture.

addition to Lohmann (1910), others attempted to make a systematic scheme of fossilized egg capsules. These were illustrated on the basis of remains recovered from modern sediments and it is very difficult to know their corresponding adult worms. On the other hand, many studies of various Turbellaria have been carried since a long time ago, but not so much attention has been paid to their egg capsules; for example, the egg capsules have been briefly illustrated as just ovoidal shaped with/without stalks (filaments). In addition to this, most fossilized egg capsules preserved after hatching lose the operculum and this may cause morphological changes from the original shape of egg capsules. At present, it is impossible to identify the parent turbellaria based on the fossilized egg capsules (Fig. 4).

3-2-1 Stalk Group

Mainly three types of stalks can be seen on modern turbellarian egg capsules: filament type (rather longer and slender), spine type (short and stout), and short and broad type. Sometimes the stalks are incomplete due to be cut on a way, because the attachment structures are missing.

The modern ellipsoidal type with stalk is identical to illustrations and photographs provided by Lohmann (1910, fig. 15b and probably fig. 15a as a complete form), Warner (1989, fig. 8a), Haas (1996, fig. 11, m as *Gyratrix hermaphroditus*), Hartman et al. (2018, pl. 5 fig. 17-19;

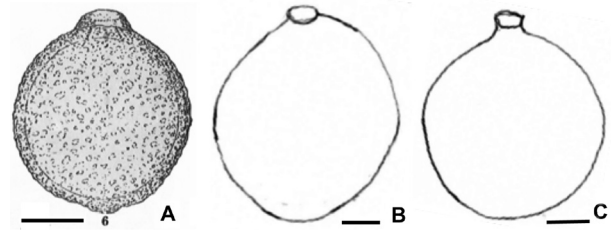


Fig. 6 Fossil and modern *Palaeostomocystis sphaerica* Deflandre 1937.

A, *Palaeostomocystis sphaerica* Deflandre 1937 (fig. 6, holotype) from Cretaceous. B, *Palaeostomocystis sphaerica* Deflandre, drawing from Hartmann et al. (2018, pl. 5, fig. 22). C, *Palaeostomocystis sphaerica* Deflandre, drawing from Warny (2009, pl.1, fig.6). Note: all specimens have a small aperture with collar.

very short stalk), Matsuoka et al. (2017, fig. 21), da Silva et al. (2017, fig. 4B-E), Mudie et al. (2000, figs. 5, 8, 12) and others (Fig. 5).

The modern cup-shaped type with a long or short stalk is similar to (Lohmann 1910, fig. 16a, b), Harmsworth (1968, fig. 7, 15), Zapata and Várela (1981), Haas (1996, fig. 1;n, o as *Gyratrix hermaphroditus*), Roncaglia and Kuijpers (2006, fig. 3e), Head (2007, fig. 12m), Gelorini et al. (2011, pl. viii, T. 1221), Chaweeapak et al. (2019, fig. 2-11), Mudie et al. (2020, fig. 11-9,12), McCarthy et al. (2021, fig. 5h as *Gyratrix* sp.), and others.

The modern spherical type with a stalk was illustrated by Haas (1996, fig. 1p as *Neorhabdocoela*, Unknown). This type with a long and flexible stalk was also recorded in surface sediments of West Japan, and it was pointed out that this remain was apparently similar to an Acritarch *Domasiella* (Matsuoka, 1994, pl. 2, fig. 5). However, *Domasia discophorai* Cookson and Eisenack, which has a subspherical to elongate body with a stalk distally divided into two appendages, was found from Cretaceous sediments of Australia and initially described as an Acritarch by Cookson and Eisenack (1962) All specimens of *Domasa* shown by Cookson and Eisenack (1962) have no aperture at the apex. Since some of them have one or two stalks at the antapex, a few different species may be included in *D. discophora*. Later, Eisenack et al. (1973) transferred them to the new genus *Domasiella* (Fig. 6).

3-2-2 Non-Stalk Group

This group is also morphologically divided into three types, like the Stalk Group.

