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REDEFINITION OF *Ceratoperidinium* AND *Pseliodinium* (CERATOPERIDINIACEAE, DINOPHYCEAE) INCLUDING REASSIGNMENT OF *Gymnodinium fusus*, *Cochlodinium helix* AND *C. pirum* TO *Pseliodinium*

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ABSTRACT. The dinoflagellate genus *Cochlodinium* is polyphyletic, and several bloom-forming species in this genus, such as *Cochlodinium helix* and *C. convolutum*, are in need of reclassification. The molecular data revealed that the polymorphic species *Gymnodinium fusus* (=*Ceratoperidinium falcatum*, *Gyrodinium caudatum*, *Gyrodinium falcatum*, *Gyrodinium sugashimanii*, *Pseliodinium vaubanii*) is closely related to *Cochlodinium helix*/*C. convolutum*. There are significant morphological differences among the type species of *Ceratoperidinium*, *C. margalefii*, and the aforementioned species. The recent proposal of the genus *Kirithra* reinforces the need of the generic split between *C. margalefii* and *Gymnodinium fusus*/*C. helix*/*C. convolutum*, instead of placing all the species under the genus *Ceratoperidinium*. *Pseliodinium* is considered the earliest available generic name, and new combinations of *Pseliodinium* are proposed for *Gymnodinium fusus*, *Cochlodinium helix* and *C. pirum* (the latter considered co-specific with *C. convolutum*)

Keywords: *Kirithra*, Dinophyta, HABs, harmful algal blooms, new combinations, red tides, unarmored dinoflagellates.

Redefinición de *Ceratoperidinium* y *Pseliodinium* (Ceratoperidiniaceae, Dinophyceae), incluyendo la reasignación de *Gymnodinium fusus*, *Cochlodinium helix* y *C. pirum* a *Pseliodinium*

RESUMEN. El género de dinoflagelados *Cochlodinium* es polifilético, y varias especies formadoras de proliferaciones como *Cochlodinium helix* y *C. convolutum* requieren reclasificación. Los datos moleculares muestran que la especie polimórfica *Gymnodinium fusus* (=*Ceratoperidinium falcatum*, *Gyrodinium caudatum*, *Gyrodinium falcatum*, *Gyrodinium sugashimanii*, *Pseliodinium vaubanii*) está estrechamente emparentada con *Cochlodinium helix*/*C. convolutum*. Hay diferencias significativas en la morfología entre la especie tipo de *Ceratoperidinium*, *C. margalefii* y las especies mencionadas anteriormente. La reciente propuesta del género *Kirithra* refuerza la necesidad de una separación genérica entre *C. margalefii* y *Gymnodinium fusus*/*C. helix*/*C. convolutum*, en lugar de emplazar todas las especies en el género *Ceratoperidinium*. *Pseliodinium* se considera como el primer nombre genérico disponible, y se proponen nuevas combinaciones de *Pseliodinium* para *Gymnodinium fusus*, *Cochlodinium helix* y *C. pirum* (esta última especie es considerada conespecífica de *C. convolutum*).

Palabras clave: *Kirithra*, Dinophyta, proliferaciones algales nocivas, nuevas combinaciones, mareas rojas, dinoflagelados desnudos

Gómez, F. 2018. Redefinition of *Ceratoperidinium* and *Pseliodinium* (Ceratoperidiniaceae, Dinophyceae) including reassignment of *Gymnodinium fusus*, *Cochlodinium helix* and *C. pirum* to *Pseliodinium*. *CICIMAR Oceánides*, 33(1): 1-11.

INTRODUCTION

In the earlier studies on dinoflagellates, Pouchet (1885, 1887) described the morphological plasticity of some unarmored dinoflagellates. Pouchet (1885, his Figs. 4a–d) illustrated several conspecific cells with different morphologies, and enclosed in a hyaline membrane (Figs. 1–5). Pouchet (1887) also described *Gymnodinium helix* C.H.G. Pouchet as a bloom-forming species enclosed in a hyaline membrane. If Pouchet's illustrations are turned upside down, specimens show high cingular displacement, round apex, and asymmetric antapex with an outstanding posterior process (Figs. 27–28). Schütt (1895) recorded the morphological plasticity of *G. helix* with several illustrations (Figs. 30–32), and described *G. pirum* F. Schütt, a closely related species enclosed in a hyaline membrane (Fig. 54). Schütt (1895) also described *Gymnodinium fusus* F. Schütt with two distinct morphotypes (Figs. 6–7). That species corresponded to the taxon that Pouchet (1885) described as a dinoflagellate enclosed in a hyaline membrane (Figs. 1–5).

