
Rediscovery of the dinoflagellate genus *Pavillardia* Kofoid & Swezy and its synonymy with *Gyrodinium* Kofoid & Swezy (Dinophyceae)

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Abstract :

Amongst the dinoflagellates, the heterotrophic unarmoured species are the group that has received less attention. The species *Gyrodinium postmaculatum*, *G. rubricaudatum* and the genus *Pavillardia* remain unreported since the original description in 1921. During on-board observations of living plankton in the Agulhas Current in the continental shelf off eastern South Africa, we observed individuals that fit with the description of *Pavillardia*, *G. postmaculatum* and *G. rubricaudatum*, and other intermediate forms. The posterior extension of *Pavillardia tentaculifera* was not movable, it detached and the cell remained viable. The diagnoses of *G. postmaculatum* and *G. rubricaudatum* were based on red colouration, but this feature was highly variable. *Pavillardia* devoid of the posterior extension is indistinguishable from *G. postmaculatum*. There are no significant differences in the morphology among *Pavillardia tentaculifera*, *G. postmaculatum*, and *G. rubricaudatum*. *Pavillardia* is considered a synonym of *Gyrodinium*, and the name *G. postmaculatum* is proposed for these three species.

Highlights

► First observations of living individuals of the athecate [dinoflagellate](#) genus *Pavillardia* and *Gyrodinium postmaculatum*, and *G. rubricaudatum* since the original description in 1921. ► *Pavillardia* is able to detach its posterior extension, and it is not a moveable tentacle. ► The colouration is an unstable diagnostic character in heterotrophic gymnodinoid dinoflagellates. ► The genera *Pavillardia* and *Gyrodinium* are considered synonyms. ► *Gyrodinium postmaculatum*, *G. rubricaudatum*, and *Pavillardia tentaculifera* are forms of the same species.

Keywords : Agulhas current, heterotrophic dinoflagellate, Indian ocean, *Gyrodinium*, *Pavillardia*, Phytoplankton, South Africa

1. Introduction

Dinoflagellates represent a major group of microalgae in marine habitats. Two major groups of dinoflagellates are distinguished: thecate or armoured species with thecal plates on the cell surface, and athecate, unarmoured or 'naked' species without thecal plates. The morphology of thecate dinoflagellates is less affected by net sampling and the tabulation, i.e. arrangement and shape of the thecal plates, can be used for species diagnosis. On the other hand, the unarmoured dinoflagellates tend to be delicate, and are easily damaged by net sampling, and individuals may be distorted by preservation, inducing confusion on their identity (Taylor, 1963). The establishment of cultures of autotrophic species is easier than those of heterotrophic species, allowing detailed studies. In contrast, the cultures of heterotrophic species are not stable due to the requirement of suitable prey. As a consequence, there is a clear gap in the knowledge of the heterotrophic unarmoured dinoflagellates (Gómez, 2020).

Kofoed and Swezy (1921) examined living cells of unarmoured dinoflagellates collected in the summer of 1917 offshore San Diego, California. They described 40 and 25 new species of *Gymnodinium* and *Gyrodinium*, respectively, among other species. The new species were accompanied by detailed colour illustrations. However, descriptions were often based on the observation of a single or few individuals, omitting intraspecific variability, such as changes of shape. For example, Kofoed and Swezy (1921) proposed eight new species as morphotypes of *Balechina gracilis* (Gómez et al., 2021). Kofoed and Swezy (1921) used colouration as a diagnostic character, but this character can vary according to pigmentation ratios, the physiological state, or the type and quantity of ingested prey. They proposed the new genus *Gyrodinium* for gymnodinioid cells with cingulum ends displaced more than 0.2 times the length of the cell, and the subgenus *Gyrodinium* for cells with longitudinal striae on the cell surface. In the dichotomous key,