The fossil elongate type was shown by Bujak (1984, pl. 4, fig. 12-14 as *Beringiella fritilla*), Warner (1989, Fig. 8b as *Microdalyellia*-type), Haas (1996, fig. 1a-f as *Microdalyellia armigera* including five morphotypes), Roncaglia (2004, fig. 2j as *Palaeostomocystis fritilla*), Roncaglia & Kuijpers (2006, fig. 7d-f), Warny (2009, pl. 1 fig. 6-8), Hartman et al. (2018, pl. 5 figs. 10-13, 14-16), Gelorini et al. (2011, pl. viii, T1221, T1223), Matsuoka and Ishii (2018, fig. 4c, d), Mudie et al. (2020 fig. 14 as *Beringiella* Bujak 1985), MacCarthy et al. (2021 as *Microdalyellia*), Head (2007, fig. 12l) and others.

3-2-3 *Beringiella* or *Palaeostomocystis* (Table 2)

However, morphotypes of fossilized egg capsules that are mostly similar to those of modern turbellarians described above are also found, and sometimes similar morphotypes are classified as Acritarcha and called by several different names. For example, the ellipsoidal type like that of *Gieystoria* sp. without a stalk is similar to the acritarch genus *Beringiella* or *Palaeostomocystis*. *Beringiella fritilla* Bujak as a new genus and species was firstly described from Pleistocene marine sediments by Bujak (1984). *B. fritilla* is ornamented with a thick, foveolate wall with a rather wide aperture and a free operculum (Bujak 1984). Later, Roncaglia (2004) transferred *Beringiella* to *Palaeostomocystis*, which is also characterized by a thick, foveolate or reticulate wall and a rather wide aperture without a collar. Roncaglia (2004) also described a new species, *Palaeostomocystis subtilitheca*, characterized by a transparent wall and larger aperture with concentric ring, from Pleistocene sediments and suggested that this palynomorph was not a ciliate lorica but a cyst form (Fig. 7).

Palaeostomocystis is one of the organic microfossils established by Deflandre in 1937. Since then, there has been much debated about whether *Palaeostomocystis* is a dinoflagellate cyst or not. For example, Stover and Evitt (1978) considered it as a dinoflagellate cyst, however it is now treated as an Acritarch (Fensome et al., 2019). The type species of this genus is *Palaeostomocystis reticulata* Deflandre, but at the same time Deflandre (1937) also described *Palaeostomocystis sphaerica* Deflandre as another new species. Besides

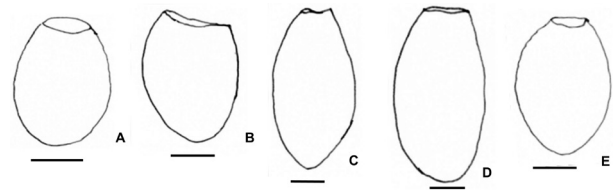


Fig. 7 Morphological variation of *Palaeostomocystis fritilla* (Bujak) Roncaglia.

A, drawing from Bujak (1984, pl. 4, fig 14; holotype). B, drawing from Roncaglia and Kuijpers (2006, fig. 7d). C, drawing from Roncaglia and Kuijpers (2006, fig. 7e). D, drawing from Roncaglia and Kuijpers (2006, fig. 7f). E, drawing from Roncaglia (2004, fig. 2j).

the surface decoration, the morphology of the opening is significantly different between these two species. The opening of *Palaeostomocystis* is described as a pore or a more-or-less large opening with or without a variably developed collar. The type species *P. reticulata* (Deflandre, 1937, fig. 5) has a more-or-less large opening. Since *P. sphaerica* (Deflandre, 1937, fig. 6) has a pore with collar, the structure of the openings of these two species is clearly different. Although a pore with collar is not known in the modern Rhabdocoela egg capsule, eggs produced by Trematoda (Neoophora) species are known to be considerably smaller than the Turbellaria egg capsules, which are usually over 100 μm and rarely less than 100 μm (57-63 x 41-50 μm for *B. fritilla*). For example, *Clonorchis sinensis* (Clonorchiasis), a species that has a pore with collar, is sometimes detected in sediments and forms residual eggs. The egg (30 x 16 μm) is an elongated ellipsoid with a small opening at the top and a collar around the opening (Uddin et al. 2012). Many human parasites belong to Trematoda, and their eggs have also been detected in sediments (e.g. Kanehara and Kanehara, 1994; Le Baully et al., 2007). Some of these eggs (*Diphylobothrium* sp., *Fasciola* sp., and *Opisthorchis* sp.) illustrated by Le Baully et al. (2007) have quite similar morphology of *Beringiella*. In addition, fish schistosomiasis is known to be caused by a member of Trematoda (e.g., Ogawa and Egusa, 1986; Ogawa, 2010). Therefore, it is possible that an unknown parasite egg belonging to Trematoda is preserved in aquatic sediments. On the other hand, Hartman et al. (2018) proposed that *P. sphaerica* might

Table 2 Modern turbellarian ellipsoidal to cup-shaped egg capsule in the group without stalk and morphologically similar fossils identical to the genera *Beringiella* and *Palaeostomocystis*.

