THE BIOLOGY AND ECOLOGY OF TINTINNID CILIATES

MODELS FOR MARINE PLANKTON

EDITORS:

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WILEY-BLACKWELL
A John Wiley & Sons, Ltd., Publication

Wiley-Blackwell is an imprint of John Wiley & Sons, formed by the merger of Wiley’s global Scientific, Technical and Medical business with Blackwell Publishing.

Registered office: John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial offices: 9600 Garsington Road, Oxford, OX4 2DQ, UK

The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

111 River Street, Hoboken, NJ 07030-5774, USA

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Library of Congress Cataloging-in-Publication Data

The biology and ecology of tintinnid ciliates: models for marine plankton / edited by John R. Dolan ... [et al.].

p. cm.

Includes bibliographical references and index.

ISBN 978-0-470-67151-1 (cloth)

1. Tintinnida. I. Dolan, John R. (John Richard), 1955–

QL368.T55B56 2012

579.4'9–dc23

2012010713

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover image: Morphological diversity in the plankton. A view of a single microscope field (20× objective) of plankton net tow material from the Bay of Villefranche in January 2011. Image by J.R. Dolan.

Cover design by: Simon Levy Associates

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Chapter 1

Introduction to Tintinnids

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1.1 WHY A BOOK ON TINTINNID CILIATES?

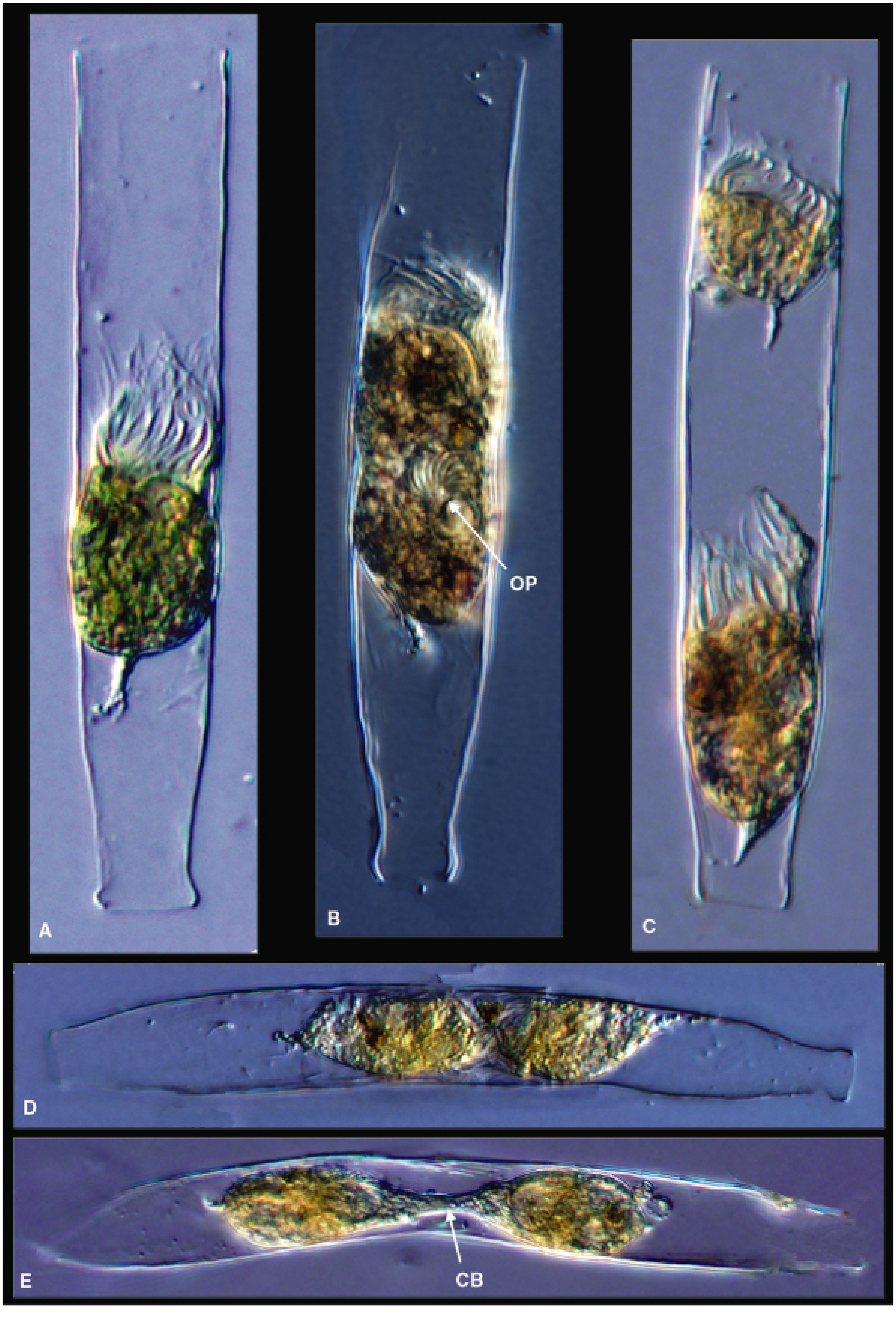
Tintinnids are “curious” because their morphology is unusual for planktonic organisms: it is a shelled cell. There are other groups of shelled organisms in the plankton, such as foraminifera and pteropods, but very few are as diverse as the tintinnids. They show an astounding variety of forms in their shells (loricae), and dozens of different types can be found in just a few liters of seawater (Dolan & Stoeck 2011). Nonetheless, all have a similar fundamental trophic role in the pelagic ecosystem: that of grazers at the base of the food web feeding on nanoplankton, for the most part. They are, therefore, ecologically united as planktonic ciliates, mainly consumers of nanoplankton, and morphologically and phylogenetically united as shelled, choreotrich ciliates. The biology and ecology of this group merit investigation if we are to understand how species-rich planktonic food webs work.

