

Torodinium and *Pavillardia* (Gymnodiniales, Dinophyceae): two unarmoured dinoflagellates with a body extension, collected from the open Pacific Ocean

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Summary

In several regions of the warm open Pacific Ocean, specimens of the unarmoured dinoflagellate genus *Torodinium* showed an elongated protuberance, the peduncle that protrudes from the sulcal-cingular region. In addition to the peduncle, a tentative organelle for ingestion, the occurrence of hair-like filaments (known as a “feeding veil”), and accumulation bodies (tentative food vacuoles) suggest a mixotrophic behaviour. There have been no records of the genus *Pavillardia* since the original description in 1921. One specimen that showed a wider cell body than the type species, *P. tentaculifera*, with a short antapical extension, has been assigned to this genus. The function of the antapical extension is unknown.

Key words: unarmoured dinoflagellates, *Torodinium*, *Pavillardia*, body extension

Introduction

In the summer of 1917, Kofoid and Swezy (1921) investigated the unarmoured dinoflagellates collected by net sampling off the Californian coast. With detailed illustrations, they described numerous new species from one or a few specimens that temporally survived to the stress of the collection, transport and manipulation. Most of the species described by Kofoid and Swezy (1921) were never subsequently reported. This is the case for *Pavillardia* Kofoid et Swezy, a monotypic genus, known only from the original description. Kofoid (1920) placed the genus *Pavillardia* in the order Noctilucales Haeckel, because he interpreted that the moveable antapical extension was related to

the tentacle of *Noctiluca scintillans* (Macartney) Kofoid. This doubtful interpretation was adopted by subsequent authors (Schiller, 1933; Chatton, 1952; Tappan, 1980; Taylor, 1987), while others placed *Pavillardia* in the order Gymnodiniales (Sournia, 1986; Chrétiennot-Dinet et al., 1993; Fensome et al., 1993).

Kofoid and Swezy (1921) also erected the genus *Torodinium* Kofoid et Swezy to house species characterized by a very large episome that occupied most of the cell body, a posterior cingulum and a much reduced hyposome. Exceptionally the sulcus extended only along the episome. These authors proposed *Torodinium teredo* (Pouchet) Kofoid et Swezy based on *Gymnodinium teredo* Pouchet and the new species *Torodinium robustum* Kofoid et Swezy.

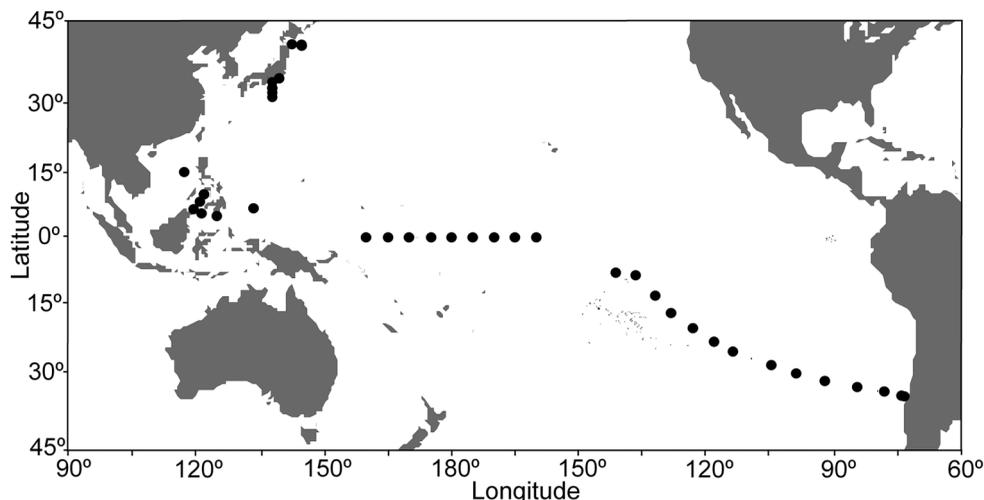


Fig. 1. Geographic location of the sampling stations in the Pacific Ocean (marked by circles).