Schütt (1896) erected the genus *Cochlodinium* F. Schütt, and he proposed *C. strangulatum* (F. Schütt) F. Schütt and *C. geminatum* (F. Schütt) F. Schütt. Later, Lemmermann (1899) proposed *C. helix* (F. Schütt) Lemmermann and *C. pirum* (F. Schütt) Lemmermann. The species concept of Kofoid and Swezy (1921) allowed no extensive intraspecific variability.Without conducting their own observations, they proposed the new name *Gyrodinium falcatum* Kofoid & Swezy and *C. schuettii* Kofoid & Swezy for of Schütt's illustrations of *G. fusus* (Fig. 7) and *C. helix* (C.H.G. Pouchet) Lemmermann (Fig. 34), respectively. Lebour (1925) illustrated *G. falcatum* (Fig. 9) and proposed *C. helicoides* M. Lebour for another one of Schütt's illustration of *G. helix* (Fig. 50). Kofoid and Swezy (1921) described other species similar to *C. helix*, also enclosed in hyaline membranes, including *C. convolutum* Kofoid &

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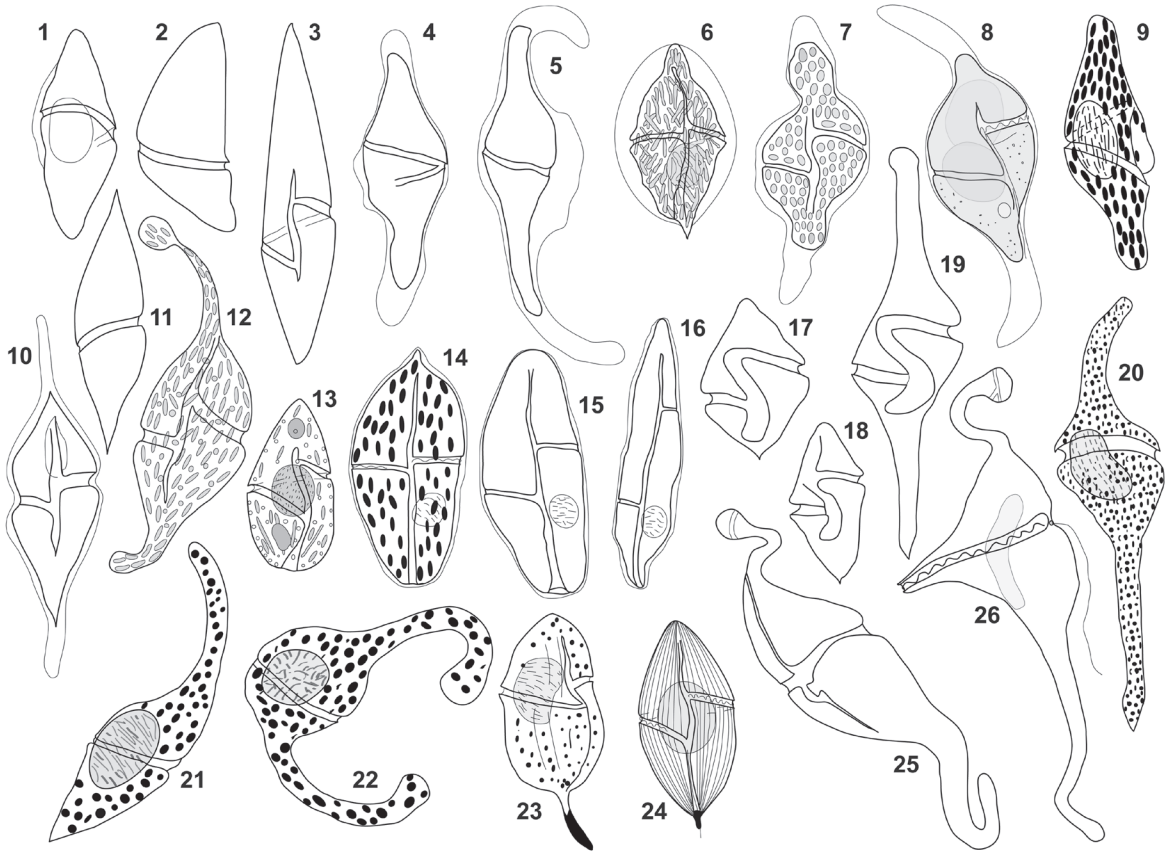
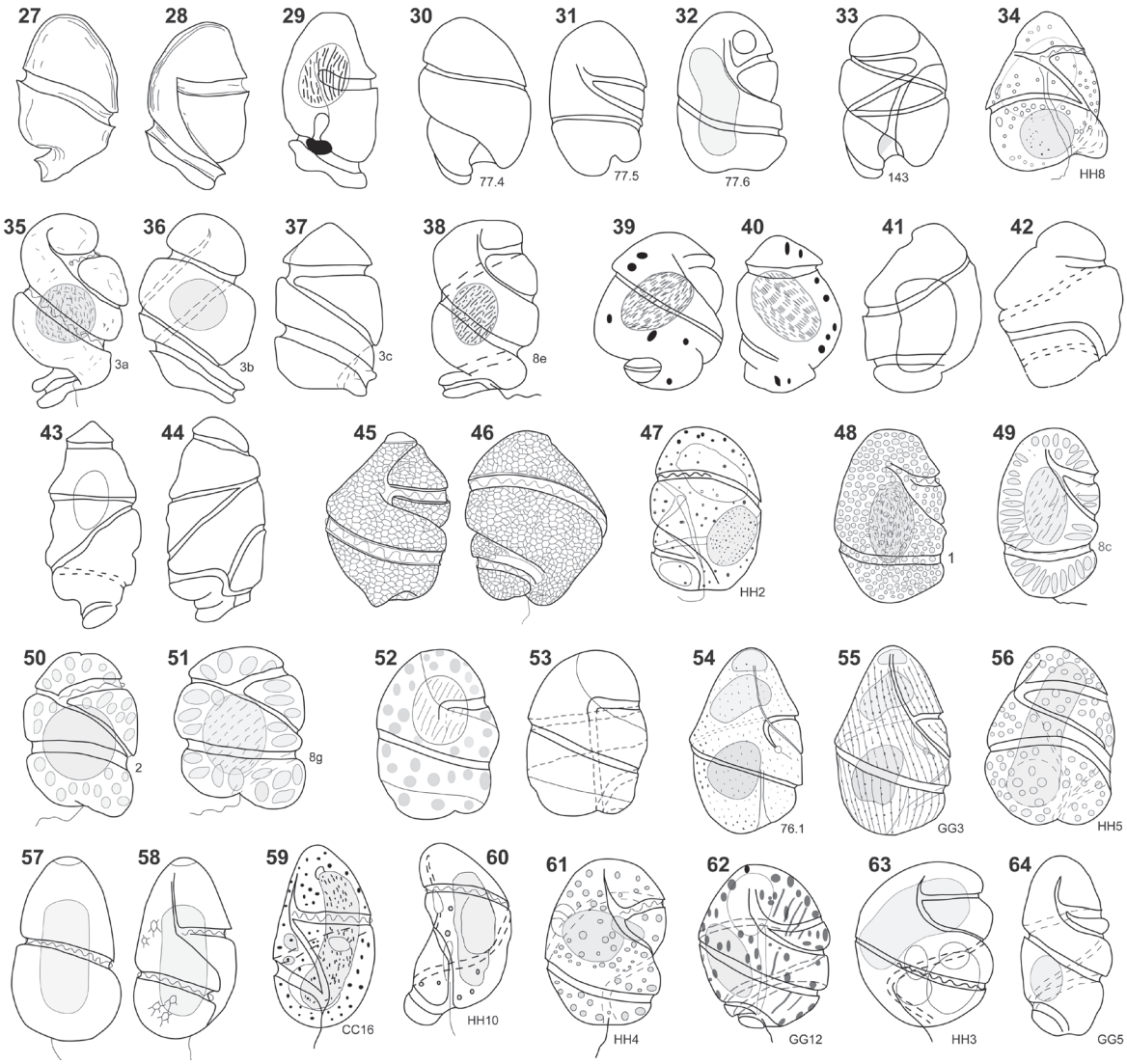