Kofoid and Swezy (1921) proposed *Gyrodinium rubricaudatum* for individuals with scattered coral red pigment, and pigment accumulation at the antapex, and *Gyrodinium postmaculatum* for individuals with a purplish or violet, and colour amaranth purple, sometimes accumulated at the antapex. Kofoid and Swezy (1921) proposed a new genus, *Pavillardia*, based on the observations of a few individuals possessing a posterior body extension with red pigmentation that they interpreted as a mobile tentacle. Kofoid and Swezy (1921) considered that the body shape, displacement of the cingulum, and the surface striation resembled *Gyrodinium*. However, they classified *Pavillardia tentaculifera* and *Noctiluca scintillans* in the family Noctilucaceae based on the common occurrence of a tentacle. Despite its distinctive morphology, the records of *Pavillardia* have almost disappeared from the literature. Takayama (1998, plate 33, figs 7–9) presented scanning electron microscopy pictures of a cell identified as *Pavillardia* sp. lacking information on the colouration. His individual was laterally flattened, with a smooth surface, anterior cingulum with low level of displacement, and a thick posterior protuberance on the dorsal side. This morphology differed from *Pavillardia*, which is a non-compressed cell, with longitudinal striae on the surface; a median cingulum with high displacement, and a thin posterior body extension. Gómez (2009) reported a cell identified as *Pavillardia* sp. with a conical episome, median cingulum and a hemispherical hyposome with a thin posterior body extension. Information on the cell colouration was not available because the sample was preserved with acid Lugol's solution. Gómez (2009) considered that the classification of *Pavillardia* in the order Noctilucales was unfortunate because it is closer to the morphology of *Gyrodinium*. To the best of our knowledge, *Gyrodinium rubricaudatum* and *G. postmaculatum* have not been further reported in the literature, and besides those unconfirmed records by

Takayama (1988) and Gómez (2009), there is no report of living cells of *Pavillardia* since the original description.

2. Materials and methods

The research cruise RESILIENCE (MD#237) took place on board R/V ‘Marion Dufresne’ from April 19 to May 24, 2022, between Réunion Island, Mozambique and eastern South Africa. The main goal of the project RESILIENCE was to study oceanic fronts on the edge of eddies in the Mozambique Channel and off the eastern coast of South Africa focusing on the interactions between ocean physics and biology at a ‘small scale’ (~10 km). (<https://en.ird.fr/resilience-cruise-aboard-marion-dufresne>). These cyclonic eddies are highly productive systems (Ternon et al., 2014). Plankton samples were collected in the South Africa continental shelf and oceanic waters influenced by the Agulhas current, from 80 m depth to the surface with a phytoplankton net (20 µm mesh size). Aliquots of living cells were left to settle in a composite settling chamber, examined on-board with an inverted microscope (Eclipse TS-100, Nikon Inc., Tokyo, Japan), and photographed at 60× or 100× magnification with a digital camera (Nikon D5000). Cell sizes were measured with Photoshop CS3 (Adobe Systems, San José, CA, USA) after calibration with pictures of a stage micrometre at each magnification.

3. Results

3.1. *Pavillardia tentaculifera*

The plankton samples were dominated by diatoms, accompanied by numerous heterotrophic dinoflagellates such as the armoured *Protoperidinium* spp. and the unarmoured *Gyrodinium* spp. Cells with a *Gyrodinium*-like morphology showed partial or total red pigmentation. Several individuals possessed a red-coloured antapical extension which is the main diagnostic character of the genus *Pavillardia* (Fig. 1). Two