Tintinnids attracted the attention of some of the first microscopists, who were fascinated by such “shelled infusoria”. From the early oceanographic expeditions, the variety of forms of their loricae catalogued from the plankton net-tow material served as an example of biodiversity in the plankton. As they are among the few protist organisms sampled using plankton nets, they were for a time considered a major component of the microzooplankton (zooplankton ranging in size from 20 to 200 µm), grazers of the smallest planktonic algae in the ocean (Beers 1982). Beginning in the 19th century and still today, tintinnids have been the focus of detailed studies that together form a considerable body of literature consisting of hundreds of reports. In recent years, monographic treatment of tintinnids has seen something of a renaissance with the appearance of comprehensive works on tintinnids of the South Atlantic (Alder 1999), Brazilian territorial waters (Gomes et al. 2006), Lebanese coastal waters (Abboud-Abi Saab 2008), and the Adriatic Sea (Krsinic 2010). The literature on tintinnids constitutes a wealth of information covering a surprisingly wide range of topics and approaches. This information has, however, remained scattered across hundreds of journal articles and monographs published over nearly 150 years.

This volume is an attempt to bring together material covering distinct aspects and topics to allow a comprehensive view of the biology and ecology of tintinnids. The ultimate goal in assembling this material is to provide a digest (a complete compendium would required a much longer book) showing the complexity of the different facets of a well-circumscribed group of single-celled eukaryotes, organisms of the marine plankton.

Although tintinnid ciliates are characteristic of the marine plankton, there are a few species found in freshwaters. Freshwater tintinnids often appear to be ephemeral in lake plankton, blooming and then virtually disappearing. In this book, we focus on marine plankton; freshwater forms will not be treated, but mentioned only in passing.

Fig. 1.1 Life-cycle stages in *Eutintinnus inquilinus*. (a) A trophont (feeding stage) cell. (b) An early stage of binary fission showing the oral primordium (OP), which will develop into a new mouth. (c) The final stage of cell division. (d) An early stage of conjugation. (e) A conjugating pair showing a well-developed cytoplasmic bridge (CB) through which nuclear material will be exchanged. Loricae are about 100 μm long. Images are of Lugol’s-fixed cells; sample from a mixed culture provided by F. Lombard.