Figures 1–26. Line drawings of unarmored dinoflagellates. **1–5**. Encysted dinoflagellate redrawn from Pouchet (1885). **6–7**. *Gymnodinium fusus* redrawn from Schütt (1895). **8**. *Gyrodinium caudatum* redrawn from Kofoid and Swezy (1921). **9**. *Gyrodinium falcatum* redrawn from Lebour (1925). **10–11**. *Gymnodinium fusus* redrawn from Schiller (1933). **12**. *Gyrodinium falcatum* redrawn from Kofoid (1931). **13**. *Gyrodinium citrinum* redrawn from Kofoid (1931). **14–16**. *Gymnodinium fusus* redrawn from Elbrächter (1979). **17–20**. *Gyrodinium falcatum* redrawn from Okolodkov and Dodge (1997). **21**. Indeterminate dinoflagellate redrawn from Sournia (1972). **22**. *Pseliodinium vaubanii* redrawn from Sournia (1972). **23**. *Pavillardia tentaculifera* redrawn from Kofoid and Swezy (1921). **24**. *Gyrodinium rubricaudatum* redrawn from Kofoid and Swezy (1921). **25–26**. *Gynogonadinium aequatoriale* redrawn from Gómez (2007a).

Swezy (Fig. 55), *C. cavatum* Kofoid & Swezy (Fig. 60), *C. lebouriae* Kofoid & Swezy, and *Gyrodinium flavescens* Kofoid & Swezy (Fig. 59), among others. Kofoid and Swezy (1921) circumscribed the genus *Cochlodinium* to species whose cingulum encircles the cell more than one and a half times and is lacking the ocelloid. They divided the genus *Cochlodinium* into three subgenera and proposed the subgenus *Glyphodinium* Kofoid & Swezy, with *C. cavatum* as type species, for *C. helix*, *C. schuettii*, *C. convolutum*, *C. rosaceum* (Fig. 61), *C. vinctum* Kofoid & Swezy (Fig. 63) and others. Schiller (1933, pp. 362) created confusion when he considered *Gyrodinium falcatum* as a synonym of *G. fusus* (Figs. 10–11), while in page 460 he reported *G. falcatum* as an independent species.

Sournia (1972) described *Pseliodinium vaubanii* Sournia from samples preserved in Lugol's solution as an open bracelet-shaped unarmored dinoflagellate (Fig. 22), and illustrated intermediate forms between that species and *Gymnodinium fusus* (Fig. 21). Elbrächter (1979) observed the intraspecific changes in cell shape in live cells of *G. fusus*, and documented the intraspecific variability of the cingular displacement from one to more than eight cingular widths (Figs. 14–16). Elbrächter confirmed *Gyrodinium falcatum* as a synonym of *G. fusus*. Yoshimatsu (1990) also confirmed this morphological variability from a culture. Despite this, the name *G. falcatum* has persisted in the literature (Okolodkov & Dodge, 1997; Figs. 17–19). Other studies have reported *P. vaubanii* as a morphotype of *G. fusus* (Konovalova, 2003; Gómez, 2007b; Gárate-Lizárraga *et al.*, 2010). The species *Gymnodinium fusus* and *Cochlodinium helix* are widespread in polar (Okolodkov, 1998; Figs. 39–40), temperate [Paulsen, 1908 (Fig. 33); Dodge, 1982 (Fig. 38); Hansen and Larsen, 1992 (Figs. 52–53); Paulmier, 1994 (Figs. 43–44)] and tropical waters (Gómez, 2007b; Gárate-Lizárraga *et al.*, 2010, 2011). Blooms of *Cochlodinium*