Species	Taxonomy	Morphology	Age	Reference	Remarks
modern					
<i>Neorhabdocele</i>	Rhaditophora Rahidocoela		FW sediment (Holocene)	Harmsworth 1968	
<i>Micratalyella</i> type	Rhaditophora Rahidocoela		FW sediment (Holocene)	Warner 1989	
<i>Micratalyella armigera</i> Schmidt	Rhaditophora Rahidocoela	ellipsoidal or ovoidal; width range: 70-120 µm, length range: 100-210 µm, wide aperture; with fine operculum suture			Five types; 1 A-E (different ornaments)
<i>Greysortia virgulifera</i> Plotnikow	Rhaditophora Rahidocoela	truncated pyramid, wide aperture	FW sediment (Holocene)	Haas 1996	Two types; 1 A-B (different ornaments)
<i>Strongylostoma radiatum</i> Müller	Rhaditophora Rahidocoela	spherical, wide aperture			Some other <i>Mesostoma</i> species included
<i>Mesostoma lingua</i> Ahlbgaaud	Rhaditophora Rahidocoela	spherical, radial operculum suture			
<i>Diphylobothrium</i> sp.	Rhaditophora Cestoda	elongate ovoidal with polar opening; 57 x 40 µm	Archeological site (human coprolites)	Le Bailly et al. 2007	Morphologically similar to <i>Beringiella</i>
<i>Opisthoris</i> sp.	Rhaditophora Cestoda	elongate ovoidal with polar opening; 120 x 70 µm, 27x13	(Holocene)		Type UG-1221, UG-1222 and UG-1223 are probably related to the oocyte types
<i>Gyatrix hermaphroditus</i> Erhenberg	Rhaditophora Rahidocoela		FW sediment (Holocene)	Gelorini et al. 2011	
<i>Micratalyella</i> sp.	Rhaditophora Rahidocoela		FW sediment (Holocene)	McCarthy et al. 2021	
fossil					
<i>Palaeostomocystis reticulata</i> Deflandre*	Acritarch	smaller aperture with operculum	Cretaceous	Deflandre 1937	Type species for <i>Palaeostomocystis</i>
<i>Palaeostomocystis crataeca</i> (O. Wetzel)	Acritarch		Late Cretaceous	Deflandre 1937	Transferred from <i>Trachelomonas</i> ?
<i>Palaeostomocystis sphaerica</i> Deflandre	Acritarch	fine-meshed reticulate network of muri	Cretaceous	Deflandre 1937	
<i>Palaeostomocystis punctulosa</i> Deflandre	Acritarch		Jurassic	Deflandre 1941	
<i>Palaeostomocystis ovata</i> (Wilson)	Acritarch		Paleocene	Eisenack 1971	Transferred from <i>Leiosphaeridia</i> to <i>Palaeostomocystis</i> .
<i>Palaeostomocystis pachyca</i> Cookson & Eisenack	Acritarch		Middle Cretaceous	Cookson and Eisenack 1971	
<i>Palaeostomocystis minor</i> Jiabo	Acritarch		Paleocene (early Tertiary)	Jiabo 1978	
<i>Beringiella fritilla</i> Bujak	Acritarch		M. sediment (Pleistocene)	Bujak 1984	
<i>Palaeostomocystis faeolata</i> Slimani	Acritarch		Late Cretaceous	Slimani 1994	
<i>Palaeostomocystis globosa</i> Louwye	Acritarch		late Miocene	Louwye 1999	
<i>Palaeostomocystis subtilitheca</i> Roncaglia	Acritarch	Ovoidal to obtuse-coniform, unilayered, thin-walled vesicle with circular to oval equatorial outline, circular aperture	M. sediment (Holocene)	Roncaglia 2004	as new species
<i>Palaeostomocystis fritilla</i> (Bujak)	Acritarch	One of the poles is lost by the development of a large aperture			as new combination
<i>Palaeostomocystis fritilla</i> (Bujak)	Acritarch	wider aperture	M. sediment (Holocene)	Roncaglia and Kuijpers 2006	
<i>Tintinnid lorica</i>	tintinnid	rather smaller aperture comparing with Deflandre with callor	M. sediment (Late Pleistocene; Eemian)	Head 2007	
<i>Palaeostomocystis reticulata</i> Deflandre	Acritarch	wider aperture	M. sediment (Late Pleistocene)	Wamy 2009	
<i>Palaeostomocystis</i> sp. 1	Acritarch	with callor			
<i>Palaeostomocystis fritilla</i> (Bujak)	Acritarch	with callor			
<i>Palaeostomocystis sphaerica</i> Deflandre	Acritarch	wider aperture, lack a faeolate wall; more slender, reticulate surface-wall ornamentation, conical antapex	M. sediment (Late Pleistocene)	Penkowski et al. 2012, 2020	Egg capsule of turbellaria
<i>Palaeostomocystis fritilla</i> (Bujak)	Acritarch	one polar collared pylome			
<i>Palaeostomocystis</i> sp. C	Acritarch	a single collared pylome, frustoconical collar; covered with outer membrane			
<i>Palaeostomocystis sphaerica</i> Deflandre	Acritarch	yellowish, ovoidal vesicle with one polar aperture			
<i>Palaeostomocystis</i> sp. B	Acritarch	operculum suture			
Tintinnomorph	tintinnid				
<i>Beringiella fritilla</i> Bujak (possibly)	Ciliate				Resting stage of ciliate protists