A
B
OP
C
D
E
CB

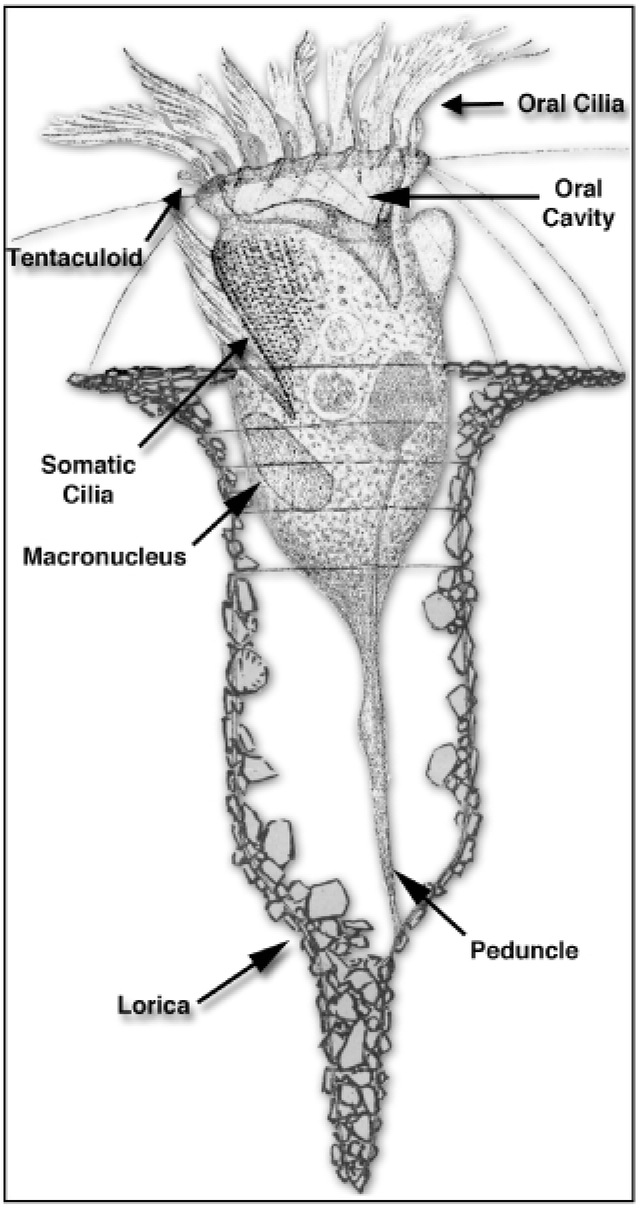
1.2 WHAT IS A TINTINNID CILIATE?

Formally, tintinnids are ciliate protists of the class Spirotrichea, subclass Choreotrichida, order Tintinnida. Among the unicellular eukaryotes, the common characteristics of ciliates are possession of cilia during all or some part of the life cycle, nuclear dualism (macro- and micronuclei), and sexual recombination through conjugation, separate from reproduction which in tintinnids and most other ciliates is through binary fission (Fig. and Plate 1.1). Ciliates in the marine plankton are largely dominated by members of the class Spirotrichea, all of which have mouth cilia in the form of polykinetids (trichia), which are compound cilia that resemble bristles more than fine hairs arranged in a rough circle, more or less a spiral, around the oral cavity. Most marine planktonic ciliates are members of either the subclasses Choreotrichia or Oligotrichia. In both groups the oral polykinetids are well developed, serving both for locomotion and feeding. The subclass Oligotrichia (meaning “few trichia”), comprises forms with the oral polykinetids arranged in an open circle around the oral cavity and few cilia on the cell, such as in the familiar (often cone-shaped) oligotrichs of the genera *Strombidium* and *Laboea*. In contrast, species in the Choreotrichia have oral polykinetids arranged in closed circle around the oral cavity and usually relatively conspicuous rows of cilia on the cell surface. Choreotrich ciliates include species of the genera *Strobilidium* (often sphere-shaped), *Strombidinopsis* (often carrot-shaped), as well as species in which the ciliate cell is always surrounded by a shell (lorica), the tintinnid ciliates.

Besides the lorica, there are cytological characteristics that distinguish tintinnids from other choreotrichs (Fig. 1.2). The oral ciliature includes structures called tentaculoids, which appear to be related to prey capture (see Chapter 4). The posterior end of the cell is a contractile, stalk-like, peduncle which connects the cell to its lorica. The tintinnid cell surface has a distinct field of rows of short cilia, the somatic ciliature (see Chapter 3). These very brief characterizations are based on the detailed descriptions and analyses found in Lynn (2008), Lynn & Small (2000), and Corliss (1979).

Fig. 1.2 Basic morphology of a tintinnid in a cut-away drawing of *Tintinnopsis campanula*,
adapted from Fauré-Fremiet (1924).