Figures 27–64. Line drawings of *Cochlodinium helix* and allied species. **27–28**. *Gymnodinium helix* redrawn and turned upside down from Pouchet (1887). **29**. *Gymnodiniun polyphemus* var. *roseum* redrawn and turned upside down from Pouchet (1887). **30–32**. *G. helix* redrawn from Schütt (1895). 31= *C. schuettii*. 32= *C. helicoides*. **33**. *Cochlodinium helix* redrawn from Paulsen (1908). **34**. *C. helix* redrawn from Kofoid and Swezy (1921). **35–37**. *C. helix* redrawn from Lebour (1925). **38**. *C. helix* redrawn from Dodge (1982). **39–40**. *C. helix* redrawn from Okolodkov (1998). **41–42**. *C.* cf. *pupa* redrawn from Paulmier (1994). **43–44**. *C. helix* redrawn from Paulmier (1994). **45–46**. *C.* cf. *helix* redrawn from Reñé *et al.* (2013). **47**. *C. schuettii* redrawn from Kofoid and Swezy (=*G. helix* in Schütt, fig. 77.6). **48**. *C. schuettii* redrawn from Lebour (1925). **49**. *C. schuettii* redrawn from Dodge (1982). **50**. *C. helicoides* redrawn from Lebour (1925) (=*G. helix* in Schütt, fig. 77.5). **51**. *C. helicoides* redrawn from Dodge (1982). **52–53**. *C. helicoides* redrawn from Hansen and Larsen (1992). **54**. *Gymnodinium pirum* redrawn from Schütt (1895). **55**. *G. pirum* redrawn from Kofoid and Swezy (1921). **56**. *C. convolutum* redrawn from Kofoid and Swezy (1921). **57–58**. *C. convolutum* redrawn from Iwataki *et al.* (2005). **59**. *Gyrodinium flavescens* redrawn from Kofoid and Swezy (1921). **60**. *C. cavatum* redrawn from Kofoid and Swezy (1921). **61**. *C. rosaceum* redrawn from Kofoid and Swezy (1921). **62**. *C. radiatum* redrawn from Kofoid and Swezy (1921). **63**. *C. vinctum* redrawn from Kofoid and Swezy (1921). **64**. *C. cereum* redrawn from Kofoid

helix, *C. convolutum* and *Gymnodinium fusus* have also been reported (Hallegraeff, 1992; McEwan *et al.*, 1998; Matsuoka *et al.*, 2008; Gárate-Lizárraga, 2014).

Takayama (1998) investigated the morphology of *Gymnodinium fusus* (as *Gyrodinium falcatum*), *Cochlodinium convolutum*, *C. vinctum* and *C.* cf. *cereum* Kofoid & Swezy with scanning electron microscopy. These species shared a circular apical groove connected to the anterior sulcus and a smooth cell surface lacking striae. Recently, Boutrup *et al.* (2017) proposed the new genus *Kirithra* Boutrup, Tillmann, Daugbjerg & Moestrup with a detailed study of the ultrastructure of a member of the

family Ceratoperidiniaceae.

Species such as *Gymnodinium fusus* and *Cochlodinium helix* do not longer fit within the current circumscriptions of the genera *Gymnodinium* F. Stein, *Gyrodinium* Kofoid & Swezy, or *Cochlodinium* (see Gómez *et al.*, 2017). In the SSU- and LSU rDNA molecular phylogenies, the members of the family Ceratoperidiniaceae are distantly related to other dinoflagellates (de Salas *et al.*, 2003; Nézan *et al.*, 2014; Reñé *et al.* 2013, 2015; Boutrup *et al.*, 2017). Reñé *et al.* (2013) reported *Cochlodinium* cf. *helix* and *C.* cf. *convolutum* as closely related to *Gymnodinium fusus*. Reñé *et al.* (2013) then transferred *G. fusus* into *Ceratoperidinium* as *C. falcatum*, but failed to do the same for *Cochlodinium helix* and *C. convolutum.* Boutrup *et al.* (2017) described a new species in a new genus instead to place it within *Ceratoperidinium*. Boutrup *et al.* (2017, p. 599) reported "the tree topology indicates the presence of four or five distinct genera belonging to the Ceratoperidiniaceae".

The morphological similarities and close molecular association suggest that *G. fusus*, *C. helix*, *C. convolutum* should also be reclassified as belonging to the same genus, and distinct from *Ceratoperidinium*. The present study proposes to place these species under the genus *Pseliodinium*, as the earliest available generic name, and to emend the generic diagnoses of *Ceratoperidinium* and *Pseliodinium*. This study also reviews of the synonymy of some of the species such as the proposal of *Cochlodinium convolutum* as a junior synonym of *C. pirum*.