*: type species for the genus *Palaeostomocystis*

Descriptive terms for turbellarian egg capsule and ciliate cyst

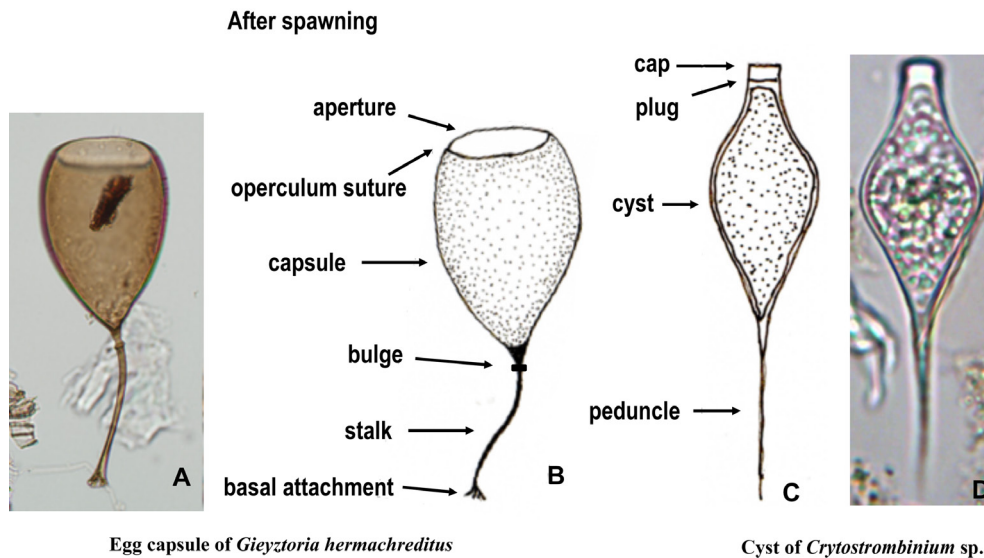


Fig. 8 Comparison between turbellarian egg capsule (A, B) and ciliate cyst (C, D). A, Egg capsule after hatching observed in surface sediment of Welu River estuary, Thailand. B, Schematic illustration of egg capsule without an operculum. C, Illustration of the ciliate cyst shown by Reid and John (1978). D, Empty ciliate cyst observed in surface sediment of Osaka Bay, Japan.

be identical to cysts of ciliates or Perkinsozoans on the basis of suggestions by Leander and Hoppenrath (2008) and Reid and John (1983). Therefore, the fact that the opening of *P. sphaerica* is not similar to turbellarian egg capsules but rather to eggs of Trematoda, cysts of ciliates or Perkinsozoans suggests that *P. sphaerica* may be in a different genus from *Palaeostomocystis*. *Palaeostomocystis* sp. C of Hartman et al. (2018) may also be different from the genus *Palaeostomocystis* because of its collared pylome. Hartman et al. (2018) described *Palaeostomocystis* sp. B characterized by elongate body ornamented with coarse reticulate structure and circular aperture (Fig. 8).