The oral cilia are comprised of oral membranelles arranged in closed circle around the funnel-shaped oral cavity. Interspersed between the oral membranelles are tentaculoids, structures presumed to be related to prey capture. The cell surface is covered in part by rows of short cilia, the somatic cilia. The macronucleus is often evident. The posterior end of the ciliate cell is attached to the lorica by a contractile peduncle.



1.3 THE LORICA AS THE DEFINING CHARACTERISTIC OF TINTINNID CILIATES

In addition to being the only choreotrich ciliates with loricae, tintinnids are also the only ciliates of the plankton with loricae. Although there are cytological characteristics that distinguish tintinnids, the defining one is its lorica or shell (although other cytological characters distinguish tintinnids from other choreotrichs or "naked oligotrichs": see Chapter 3). The lorica, although of various shapes ranging from tubular to vase- or bowl-shaped, is always open at one end, the oral end, and closed or tapered at the opposite, or bottom end. Within the lorica the tintinnid cell is attached near the bottom end by a contractile portion of the ciliate cell, a pedicle or peduncle (see Fig. 1.1). While feeding, the cell extends out of the lorica and the tintinnid is propelled mouth-end forward. If disturbed, the cell retracts into the lorica.

The contractile behavior and the lorica as the defining character were apparent in the text of the first description of a tintinnid by O.F. Müller published in 1778 (Box 1.1). The "creature" was described as *Trichoda inquilinus*; all ciliates were placed in the genus *Trichoda* by Müller; *inquilinus* – "lodger" or "occupant" – refers to the ciliate as the inhabitant of a structure. Remarkably, not only was the contractile behavior noted but also that reproduction was by cell division. Müller noted that the "mother cell" (the proter that retains the original mouth) abandons the lorica to the newly formed daughter cell. The form he described might be the species now called *Eutintinnus inquilinus* (shown in Fig. 1.1), known to attach to particles (Fauré-Fremiet 1908; Jonsson et al. 2004). The appellation *Tintinnus inquilinus* was given to the species by Schrank (1803) who removed it from *Trichoda*, giving it its own genus, without unfortunately noting why he chose the term "*Tintinnus*", which most commonly refers to the ringing of a bell.

BOX 1.1 Translation of the 1779 Latin text of O.F. Müller

Trichoda Inquilinus (T. Lodger): a Sheathed Trichoda, with a Hyaline, Cylindrical, Shell and a Little Footstalk

This is among the smallest creatures, and with the slow work of a simple lens, the eye observes a very small point with great mobility. The shell, whether egg-shaped, oblong, smooth, is so glassy transparent that otherwise invisible things might be seen. For this creature is a swimmer, which you might say has a pivoted footstalk …

I have been able to observe these things for a long time with my eyes unaided, being apparent in great numbers. The most apt name should account for the quick motion and the rotation of the hairs. Often the organ of the hairs is spread out resembling a comb, then the more distinct, outermost, blackish teeth, in the hyaline jelly of the true center, which are show various movements, are seen.

The clear footstalk runs through the middle of the sheath, fixed though at the wide base. Often it is contracted, the hairs are together, the little head is submerged, and the side strings of the sheath stand forth like a pregnant creature stretching. Slowly the head retreats back, with the hairs, whether thin tentacles or spread about, extend, barely occupying the entrance of the sheath, intently moving for nutrition. I saw it withdraw within the sheath and be spread out at the top of the head.

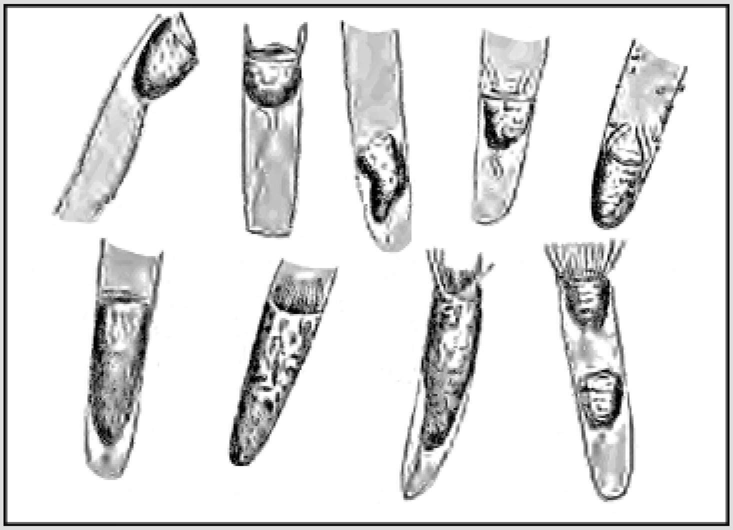
Having been disturbed by dust (and I don’t know where the center is), it becomes very bare, it adheres to very many things and moves about slowly; it swims around vehemently with the head clinging on to the outside of the sheath with the work of the hairs; if it is clinging on to the base of the sheath, fixed only a little, whether extended in a perpendicular or oblique fashion, an alternate movement of the top of the head follows, moving in water continuously or less so.