Records of *Torodinium* are numerous, whereas the information on *Pavillardia* is restricted to the original description, with the exception of Takayama (1998) who, with doubts, named a gymnodinioid cell with an antapical protuberance *Pavillardia* sp. Based on scanning electronic microscopy, Takayama (1998) illustrated the morphology of *T. teredo*. However, the study is not easily accessible; it is only available in a thesis dissertation in Japanese.

The present study illustrates specimens in which the episome unequivocally corresponds to *Torodinium*, while showing a previously unreported elongated extension that emerged from the sulcal-cingular region. A globular gymnodinioid cell with a short antapical extension has been tentatively assigned to the genus *Pavillardia*.

Material and methods

The specimens were collected during 12 research cruises in several regions of the open Pacific Ocean: Oyashio and Kuroshio Currents; Philippines; Celebes; Sulu and South China Sea; western and central equatorial Pacific; subtropical Pacific in the vicinity of the Marquesas Islands Archipelago; South Pacific Gyre; and the Perú-Chile Current (Fig. 1). The specimens were immediately fixed with acetic Lugol's solution and analyzed following the methodology described in previous studies (Gómez et al., 2005; Gómez, 2006, 2007).

Results

TORODINIUM

The identification of *Torodinium* is relatively easy. The episome occupied more than 4/5 of the cell length. The cingulum was very posterior and

the inverted-cone shaped hyposome was highly reduced. In ventral view, the oblique base of the cone descended right. Depending on the view, a lateral protuberance was observable near the apex. This protuberance is here named the "bill-like projection" following the terminology established by Takayama (1998) based on the resemblance with a bird bill. The episome showed longitudinal pigmented bands that Kofoid and Swezy (1921) named rhabdosomes. This is the typical morphology of *Torodinium* that can be found in the literature (Fig. 2, A). However, the present study focused on the specimens which differed morphologically from that previously reported in the literature.

In some specimens, the inverted-cone shaped hyposome was almost indiscernible and showed a round-tip protuberance from the sulcal-cingular region (Fig. 2, B-J). This structure is considered a peduncle following the terminology proposed by Spero (1982) for the freshwater phagotrophic dinoflagellate *Gymnodinium fungiforme* Anissimova. In other specimens the peduncle was more elongated and even reached about one half of the length of the episome (Fig. 2, E-J). The dimensions of the specimens, excluding elongated hyposome, were 55-70 μm in length and 22-40 μm in width; commonly, the specimens were 60 μm long and 25 μm wide. The nucleus can be discerned as a pale region extending longitudinally in the central episome (Fig. 2, B, D, G).

The pigmentation of most of the Lugol-fixed specimens was brown, suggesting the presence of peridinine as an accessory pigment. One of the specimens with olive-green pigmentation showed three dark corpuscles, here considered as accumulation bodies (Fig. 2, D). It is uncertain whether they correspond to food vacuoles (Fig. 2, D, J). Another specimen with a dark brown pigmentation also showed three accumulation bodies of similar size and disposition (Fig. 2, J) to