MATERIALS AND METHODS

Cells were collected and analyzed according to the methods described in Gómez *et al.* (2017).

RESULTS AND DISCUSSION

Identity and synonymy of *Gymnodinium fusus*

The synonymy of *Gymnodinium fusus* has been reported in previous studies (Konovalova, 2003; Gómez, 2007b). Pouchet (1885) and Schütt (1895) described the high morphological variability in this species in observations of live cells. The taxonomic literature regarding these species was complicated by splitter taxonomists which often described morphological variants of the same species as distinct species (Kofoid, 1931; Kofoid & Swezy, 1921; Sournia, 1972; Cachon *et al.*, 1989). For example, *Gyrodinium caudatum* and tentatively *Gyrodinium citrinum* Kofoid, *Gymnodinium scopulosum* Kofoid & Swezy and *Gyrodinium truncatum* Kofoid & Swezy are junior synonyms of *G. fusus.*In the apparent absence of their own observations, Kofoid and Swezy (1921) used one of Schütt's illustrations of *Gymnodinium fusus* (Fig. 7) to describe *Gyrodinium falcatum.* Although Kofoid and Swezy (1921) also observed genuine *Gymnodinium fusus*, they described that species as *Gymnodinium caudatum* (Fig. 8), and it is possible that they also identified *Gymnodinium fusus* cells as *Gyrodinium citrinum* (Fig. 13), *Gymnodinium scopulosum*, and *Gyrodinium truncatum*, as their descriptions could have corresponded to various forms of *G. fusus* with contracted body extensions. Pouchet (1885, his fig. 4a–d) was the first to illustrate the species, and Schütt (1895) described it as *G. fusus.* As the name *Gymnodinium fusus* is the basionym, upon transfer into another genus, the new combination should include the epithet '*fusus*' (except in case of homonymy).

Identity and synonymy of *Cochlodinium helix* and *C. convolutum*

The taxon *Cochlodinium helix* and allied species have a complicated taxonomic history as *Gymnodinium fusus* as the same authors were involved in describing species in this clade. These descriptions were further complicated by the intraspecific plasticity in key taxonomic features such as the number and locations of cingular and sulcal turns as well as changes in cell size and shape that occurs when the cells feed mixotrophically. The original line drawings in Pouchet's description were imprecise (Figs. 27–28) and showed a confusing similarity with *Gymnodinium polyphemus* var. *roseum* C.H.G. Pouchet (currently a *Warnowia* Er. Lindemann species) as illustrated by Pouchet (1887) (Fig. 29). Schütt (1895) described in detail the intraspecific variability of *Gymnodinium fusus*, probably based on live samples collected from the Gulf of Naples, Mediterranean Sea. Some authors described the morphotypes of *Gymnodinium helix* as independent species. Schutt's figure 77.6 showed an ovoid cell with flattened basis of the hyposome (Fig. 47) that was named as *C. schuettii* (Kofoid & Swezy, 1921), while Schütt's figure 77.5 showed an asymmetrical hyposome with a lobe as *C. helicoides* (Fig. 50) (Lebour, 1925). These species are separated by the degree of cingular turns around the cell, but this character is difficult to observe.

In addition to *Gymnodinium helix*, Schütt (1895) described the closely related species,*Gymnodinium pirum*, which showed a more regular cell contour, surface granules, and vacuoles that suggested mixotrophic behavior (Fig. 54). When Kofoid and Swezy (1921, pp. 375) observed this species, they clearly stated that it lacked surface striae, but nevertheless illustrated it with surface striation (Fig. 55). Nobody has ever observed a photosynthetic dinoflagellate with yellow greenish pigmentation and surface striation enclosed in a hyaline membrane, and *Cochlodinium pirum* (F. Schütt) Lemmermann has anomalously disappeared from the scientific literature. The observations of *C. pirum* were assigned to *C. convolutum*, which is similar, but lacking the striae. In the proliferations of *C. pirum*, the cells showed a granulated surface and scarce pigmentation (Figs. 72–79). When cells contained a large vacuole, the nucleus changed its shape from ellipsoidal to sphe-

rical (Fig. 78). Kofoid and Swezy (1921) described the species *C. cavatum* from the observation of a single individual that showed an elongated nucleus prior the karyokinesis (Fig. 60). This species corresponded to a dividing cell of *C. pirum* (Fig. 74).