I have found two swimming together lengthwise. Whether it was at the base of the sheath, or lying higher up, or lower than the top, and the head was pulled about in every sense: at length it tore itself apart, front from back.

I saw a certain one, the heads of which were more than threefold, and they fully occupied the whole sheath even with the footstalk inconspicuously or for a short time; also two by two the little creatures lived in the sheath with their own footstalks.

An extension developed, while I watched the little creature growing. The head is divided in the middle and the bottom at the base of the footstalk, while what happens must be due to the workings of the hairs. By what means the middle of the sheath is truly divided I know not even though keeping them in clean and pure sea water, even in entirely non-renewed water, through the whole of winter 1776, 1777 and 1778.

Fig. B1.1 The lodger occupies various places; small, scaly sheaths called Monads are found together and sticking together in the fifth image. A series of fertile mothers having taken positions to divide, laden and mature, and at the last image a mother is now swimming away. *O.F. Müller (1779) pp. 8–9 (Latin translation by B. Scott, University of Liverpool).*



Very early on it was noted that distinct types of lorica exist among tintinnids and that these may represent natural groups (Claparède & Lachmann 1858). A completely lorica-based taxonomy and phylogeny was introduced by Kofoid & Campbell (1929, 1939) and identifications are today still based on lorica morphology. However, culture studies and recent molecular phylogenies have shown that lorica characteristics do not always reflect phylogenetic relationships (see Chapters 2 and 3). Nonetheless, for practical reasons, tintinnids traditionally have been divided into two groups corresponding to easily distinguished lorica types: one with agglutinated (or agglomerated) loricae composed of particles and another, those with hyaline, generally transparent, loricae. The two lorica types very approximately correspond to different habitats in which tintinnid species with the different loricae are the dominant forms: coastal and open waters (see Chapter 10).

Mineral particles are used in the “agglutinated” loricae of species in the genera *Tintinnopsis*, *Stenosemella*, *Tintinnidium*, and *Leprotintinnus*. These forms are generally restricted to coastal waters. In some genera there are species that incorporate the hard parts of some microalgae. The coccoliths from coccolithophorid algae are used by some species (*Codonella*, *Dictyocysta*, *Codonellopsis*, and *Acanthostomella*) or the remains of diatoms (*Laackmanniella*). The arrangement of “agglutined particles” can be quite precise. For example, in *Codonella elongata*, the coccolithophores are all oriented in the same “face-out” direction (Fig. 1.3). However, not all species show precision in particle use. Examples of the variety of forms with agglutinated lorica are shown in Fig. and Plate 1.4. These species generally dominate tintinnid assemblages in coastal waters but some can be found in open waters.