As discussed from the viewpoint of morphology, species belonging to *Palaeostomocystis* excluding *P. sphaerica* are not ciliate cysts and is possibly identical to turbellarian egg capsules. This suggestion is also supported by the chemical composition of *B. fritilla* shown by Mudie et al. (2021).

On the other hand, Le Baully et al. (2007) reported ellipsoidal eggs morphologically similar to *Beringiella* from human coprolites of the Neolithic archeological sites

and identified them as parasitic *Diphyllbothrium* sp. and *Opistorchis* sp. together with *Taenia* sp., *Capillaria* sp., and *Diocotophyma* sp. of Tremadoda, Neophora. This suggests that morphologically similar but ecologically different eggs or egg capsules of turbellarians exist in sediments. Therefore, for understanding the origin of *B. fritilla*, further investigation of egg capsules and eggs of modern turbellaria and trematode is needed.

4. Turbellarian egg capsule remains as environmental indicator

According to the summary of Platyhelminthes provided by Norena et al. (2015), modern turbellarians inhabit extremely diverse environments: marine, brackish, freshwater, wetland, water film of moss, decomposed leaves, or debris, and the majority of them are basically carnivores, but some of them are ectoparasitic or symbiotic in association with other invertebrates. Interestingly, egg-capsule-forming turbellarians inhabiting freshwater include both free living and ectoparasitic or symbiotic species. *Gyratrix*

hermaphroditus, which is known to produce egg capsules from sediments, is a free living turbellarian belonging to the Family Dalyelliidae. It is also well known that free-living turbellarians inhabit a large number of sea areas, but the family Umagillidae members, *Anopodium hymanae*, *Syndesmis dendratorum*, and *Wahlia pulchella*, which can produce egg capsules that are preserved in sediments as remains (fossils), are endosymbionts of sea cucumbers and sea urchins (Shinn, 1985; 1986; 1988. Kozloff and Shinn, 1987) (Table 1).

Fossil turbellarian egg capsules formerly called tintinnomorphs have so far been observed in various environmental areas, from low latitudes (e.g., Banda Sea (van Waveren, 1994) to high latitudes (e.g., Pieńkowski et al., 2011; 2013; 2020, Roncaglia and Kuijpers, 2004, and from freshwater (e.g., Warner, 1989; Haas, 1996; Gelorini et al., 2011), tidal marsh (e.g., Matsuoka et al., 2017, Chaweeapak et al., 2019), coast (e.g., da Silva et al., 2017, Matsuoka and Ishii, 2018, Mudie et al., 2020) to offshore (e.g., van Waveren, 1993 Banda Sea). However, most of these reports have not identified egg capsules as genus or species levels, because taxonomic and ecological studies of each morphotype have been not fully progressed. This suggests that the turbellarian egg capsules are not so helpful for paleoenvironmental reconstruction at present.

Since the report of Harmsworth (1968), several reports described the turbellarian egg-capsules from freshwater sediments. For example, Kadota (1973) conducted a paleontological study of a sediment core collected from Lake Biwa-ko, Japan and reported the density of turbellarian egg-capsules as 389 individuals / cc of sediment. Haas (1996) recorded 3500 oocysts / cc as the highest density of *Gytratrix hermaphroditus* Ecotype 1-A from the Holocene freshwater lake sediments near Zürich. According to Eeckhaut et al. (2004), 128 out of the 202 inspected sea cucumbers contained at least 6 and up to 10,000 egg capsules (mean of 1,433) and Doignon and Jangoux (2001) reported that *Anopodium parasite*, of which the egg capsule shape had not been clearly known, produced 183,455 capsules per year. Thus, a considerable number of turbellarian egg capsules seem to be produced near shallow coastal areas. However, in marine off-shore sediments, turbellarian egg capsules are not dominant among aquatic palynomorphs, constituting less than 10 individuals per sample as the originally counted

number (van Waveren, 1993) and only around 100 egg capsules / dry sediment weight in Beppu Bay (Matsuoka, unpublished data). For understanding paleoenvironmental significance of turbellarian egg capsules particularly in marine sediments, further studies of morphology, ecology and physiology of each species are needed as suggested below.