Iwataki *et al.* (2005) reported line drawings of *C. convolutum* showing less than 1.5 turns of the cingulum around the cell, and an elongated nucleus (Figs. 57–58). Their line drawings resembled *Gyrodinium flavescens* (Fig. 59). The light microscopy pictures of *C. convolutum* in Matsuoka *et al.* (2008) strongly resembled *C. pirum*, as in the original description by Schütt (1895). Beyond the similar cell shape, cingulum, and sulcus, Schütt's figure 76.1 illustrated an accumulation body in the apex similar to that in Matsuoka *et al.* (2008, their fig. 4b). Schutt's figure 76.1 illustrated a granulated cell surface (Fig. 54), and Matsuoka *et al.* (2008, fig. 4d) illustrated the cell surface with small grains scattered in the surface. It should be noted that the amphiesma with polygonal vesicles reported for *Kirithra* may be interpreted as a granulated cell surface under light microscopy (Boutrup *et al.*, 2017).The main difference between these depictions is the shape of the nucleus, which was spherical in Schütt and elongated in Matsuoka *et al.* (2008).Schütt illustrated *C. pirum* with a vacuole that changes the shape of the nucleus (Fig. 54). This suggests that Kofoid and Swezy (1921) described *C. pirum* as the new species *C. convolutum* (Fig. 55). In the recent literature, Gárate-Lizárraga *et al.* (2011) used the names *C. helicoides* and *C. convolutum* for cells of *C. helix* and *C. pirum*, respectively. Gárate-Lizárraga (2014, his fig. 3f) subsequently illustrated the same cells of *C. convolutum* under the name *C. pirum*, and obviously without striae in the cell surface. Reñé *et al.* (2013) provided a LSU rRNA gene sequence of a cell identified as *C.* cf. *convolutum* (their fig. 3d–e). Their cells showed an asymmetrical hyposome, with a lobule that corresponds to the morphology of *C. helix* (Figs. 30, 33). The scanning electron microscopy images identified as *Cochlodinium* cf. *helix* in Reñé *et al.* (2013, their fig. 4a–b) showed a symmetric hyposome (Figs. 45–46) that its closer to the morphology of *C. pirum* (Figs. 54–56). Consequently, the species in Reñé *et al.* (2013) *C. helix* and *C. pirum* (as *C. convolutum*) may reciprocally misidentified as each other.

Molecular phylogeny and diagnostic characters

In the LSU rRNA gene phylogeny, the species *Gymnodinium fusus* (=*Gyrodinium falcatum*), *Cochlodinium helix* and *C. pirum* (=*C. convolutum*) branched together with high support in a clade while the type of *Ceratoperidinium*, *C. margalefii*, and *Gymnodinium* sp.2, and *Kirithra* are placed in other clades within the family Ceratoperidiniaceae (Reñé *et al.*, 2013, 2015; Boutrup *et al.*, 2017).