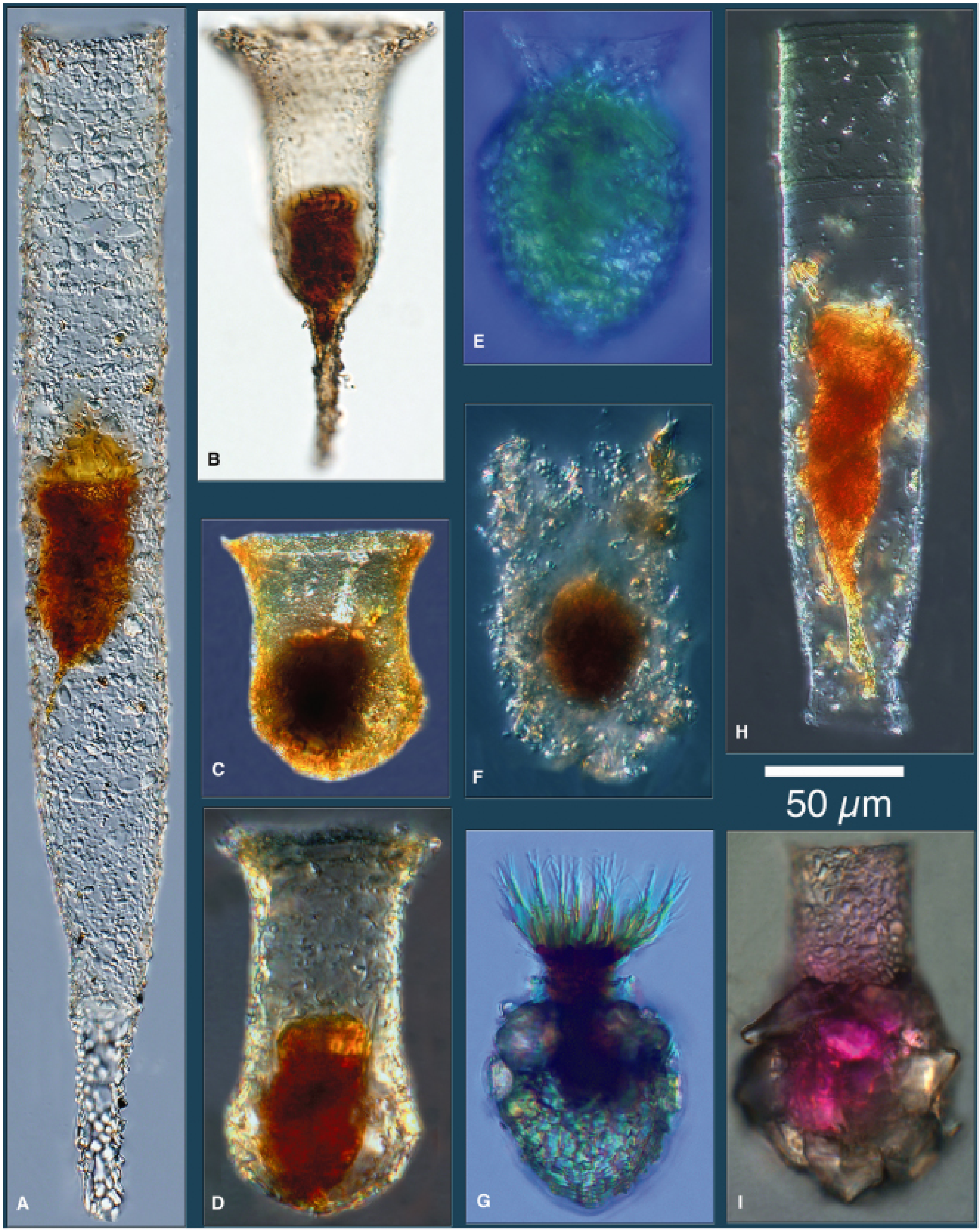
Fig. 1.3 Scanning electron micrograph of a specimen of *Codonella elongata* from the Bay of Villefranche. The upper panel shows the lorica with a bottom portion cut away with a high-energy electron beam. The lower panel shows the interior surface of the lorica. Note that the lorica is agglomerated with the coccolithes of *Helicosphaera carteri* oriented as they are on the living algae.

Images are courtesy of François Guyot and Charles Bachy.

An image of a live specimen of *C. elongata* is shown in Fig. 1.4.