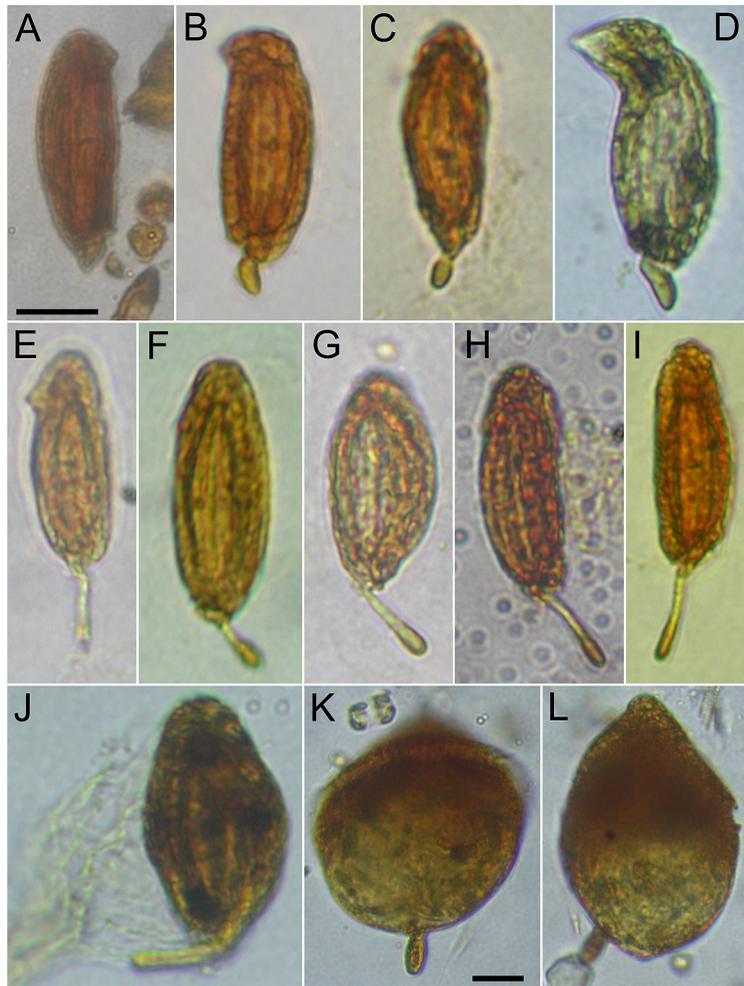


Fig. 2. Photomicrographs of *Torodinium teredo* (A-J) and *Pavillardia* sp. (K-L), bright field optics. A - Typical specimen of *T. teredo*; B-D - specimens with a short peduncle (note the green pigmentation and accumulation bodies, tentatively food vacuoles, in the figure D); E-J - specimens with long peduncle. Scale bars: 20 μm (A-J - at the same scale).

the olive-green pigmented specimen (Fig. 2, D). Some specimens showed hair-like filaments that emerged laterally (Fig. 2, H, J) or posteriorly (Fig. 2, C). These filaments resembled the “feeding veil” that can be found in heterotrophic dinoflagellates.

PAVILLARDIA

The monotypic genus *Pavillardia* was described with a distinctive antapical extension. However, to the best of my knowledge *P. tentaculifera* has not been recorded since its original description in 1921. From all specimens observed in the present study, only one (collected in the Bay of Sagami in the south of Japan - see Table 1) may correspond to the genus *Pavillardia*, based on the occurrence of a short antapical extension. The cell showed a hemispherical hyposome and a conical episome with a round apex.

The cell dimensions were 80 μm in width and 93 μm in length, excluding the appendix, whereas *P. tentaculifera* was smaller (58 μm long, 31 μm wide). The cingulum was well-impressed and showed a low displacement. The occurrence of an antapical round-tip extension of 13 μm in length and 5 μm in width is the morphological character that suggests the specimen may belong to the genus *Pavillardia* (Fig. 2, L-M).

Discussion

TORODINIUM

The large episome with respect to hyposome makes the genus *Torodinium* one of the more distinctive unarmoured dinoflagellates. Another distinctive character of *Torodinium* is the “bill-like

Table 1. Depth (m) and geographic coordinates (latitude, longitude) of the specimens of *Torodinium teredo* and *Pavillardia* sp. illustrated in the figures 2 A-L.