individuals were similar to the illustration in the original description (Fig. 1B) of the type species, *Pavillardia tentaculifera* in Kofoid and Swezy (1921). One individual was 67 μm long, and 42 μm wide, with a posterior extension of 20 μm long (Fig. 1A, C–J), and the other individual was 73 μm long, 40 μm wide, with a body extension of 14 μm long (Fig. 1K–Q). The cell body was colourless, with some red pigmentation near the cingulum (Fig. 1H). The most distinctive morphological character was a prominent posterior extension with intense red pigmentation (Fig. 1A, C–Q). The episome was conical with a round apex. The cingulum was median with a high displacement, about one-third of the cell length. The sulcus was slightly sigmoidal and extended from the apex to the antapex (Fig. 1E–F). The longitudinal flagellum was visible in both individuals (Fig. 1I, L). The hyposome was ovate. The cell surface was covered with longitudinal striae that were twice as numerous on the hyposome than the episome (Fig. 1C, E, G). There were 10–11 striae in each face of the episome that were 2.7 μm distant from each other near the cingulum (Fig. 1C, F). The nucleus was encapsulated and located in the middle of the cell, and slightly displaced towards to the dorsal side (Fig. 1H–J). The nucleus was almost round or bean-shaped according to the view. Condensed chromosomes were visible and oriented in distinct angles, appearing as fibrils in some parts, or as points in other parts (Fig. 1H–J). A prominent food vacuole with yellow-brown contents occupied most of the hyposome of one of the individuals (Fig. 1L–M). The morphology of the posterior extension varied between the individuals. One individual showed a thick triangular posterior body extension projected from the antapex (Fig. 1H–I). The other individual showed a thinner body extension that was laterally oriented from the posterior end of the ventral hyposome (Fig. 1K–N). Each individual was observed for more than half an hour, and movement of the posterior extension was never observed. During the observations, the posterior extension of one of the individuals was

suddenly detached (Fig. 1N). The area where the posterior extension was located initially showed a rough contour, that became smooth after several minutes (Fig. 1O–Q). Some red pigmentation remained in the antapex. The cell did not lyse and the detached posterior extension remained as an amorphous red mass (Fig. 1N).

3.2. *Pavillardia* spp.

Other individuals showed a posterior body extension, but differing from the typical morphology of *Pavillardia tentaculifera*. One individual showed the entire cell body with a red pigmentation, more intense in the antapex and the posterior extension (Fig. 1R). The cell was 49 μm long, 37 μm wide, with a pointed body extension of 10 μm long. In contrast to the previous individuals, the episome was smaller and hemispherical (Fig. 1R–V). Another individual was small (48 μm long, 32 μm wide) with a conical episome and ovate hyposome with a triangular short (~10 μm long) and thick posterior extension (Fig. 1W–X). The cell did not show a red colouration. There were yellow-brownish masses near the apex and the antapex, especially in the posterior extension.

3.3. *Gyrodinium postmaculatum* and *G. rubricaudatum*

One unarmoured individual showed two posterior body extensions of distinct size with intense red pigmentation. The posterior extension was larger in the left part of the hyposome than in the right one (Fig. 2A). The cell showed weak red pigmentation in the entire cell body, with more intensity near the apex, antapex, and cingulum. The morphology fit with the illustration in the original description of *Gyrodinium postmaculatum* (Fig. 2B). The individual coincided in the same sample with *Pavillardia tentaculifera* (Fig. 1A, Table 1). The cell size was 89 μm long and 49 μm wide. Beyond the presence of two small posterior extensions, the individual showed similar

morphological features to *P. tentaculifera*, with the median cingulum, displacement of about one-third of the cell length, and the sulcus extended from the apex to the antapex (Fig. 2A, C–E). The cell was covered with longitudinal striae that were about twice as numerous on the hyposome than in the episome (Fig. 2F–H). There were 11–12 striae in each face of the episome (Fig. 2F). The nucleus was slightly ellipsoidal and located in the middle of the cell (Fig. 2A, D). This study included the original illustration of *Gymnodinium bicaudatum* because this species was also described with two posterior body extensions (Fig. 2J). Information on the sulcus, or about a red colouration was missing in the original description (Pavillard, 1905). The illustration of *Gymnodinium bicaudatum* shows a robust cell with a premedian cingulum that differs from the cells found in our samples (Fig. 1A, C–D). Based on the scarce available information, the authors cannot consider *G. bicaudatum* as an earlier description of *Gyrodinium postmaculatum*.

Kofoid and Swezy (1921) provided a second colour illustration for *Gyrodinium postmaculatum* (Fig. 2K). In this case, the episome showed a round apex, the periphery of the cell was covered with red granules, a food vacuole with yellow-brownish masses in the hyposome, and a tiny posterior extension or elongated antapex with red pigmentation. Kofoid and Swezy (1921) also described the species *Gyrodinium rubricaudatum* (Fig. 2L). The cells showed a similar size and shape to *G. postmaculatum*, and a pointed antapex that can be interpreted as a tiny posterior extension. The red pigmentation in the cell body was missing in *G. rubricaudatum*, except in the antapex. These features suggest that *G. rubricaudatum* and *G. postmaculatum* are synonyms. The authors observed several individuals with a distinct degree of red colouration and development of the posterior extension that are considered morphotypes of *G.*

postmaculatum (Fig. 2M–R). In addition, other individuals corresponded to recently divided individuals or currently under division (Fig. 2S–X).