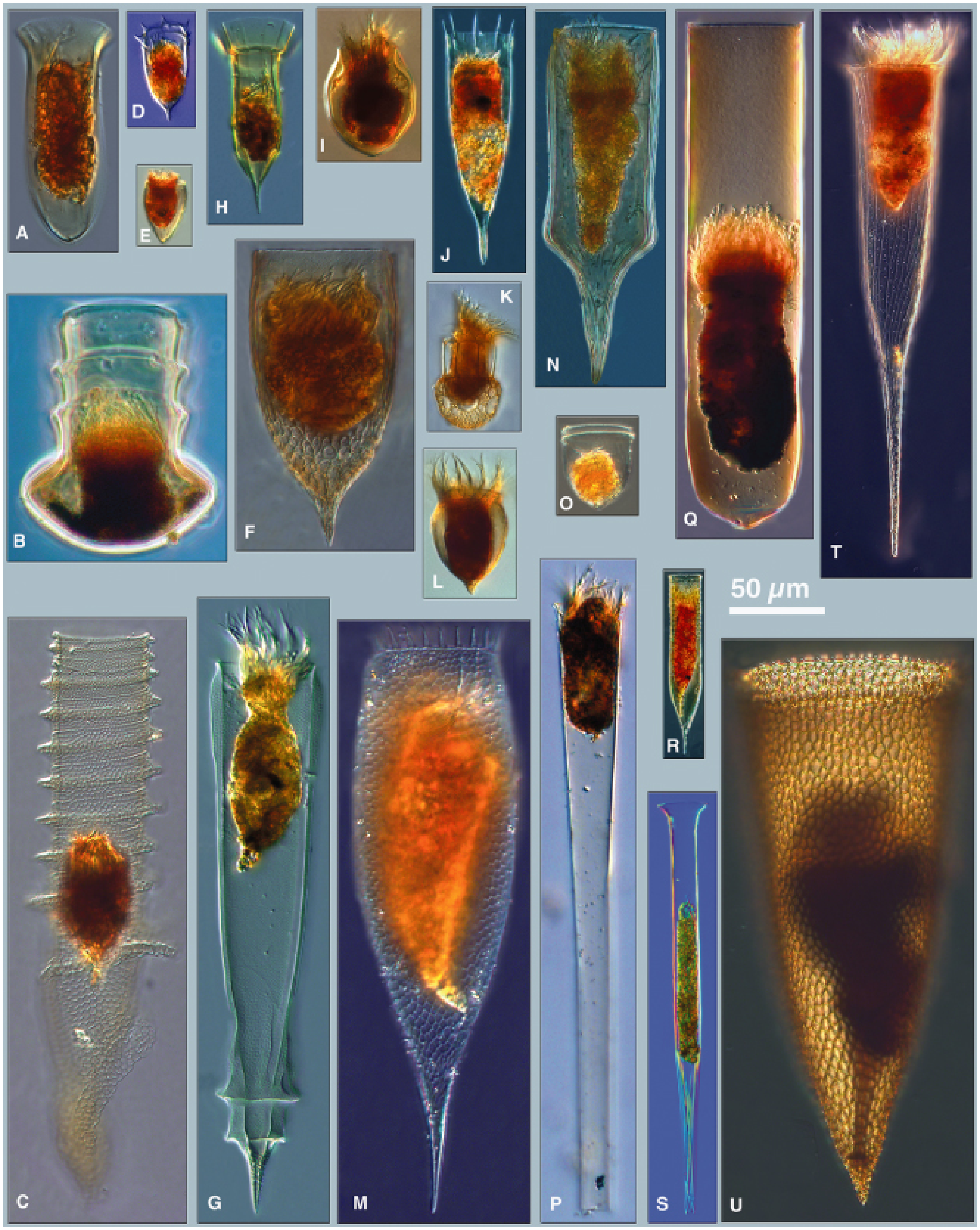
Image not available in this digital edition

Fig. 1.4 Some tintinnid species with agglutinated loricae: *Tintinnopsis radix* (a), *T. campanula* (b), *T. dadayi* (c), *T. spiralis* (d), *Codonella elongata* covered with coccoliths (e), *Tintinnidium* sp. (f), *Stenosemella ventricosa* (g), *Leprotintinnus pellucidus* (h), and *Codonellopsis schabi* (i). Species names are attributed based on lorica morphology. All the specimens are Lugol's-fixed cells except for *Codonella elongata* which was a live specimen.



“Hyaline loricae” groups tintinnids of a very large variety of shapes, sizes, and architectures whose sole common characteristic is a lack of extraneous particles in the lorica. The morphologies range from the transparent small (50 μm diameter) bowl-shaped *Ascampbellia tortulata* to the large, conical *Cyttarocylis cassis* which shows a sculpted surface. Although some hyaline lorica species are found in coastal waters (e.g. species of *Helicostomella*, *Favella*) typically they are the dominant forms in open-water tintinnid assemblages. A sampling of the diversity of hyaline-lorica forms is shown in Fig. and Plate 1.5.