5. Tintinnomorph problem

van Waveren (1994) proposed the term “tintinnomorph” for funnel-, bell-, pitcher-, and cup-shaped palynomorphs. It is speculated that tintinnids are decomposed into several parts and preserved in sediments, referring to the specimen in which *Favella serrata* illustrated by Reid and John (1978) contains a resting cyst in a lorica. It is clear that the concept of “tintinnomorph” has been obtained by artificial combine of different components. However, these palynomorphs preserved in the sediment are taxonomically, ecologically and physiologically different organism remains, namely, turbellarian egg capsules, ciliate resting cysts, and lorica, rather than the individual parts of a ‘tintinnid’ being preserved separately. Therefore, as pointed out by Mudie et al. (2021), the use of the term “tintinnomorphs” may cause confusion, when we intend to reconstruct the paleoenvironment and paleoecology based on the production of these palynomorphs. It is instead appropriate to use terms that indicate each taxon.

Morphological differences between tubularian egg capsules and ciliate cysts are as follows:

The egg capsules of modern turbellarian species are over 100 µm in size (e.g., Haas, 1996; Shinn, 1985), whereas the size of ciliate cysts identical to *Strombidium* sp. is less than 100 µm (Matsuoka and Ishii, 2018). However, *Fusopsis* collected from the North Sea was more than 100 µm but furnished with cylinder-like head (Reid and John, 1978). The modern turbellarian egg capsules are variable from orange to brown in color, but usually light to dark brown when they are extracted from sediments. The ciliate cysts are mostly colorless and transparent. The structures around the hatching and germination apparatus are also different between turbellarian egg capsules and ciliate cysts. Turbellarian egg capsules have an aperture with an operculum, whereas ellipsoidal to elongated ovoidal ciliate cysts have a plug and cap or

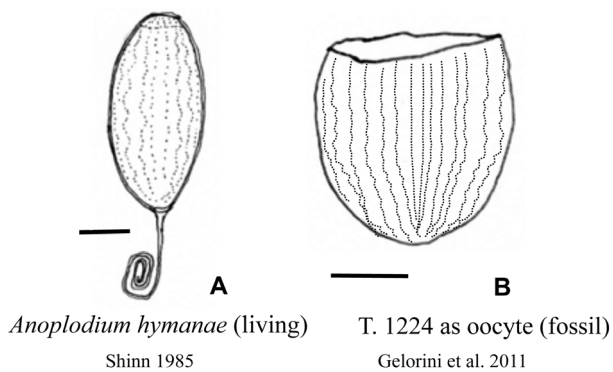


Fig. 9 Wall ornamentation on turbellarian egg capsules. A, vertical wavy lines of *Anopodium hymanae* (Shinn 1985, fig. 10). B, vertical wavy lines of fossil egg capsule of T 1224 (Gelorini et al. 2011, plate VIII).

neck with papula (Reid and John, 1978; 1983) (Fig. 7).

Therefore, it is reasonable to differentiate ciliate cysts from turbellarian egg capsules, and it is recommended hereafter to use “turbellarian egg capsules” for the brown, funnel-, bell-, pitcher-, and cup-shaped palynomorphs with or without a stalk.

6. Further study for understanding turbellarian egg capsules

Morphology of the following features are important for turbellarian egg capsules; shape, wall ornamentations, type of stalks, and a shape of basal attachments.

6-1 Morphology of egg capsules - their shape

As described above, two different types, with several subtypes, of modern turbellarian egg capsules are observed. However, further morphological studies are needed because insufficient data has been obtained for considering variations within a species. Haas (1996) illustrated several different morphotypes called “ecotypes” or “types” in a single species. For example, four Ecotypes with different shape of capsules and surface ornaments furnished with filament-like stalks were described for *Gyratrix hermaphroditus* and five types possessing different shapes of capsules and surface ornaments without stalks for *Microdalyellia armigera*. It is possible that these different types may represent

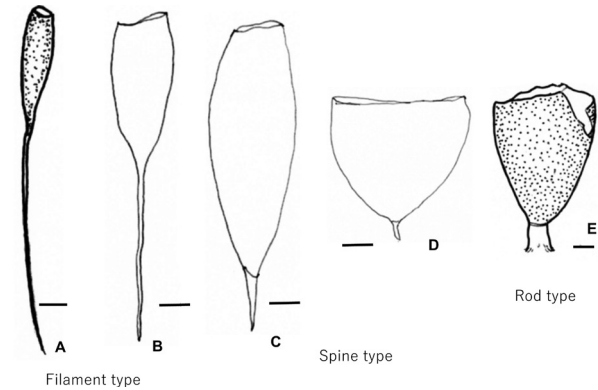


Fig. 10 Different types (filament (A, B), spine (C, D) and rod (E)) of stalks developed on turbellarian egg capsules. A from Lohman (1910, fig. 15b), B from van Waveren (1994, pl. 1, fig. 13), C from van Waveren (1994, pl. 1, fig. 16), D from Gelorini et al. (2010, pl VIII, T 1221), E from Pieńkowski et al. (2011, fig. 5 i).

independent species.