4. Discussion

The unarmoured dinoflagellates present high shape versatility, and especially heterotrophic forms, such as *Gyrodinium*, that deformed after the ingestion of prey by engulfing (Gómez et al., 2020). Cell shape is, therefore, not a stable diagnostic character for species identification and neither is colouration. Photosynthetic dinoflagellates possess carotenoid pigments, and when they reach high densities the phenomenon known as red tides occur. In the case of the heterotrophic forms, these carotenoid pigments are derived directly from the ingested preys or the ingestion products are used for the synthesis of new pigments. *Noctiluca scintillans* may show a red pigmentation derived from the prey (i.e., *Lingulodinium polyedra*), and in part due to the *de novo* synthesis of other pigments (Balch and Haxo, 1984). The red pigments of the heterotrophic thecate dinoflagellate *Protoperidinium* have been identified as granules of canthaxanthin and astaxanthin (Neveaux and Soyer, 1976; Carreto, 1985). Even less information is available for the gymnodinioid heterotrophic dinoflagellates. The cells of *Erythroperidinium* possess a red pigmentation (Gómez, 2017), and it feeds on crustacean eggs that store astaxanthin (Dall et al., 1995). All the known species of *Gyrodinium* are heterotrophic, and the pigmentation is derived from the ingested prey, directly or after new synthesis using the ingested materials as precursor. A carotenoid pigment, gyroxanthin (Bjornland et al., 2000) is regarded as unrelated to *Gyrodinium*, because it was obtained from a photosynthetic species of *Karlodinium*. Kleppel and Lessard (1992) detected astaxanthin in *Protoperidinium* and canthaxanthin in a heterotrophic ‘*Gymnodinium* sp.’ that probably corresponded to a species of *Gyrodinium*. Kleppel and Lessard (1992) reported:

“The pigment content cultured at $29 \mu\text{E m}^{-2} \text{s}^{-1}$ (low-light group) was approximately 42% of the average pigment content of the same species cultured in the same food environment but at $290 \mu\text{E m}^{-2} \text{s}^{-1}$ (high-light group). Inadvertent starvation of the cultures in the low-light group for ≤ 3 days resulted in the loss of all measurable pigmentation”. Kleppel and Lessard (1992) concluded that the levels of canthaxanthin in *Gymnodinium* sp. covaried with chlorophyll from the algal food supply. It would appear that carotenoid pigment content was dependent upon food availability. In the absence of food, carotenoids were not present in *Gymnodinium* sp. Presumably, the pigments were metabolized and could not be replaced (Kleppel and Lessard, 1992).

Pavillardia has a distinctive shape, but no light micrographs of living cells have ever been published, and the species *Gyrodinium postmaculatum* or *G. rubricaudatum* were not reported since the original descriptions in 1921. Diatoms produce numerous carotenoid pigments (Kuczynska et al., 2015), and they are consumed by the dinoflagellates. The degree of red colouration of the heterotrophic unarmoured dinoflagellates was variable, and more usually accumulated in the antapex and/or posterior extension. The process of transformation of the pigments acquired from the ingested prey remains unknown. It can be speculated that the carotenoid pigments are placed on the cell surface, especially in granules near the longitudinal striae (Fig. 2G–H) and, finally, accumulated in the antapex. From a taxonomical point of view, the presence of carotenoid pigments may vary according to the type and quantity of ingested preys and/or the light conditions if it is assumed a photoprotective mechanism of these carotenoid pigments. This variability precludes using colouration as a diagnostic character for species delimitation. Nevertheless, Kofoed and Swezy (1921) used the colouration for the diagnosis of the species *Gyrodinium rubricaudatum* and *G. postmaculatum*. They published two colour illustrations of *Gyrodinium postmaculatum*

(Fig. 2B, K), evidencing the intraspecific morphological variability because the shape, especially of the episome, and colouration varied within a single species. In the description of *G. postmaculatum*, Kofoid and Swezy (1921, p. 329) reported that the localisation of the pigment in the antapex, the interrupted striae, and size are quite similar to these features in *G. rubricaudatum* sp. nov., but the more rotund body and the purple instead of red colour differentiate the two. Considering that the main difference between *Gyrodinium postmaculatum* and *G. rubricaudatum* is the colouration, both species should be therefore considered synonymous.