Fig. 1.5 Examples of tintinnid species with hyaline loricae: *Amphorides quadrilineata* (a), *Amplectella collaria* (b), *Climacocylis scalaria* (c), *Acanthostomella conicoides* (d), *Protorhabdonella simplex* (e), *Epiplocylis blanda* (f), *Xystonellopsis paradoxa* (g), *Ormosella trachelium* (h), *Proplectella elipisoida* (i), *Dadayiella ganymedes* (j), *Dictyocysta lepida* (k), *Metacylis mediterranea* (l), *Parafavella parumdentata* (m), *Parundella messinensis* (n), *Ascampbellia tortulata* (o), *Eutintinnus stramentus* (p), *Undella hyalina* (q), *Helicostomella subulata* (r), *Salpingella acuminata* (s), *Rhabdonella spiralis* (t), and *Cyttarocylis cassis* (u). All the specimens are Lugol's-fixed cells.



The term “lorica” refers to the armor or protective clothing worn by roman soldiers. Dujardin (1841) credits Ehrenberg (1832) with using the word in his Latin text to describe the protective structures, *Panzer* in the German text, of tintinnids as well as other protists and rotifers. Indeed, the hard structures of many different protists appear early in the fossil record and likely evolved as protection against predation by other protists (Porter 2011). Among planktonic organisms, the seemingly odd morphologies of present-day forms are thought to be the result of a “watery arms race” between prey and predator (Smetacek 2001; Hamm & Smetacek 2007). In contrast, Kofoid & Campbell (1939) stated that the lorica probably did not evolve as protective device because it affords little protection against large metazoan predators such as copepods. However, tintinnids are subject to predation from a very wide range of predators (Chapter 5) as well as parasitic infections (Chapter 6). In reality, the identity of the major source of mortality for tintinnids is unknown so it is difficult to assess the possible use of the lorica as a protective device.

Many explanations other than “armor” for the lorica have been suggested. These include that of a flotation aid in the case of the hyaline lorica (Kofoid 1930; Campbell 1926), alternatively as aid in quickly sinking away from predators in the case of the agglutinated lorica of *Stenosemella* (Capriulo et al. 1982), and maintaining directionality in swimming in the case of the elongate nail or spike-shaped lorica of oceanic forms (Kofoid & Campbell 1939). A lorica, like projecting spines or trailing structures in other small zooplankton, may reduce swimming speed while enhancing the capture of food particles by increasing fluid motion around the oral cilia (Emlet & Strathmann 1985). The lorica can also serve as an attachment device. Jonsson et al. (2004) found that in some species of *Eutintinnus*, the tintinnid can reversibly attach its lorica to detrital particles thus increasing its feeding rate owing to the “tethering effect” (Strathmann & Grünbaum 2006) and reducing its susceptibility to copepod predation. Lastly, the lorica may furnish protection against ultraviolet radiation (Armstrong &

Brasier 2005), allowing tintinnids to exploit the near-surface waters. There appears no reason not accept the possibility that the variety of loricae found among tintinnids may serve a variety of functions.

1.4 HISTORY OF TINTINNID STUDIES

Early mentions of tintinnids are mostly in taxonomic treatises and consist of little more than simple listings in species catalogues of “infusoria” (i.e., Müller 1776, Schrank 1803; Ehrenberg 1832; Dujardin 1841). The first detailed consideration of tintinnids was by Claparède & Lachmann (1858–1860, part 1, pp. 192–221) who provided notes on the morphology and ecology of most of the 17 known species, and placed them all in a single genus, *Tintinnus.* They remarked on the abundance of tintinnids in marine waters compared with their rarity in freshwaters, and the diversity of lorica types. The appearance of more marine biological studies of tintinnids marked the last quarter of the 19th century.

In 1873 Ernst Haeckel published the first paper devoted exclusively to tintinnids. He not only described new species from waters off Messina (Italy) and Lanzarote (Canary Islands), but also the development and release of what he thought were reproductive spores. We now know that he was the first to describe parasites in tintinnids (see Chapter 6). A few years later appeared the observations of Herman Fol (1881, 1883, 1884) on tintinnids from the Bay of Villefranche-sur-Mer, describing investigations into the chemical nature of the lorica (see Chapter 2) and some new species. These reports were followed by a series papers from the Zoological Station in Naples first by Géza Enzt, senior (1884, 1885) and then Eugene von Daday (1886,