6-2 Morphology of egg capsules - surface ornament

Timoshkin et al. (2004) mentioned that *G. hermaphroditus* shows a world-wide distribution, but the wall of egg capsules of Eurasian populations is thinner and different from others in explaining expansion of its world-wide distribution. Gelorini et al. (2010) observed cup-shaped turbellarian egg capsules ornamented with longitudinal wavy lines on their surface from modern freshwater sediments. Interestingly, a similar structure was also found by Shinn (1985) in egg capsules of *A. hymanae*, which inhabits the coelom of a sea cucumber. Thus, the surface ornament on egg capsules is also probably an important feature for species identification (Fig. 9). Many and varied cup-shaped turbellarian egg capsules have been illustrated based on specimens extracted from sediments; however, it is possible that they may have been ellipsoidal before hatching and then became cup-shaped after hatching because a larger aperture was partially formed.

6-3 Morphology of stalks

As explained above, two groups of turbellarian egg capsules can be observed regarding whether they do or do not possess a stalk. *G. hermaphroditus* has an egg capsule with a filament-like stalk, when it is in the

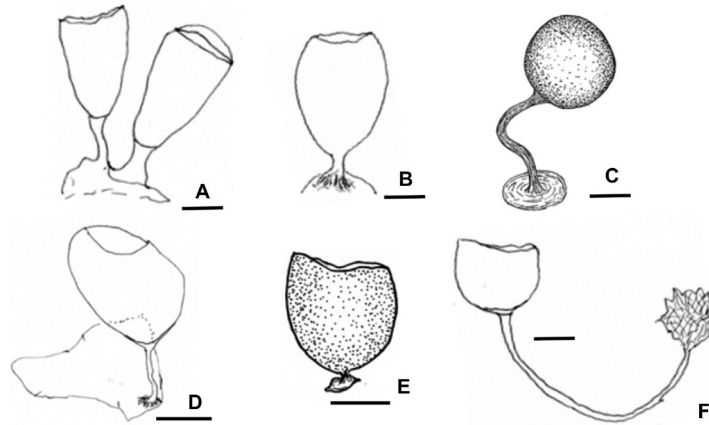


Fig. 11 Basal attachments developed in turbellarian egg capsules.

A–C, modern capsule eggs. D–E, fossil capsule eggs preserved in sediments. A, *Aegla serrana* (Amato et al. 2003, fig. 4). B, drawing from <http://dorsetmicroscopy.blogspot.com/2014/07/budding-or-not.html>. C, *Gyratrix* sp. probably with operculum (Pennak 1978, fig. 82A). D, drawing from Roncaglia and Kuijpers (2006, fig. 3e). E, drawing from Pieńkowski et al. (2011, fig. 5i). F, drawing from Matsuoka (1994, pl. II, fig. 9).