Kofoid and Swezy (1921) proposed the new genus *Pavillardia* based on the presence of a tentacle. In the description of *Pavillardia*, they did not compare it with *Gyrodinium*, and they classified *Pavillardia* together with the tentacle-bearing *Noctiluca scintillans*. Gómez (2009) concluded that the use of an antapical extension as the main diagnostic character for the erection of new a genus is questionable. In this study, the posterior extension of *Pavillardia* remained in the same position without evidence of movement. Taken into account that the posterior extension is not moveable, it does not constitute a tentacle as present in *Noctiluca* or *Spatulodinium pseudonoclituca*. Other unarmoured dinoflagellate such as *Torodinium* showed a posterior extension under oceanic conditions (Gómez, 2009). The posterior extension of *Pavillardia* was detached, probably due to stress during microscope observations (Fig. 1N). The autotomy has also been observed in other unarmoured dinoflagellates such as *Cucumeridinium* when the cells are stressed (Gómez et al., 2015; <https://www.youtube.com/watch?v=eLK5FMGNtTI>). Kofoid and Swezy (1921) reported in the diagnosis of *Pavillardia* that the longitudinal flagellum is usually absent. However, the longitudinal flagellum is present (Fig. 1I, L).

Pavillardia shed the posterior extension, it is indistinguishable from the typical cells of *Gyrodinium*. Unfortunately, the paucity of individuals of *Pavillardia* did not allow for obtaining molecular data for genetic comparison. However, the morphological evidences revealed from our study suggest that *Pavillardia* and *Gyrodinium* should be considered synonyms (Table 2). As both generic names were proposed in the same publication, priority may be given to any of these names. Because the name *Pavillardia* has been used for a single species (*P. tentaculifera*) and the name *Gyrodinium* for at least 130 species (Gómez, 2012), it would be more plausible to transfer *Pavillardia* to the genus *Gyrodinium* than vice versa. In molecular phylogeny, the sequences of *Gyrodinium* form a monophyletic group (Gómez et al., 2020). However, the name *Pavillardia* could be re-instated if further studies support the generic split of *Gyrodinium*.

The transfer of *Pavillardia tentaculifera* into *Gyrodinium* would be unnecessary if one already described species of *Gyrodinium* is considered synonym of *P. tentaculifera*. In the description of *Pavillardia*, Kofoid and Swezy (1921) did not compare it with the species of *Gyrodinium*. However, in the description of *G. rubricaudatum*, Kofoid and Swezy (1921, p. 331) reported that in *G. postmaculatum* an intermediate condition is shown, with a localized antapical pigment mass and also pigment diffused throughout the periphery. *G. rubricaudatum* leads onwards to the greater development of the same tendency in *Pavillardia*, where there is localization of the pigment in the mobile posterior tentacle. The morphology of *G. postmaculatum* corresponds to cells of *P. tentaculifera* with a less developed posterior extension (Fig. 2A, I; Table 2). The authors propose synonymy with the following priority:

Genus *Gyrodinium* Kofoid & Swezy 1921 (= *Pavillardia* Kofoid & Swezy 1921)

Gyrodinium postmaculatum Kofoid & Swezy 1921 (= *Gyrodinium rubricaudatum* Kofoid & Swezy 1921, *Pavillardia tentaculifera* Kofoid & Swezy 1921).