Specimens	Depth	Latitude	Longitude	Fig. 2
<i>Torodinium teredo</i> (typical cell)	5	34°15'N	138°E	A
<i>T. teredo</i> (short peduncle)	10	32°30'N	138°E	B
<i>T. teredo</i> (short peduncle)	5	30°30'N	138°E	C
<i>T. teredo</i> (green pigmentation)	60	0°	160°W	D
<i>T. teredo</i> (long peduncle)	80	32°30'N	138°E	E
<i>T. teredo</i> (long peduncle)	120	0°	165°E	F
<i>T. teredo</i> (long peduncle)	70	31°30'N	138°E	G
<i>T. teredo</i> (long peduncle)	125	32°30'N	138°E	H
<i>T. teredo</i> (long peduncle)	100	0°	160°E	I
<i>T. teredo</i> (feeding veil)	80	0°	175°W	J
<i>Pavillardia</i> sp.	5	34°39.2'N	139°31.3'E	K-L

projection". The present study illustrates, for the first time, that the genus *Torodinium* is able to project a peduncle, up to one half the length of the episome. This interpretation is based on Spero (1982), who observed that the freshwater phagotrophic dinoflagellate *Gymnodinium* (*Katodinium*) *fungiforme* ingested prey cytoplasm through a highly extensible structure, the peduncle that protrudes from the sulcal-cingular vicinity of the cell during feeding. Two types of feeding tubes have been described among the dinoflagellates: the peduncle and the phagopod (Hansen and Calado, 1999). In feeding cells, the peduncle is a protoplasmic strand that protrudes from the mid-ventral area of the sulcus and connects predator and prey. The peduncle is usually retracted in non-feeding cells. The phagopod is a non-cytoplasmic feeding tube. It differs also from the peduncle by remaining attached to the remnants of the prey after feeding, rather than being retracted (Hansen and Calado, 1999).

The presence of a hair-like filament that resembled the "feeding veil" that can be found in heterotrophic dinoflagellates such as *Gyrodinium spirale* (Bergh) Kofoid et Swezy (Fig. 2, J) and accumulation bodies (tentatively food vacuoles - see Figs 2, D, J), suggest the ingestion of particles. Mixotrophic behaviour has been described in numerous dinoflagellates (Stoecker, 1999). This study was carried out in the open ocean, where the availability of nutrients for an obligate photosynthetic organism is low (see nutrients distributions in Gómez et al., 2005, 2007). The ingestion of food particles may constitute a life strategy under these unfavourable conditions.

PAVILLARDIA

Despite the distinctive antapical extension, the knowledge on *Pavillardia tentaculifera* is restricted to the original description in 1921. Kofoid and Swezy (1921) observed that the antapical extension of *P. tentaculifera* was movable, and assumed that it resembled dinoflagellates with a movable tentacle that were known at that time, such as *Noctiluca scintillans* or *Spatulodinium pseudonociluca* (Pouchet) J. Cachon et M. Cachon ex Loeblich Jr. et Loeblich III.

The classification of *Pavillardia* in the order Noctilucales was unfortunate, although this has been followed by some authors until relatively recently (Tappan, 1980; Taylor, 1987). Based on the original description, the cell body of *Pavillardia* is closer to the morphology of *Gyrodinium* Bergh; even *Pavillardia* showed the distinctive surface striation of *Gyrodinium* (Kofoid and Swezy, 1921; Takayama, 1998). Beyond the brachidiniaceans, the projection of body extensions is a phenomenon that can be found in numerous unarmoured dinoflagellates in open waters (e.g. Gómez et al., 2004; Gómez, 2006, 2007). Takayama (1998) illustrated a gymnodinioid cell with a thick antapical elongation that he tentatively named *Pavillardia* sp. In contrast to *Pavillardia*, the antapical extension of the Takayama's specimen seems to be an elongation or deformation of the hyposome more than the extension or tentacle seen in *Pavillardia*. The function of the extension of *Pavillardia* is unknown and it clearly differs from that found in *Torodinium*.

Numerous gymnodinioid cells showed extensions with variable degrees of elongation. The extensions facilitate identification during the routine microscopic analysis. Nevertheless, the use of an antapical extension as the main diagnostic character for the erection of new a genus is questionable.

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