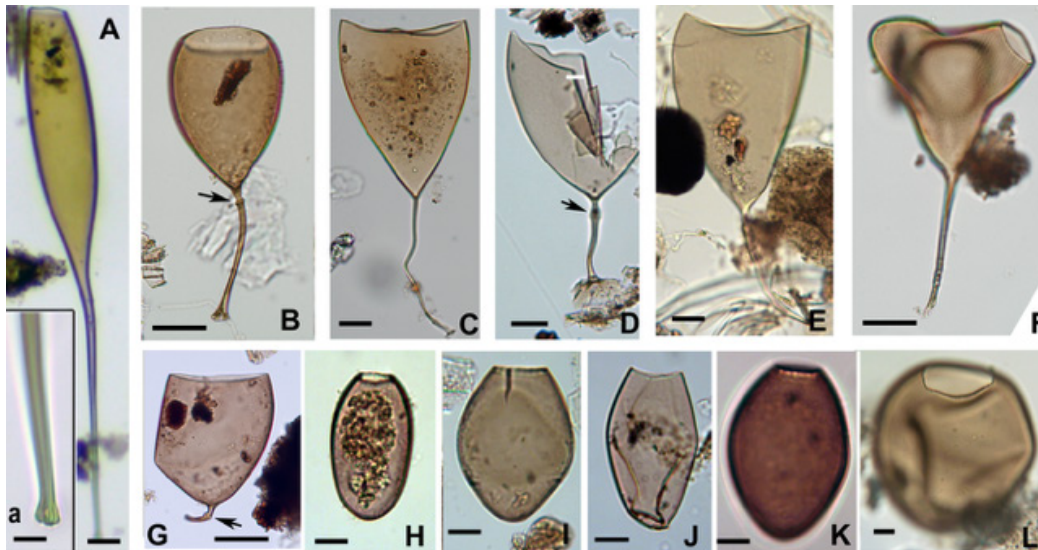


Fig. 12 Modern turbellarian egg capsules preserved in surface sediments collected from various regions.

A, Elongated capsule and long solid stalk furnished with a small basal attachment; a, enlargement of basal attachment, loc. Lake Nakaumi, Japan. B, Cup-shaped egg capsule and stalk with small bulge (arrow) and basal attachment, loc. Welu River estuary, Thailand. C, Conical egg capsule and slender stalk with tiny basal attachment, loc. Manjung River estuary, Malaysia. D, Conical egg capsule and stalk with bulge and larger basal attachment, loc. Osaka Bay, Japan. E, Conical egg capsule and long stalk, loc. Osaka Bay, Japan. F, Two-headed egg capsule and stalk, loc. Chanthburi River estuary, Thailand. G, Vase-shaped capsule and short stalk, loc. Chanthburi River estuary, Thailand. H, Ellipsoidal capsule with narrower aperture, loc. Osaka Bay, Japan. I, Ovoidal egg capsule with wider aperture, loc. Osaka Bay, Japan. J, Ellipsoidal egg capsule with wider aperture, loc. Osaka Bay, Japan. K, Ovoidal egg capsule with narrower aperture, loc. Osaka Bay, Japan. L, Spherical egg capsule with wider aperture, loc. Osaka Bay, Japan. Scale bar = 20 μm , except for A = 5 μm .

turbellarian body. On the other hand, another *Gieysztoria* sp. described by Yamazaki (2020 frontispiece 4C) does not have any stalk. In addition to this, some groups bearing a stalk have various basal attachments, which is possibly dependent on the nature of substrates that the egg capsules attach to after they are released from the body. We need further investigation for understanding the nature of these basal attachments (Fig. 10).

6-4 Morphology of basal attachment (Fig. 11)

In the group of turbellarians whose egg capsules have stalks, a basal attachment can probably be confirmed at the trailing end of the stalk, as well as formation of an aperture in the egg capsule after spawning. It can be inferred that the basal attachment is formed because the egg capsule is released from the body and then adheres to the substrate before spawning. The morphology of the basal attachment is also diverse, and may depend on the substrate to which the egg capsule is attached. For example, Zapata and Várela (1981) reported an egg capsule attached to the benthic foraminifera *Buccella frigida*. In palynological analysis, mineral particles are dissolved during the treatment process, so it is considered that the substrate to which the egg capsule is attached has been removed. Based on this premise, it will be a future task to clarify the correspondence between the substrate and basal attachment.

7. Further investigation

As shown in Table 1, most of the turbellarians that produce egg capsules belong to the Families Dalyelliidae, Typhloplanidae, and Umagillidae. According to WoRMS, the Dalyelliidae consists of five marine and freshwater genera and ten species, Typhloplanidae of mainly marine 17 genera and 38 species, and Umagillidae of 19 genera and 71 species that are all marine. However, less than 40 of these species are known to have egg capsules. In addition, the morphology of these egg capsules is rather simple: spherical to ovoidal, sometimes together with long filamentous stalks in the published literatures. On the other hand, turbellarian egg capsules recovered from sediments show wider morphological variation than those present in living organisms as shown in Fig. 12. After releasing from a main body, some of egg capsules seem to adhere to solid to soft materials like pebbles,

foraminifera shells, and plant fragments and others as illustrated by Brusca et al. (2016, fig. 10.23). This may suggest that after being released from the body to outside, egg capsules change their morphology by developing stalks and apertures, similarly to the change of the color of the egg capsules. Shape, color, stalks, surface ornaments and basal attachment of egg capsules should be investigated in more detail. Such further studies are needed to understand the significance of turbellarian egg capsules as aquatic palynomorphs.

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