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Table 1. Records of *Pavillardia tentaculifera*, *Gyrodinium postmaculatum*, *G. rubricaudatum* and related taxa during the RESILIENCE MD#237 cruise (May 2022) off eastern South Africa

Taxon	Date	Coordinates	Long; wide (μm)	Figure
<i>P. tentaculifera</i>	12/05/2022	32°16.6 S, 29°29.1 E	67; 42	Fig. 1A, C–J
<i>P. tentaculifera</i>	16/05/2022	32°27.7 S, 28°55.1 E	73; 40	Fig. 1K–Q
<i>Pavillardia</i> sp. red	03/05/2022	30°03.2S, 30°58.4 E	49; 37	Fig. 1R–V
<i>Pavillardia</i> sp. yellow	13/05/2022	32°9.3 S, 29°26.7 E	48; 32	Fig. 1W–X
<i>G. postmaculatum</i>	12/05/2022	32°16.6 S, 29°29.1 E	89; 49	Fig. 2A, C–I
<i>G. rubricaudatum</i>	13/05/2022	32°9.3 S, 29°26.7 E	73; 40	Fig. 2M–N
<i>G. rubricaudatum</i>	16/05/2022	32°27.7 S, 28°55.1 E	72; 38	Fig. 2O
<i>G. rubricaudatum</i>	13/05/2022	32°9.3 S, 29°26.7 E	78; 44	Fig. 2P–Q
<i>G. rubricaudatum</i>	15/05/2022	31°54.3 S, 29°26.7 E	73; 41	Fig. 2R
Unidentified <i>Gyrodinium</i> recently divided	10/05/2022	32°3.5 S, 29°38.3 E	62; 43	Fig. 2S–T
Unidentified <i>Gyrodinium</i> under division	12/05/2022	32°16.6 S, 29°29.1 E		Fig. 2U–V
Unidentified <i>Gyrodinium</i> under division	13/05/2022	32°9.3 S, 29°26.7 E		Fig. 2W–X

Table 2. Comparison of the morphological characters of *Pavillardia tentaculifera*, *Gyrodinium postmaculatum* and *G. rubricaudatum* observed in this study. The cingular displacement is calculated with respect to the cell length, excluding the posterior extension.

Morphological character	<i>Pavillardia tentaculifera</i>	<i>Gyrodinium postmaculatum</i>	<i>Gyrodinium rubricaudatum</i>
episome shape	conical	conical	conical
hyposome shape	ovate	ovate	ovate or conical
posterior extension	one, long (>10 μm)	one or two, short	pointed antapex
length in μm	67–73	89	62–80
width in μm	40–42	49	38–45
cingulum	median	median	median
cingular displacement	0.29–0.31	0.33	0.27–0.30
sulcus	extended into apex	extended into apex	extended into apex
#striae in episome face	10–11	11	10–12
#striae in hyposome face	20–24	22	20–26
nucleus position	central	central	central
nucleus diameter in μm	19–21	20	20–24

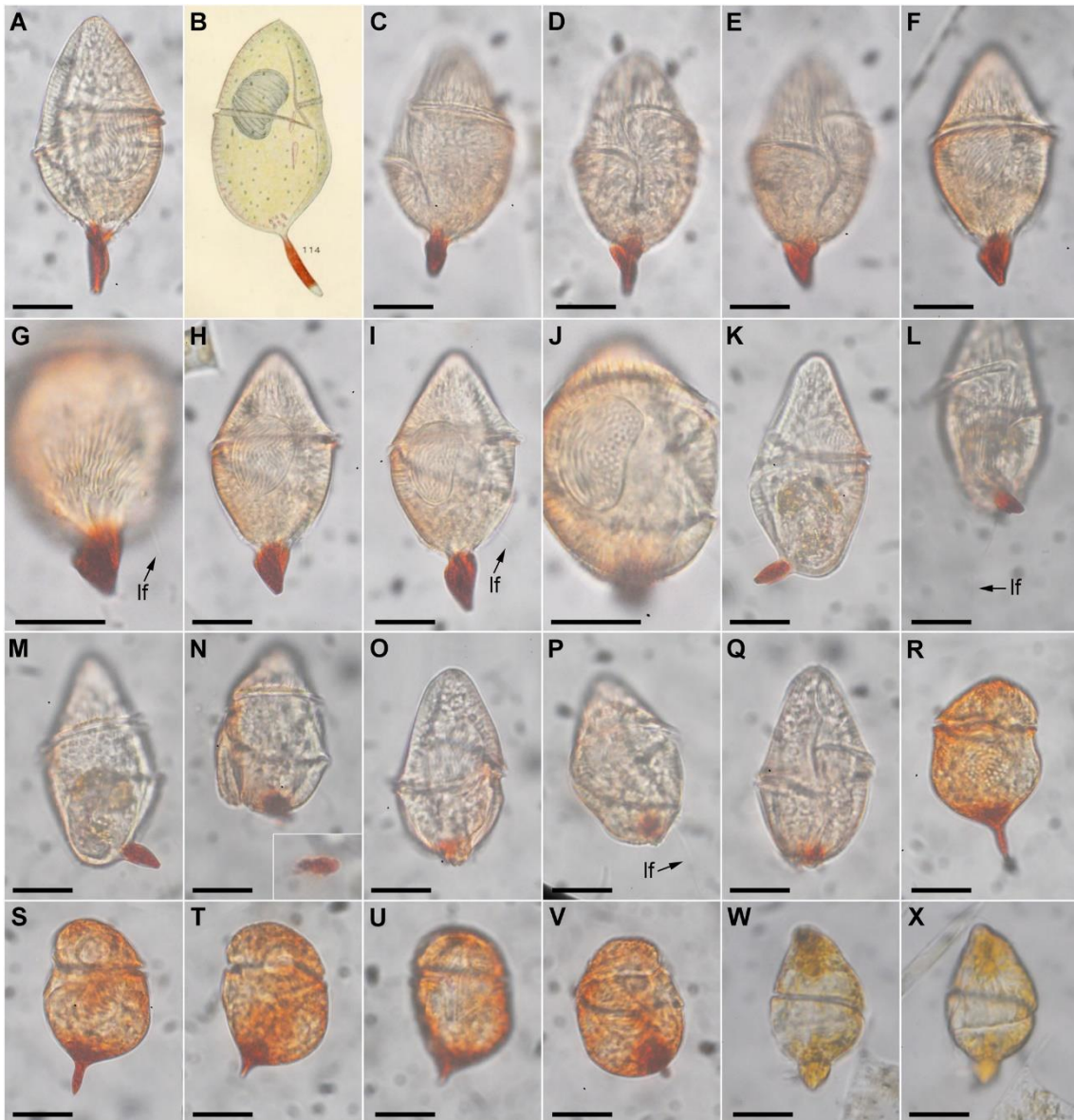


Fig. 1. Light micrographs of living cells with a posterior extension from the RESILIENCE MD#237 cruise (May 2022) off eastern South Africa, as well as a line drawing of *Pavillardia tentaculifera*. A, C–J. Different views of one individual of *P. tentaculifera*. B. Original illustration reproduced from Kofoid and Swezy (1921). K–Q. Different views of another individual of *P. tentaculifera*. N. The inset showed the detached posterior extension. R–V. A red-coloured individual tentatively belonging to the genus *Pavillardia*. W–X. A yellow-brown individual tentatively belonging to the genus *Pavillardia*. lf = longitudinal flagellum. See Table 1 for the location of the records. Scale bar = 20 μm .

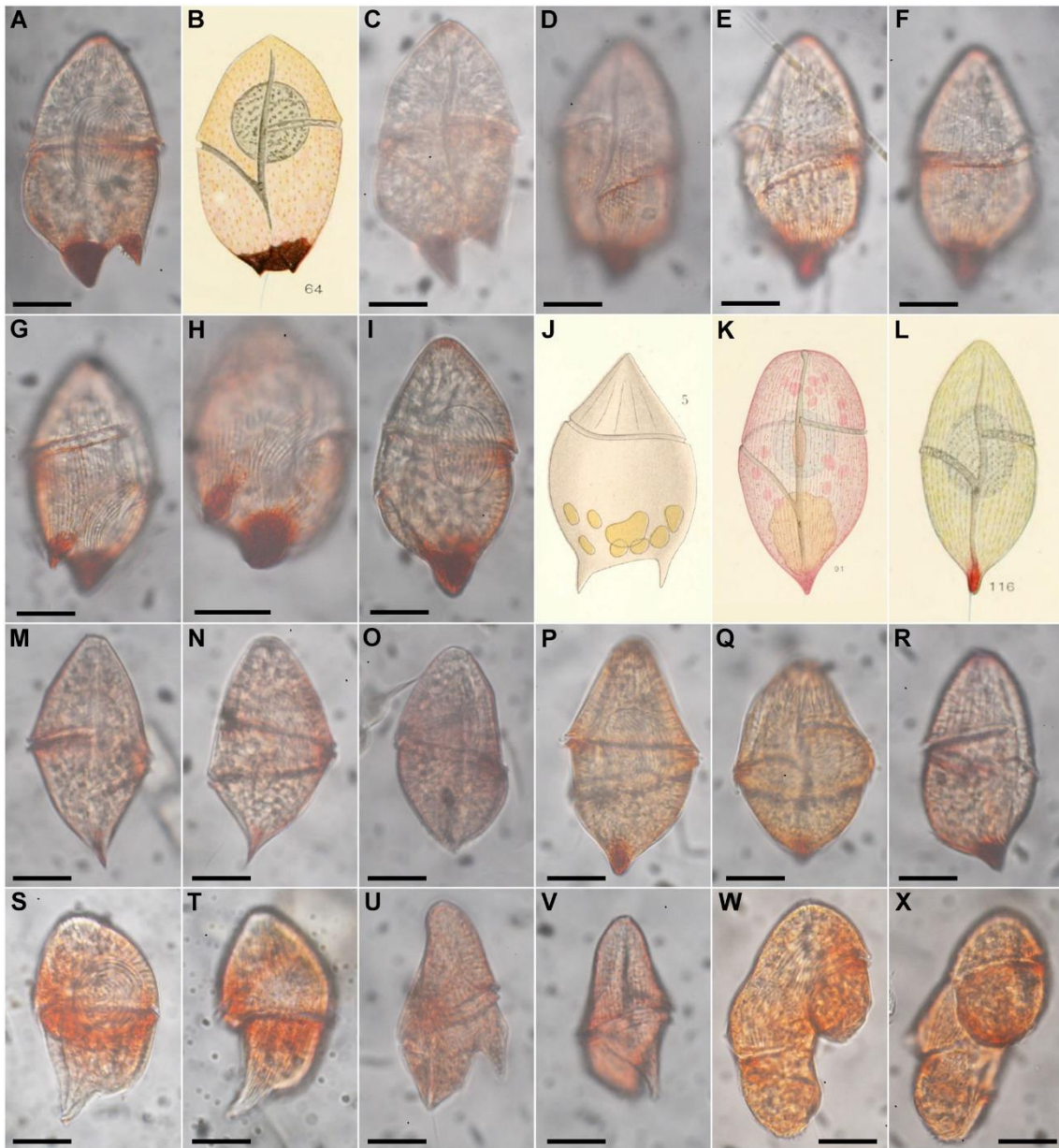


Fig. 2. Light micrographs of living cells of *Gyrodinium postmaculatum* and *G. rubricaudatum* from the RESILIENCE MD#237 cruise (May 2022) off eastern South Africa. A, C–I. One individual of *Gyrodinium postmaculatum*. B. Original illustration of *G. postmaculatum* reproduced from Kofoid and Swezy (1921, their figure 64). J. Original illustration of *Gymnodinium bicaudatum* reproduced from Pavillard (1905). K. Original illustration of *G. postmaculatum* reproduced from Kofoid and Swezy (1921, their figure 91). L. *Gyrodinium rubricaudatum* reproduced from Kofoid and Swezy (1921, their figure 116). M–N. Individual of *G. postmaculatum*. O. Individual of *G. rubricaudatum*.

P–Q. Other individual of *G. rubricaudatum*. R. Other individual of *G. postmaculatum*.
S–T. Unidentified *Gyrodinium* recently divided. U–V. Unidentified *Gyrodinium* under
division. W–X. Another individual under division. See Table 1 for the location of the
records. Scale bar = 20 μm .