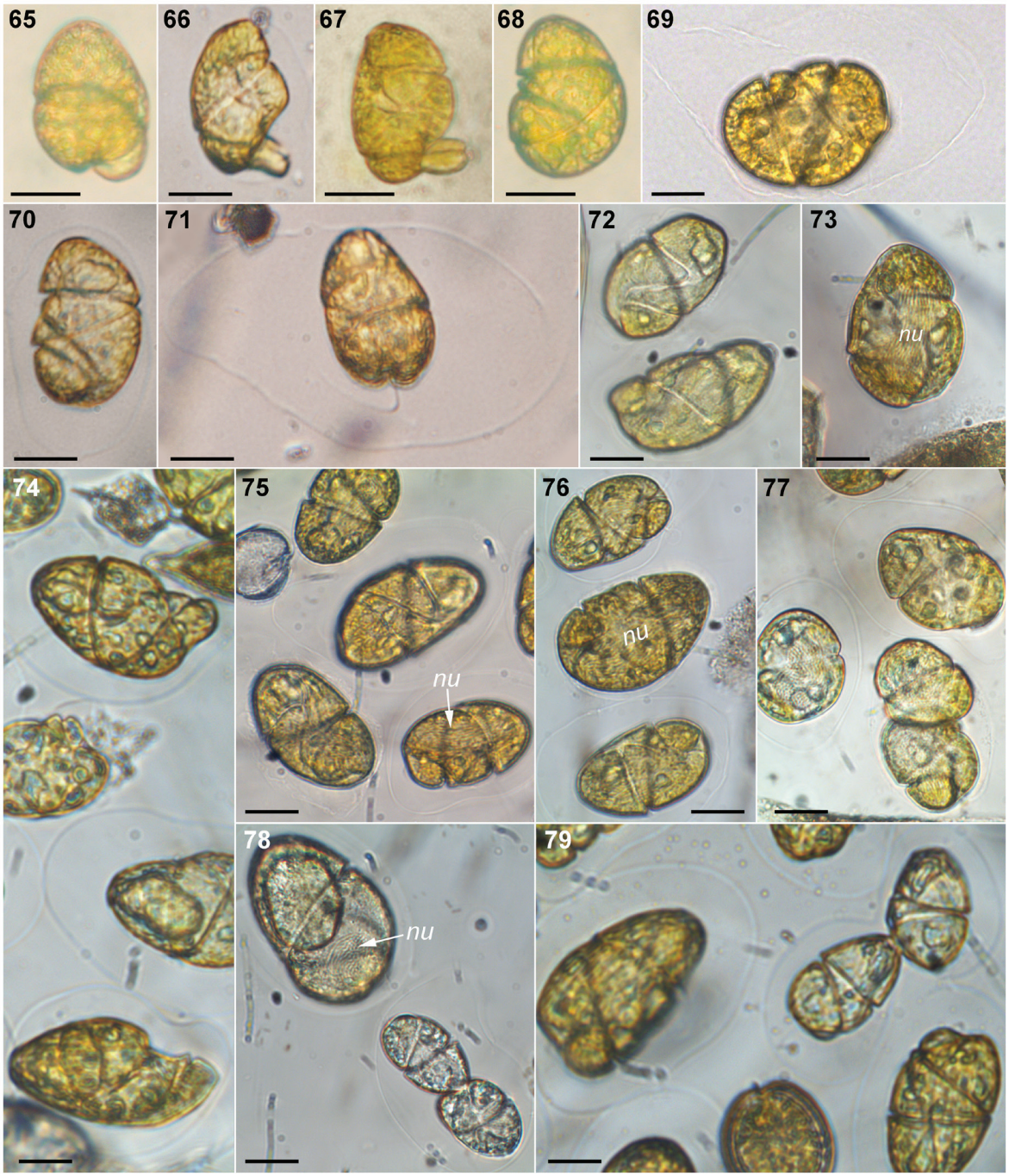
Gymnodinium helix was separated into different species based on differences in the number of turns of the cingulum and sulcus (Figs. 27–53, 65–69). The species *G. fusus*, *C. helix*, and *C. pirum* are closely related, but differ greatly in the number of turns of the cingulum and sulcus. Consequently, this is not a synapomorphic character of the clade comprising *G. fusus/C. helix*. Rather, this character appears as a recent adaptation and is lacking in species such as *Ceratoperidinium margalefii* and *Gymnodinium* sp.1-sp.2. This higher number of turns of the cingulum could be associated with increasing cell propulsion. The species *G. fusus* has developed long extensions that increase the cell surface area available for photosynthesis and nutrient uptake (Figs. 90–102). The swimming speed of *Gymnodinium fusus* is slow. In contrast, *Cochlodinium helix* is a fast swimming form, as is common in many red tide blooms, and the cingulum torsion may function to increase the swimming speed. *Gymnodinium fusus* forms a hyaline membrane that tightly surrounds the cell (Figs. 96–100), while *C. pirum* is able to swim inside a hyaline membrane that can be up to twice larger than the cell length (Fig. 71).

The shape of the nucleus is an instable diagnostic character. During a bloom of *C. pirum*, some cells showed a spherical nucleus (Fig. 78), slightly posterior, while other cells showed an elongate nucleus (Fig.76). In *G. fusus*, the nucleus is ellipsoidal in cells with elongate cell body (Figs. 90–94), but spherical when the cell body is circular, as in the form *Pseliodinium vaubanii* (Figs. 95–100).

Ceratoperidinium

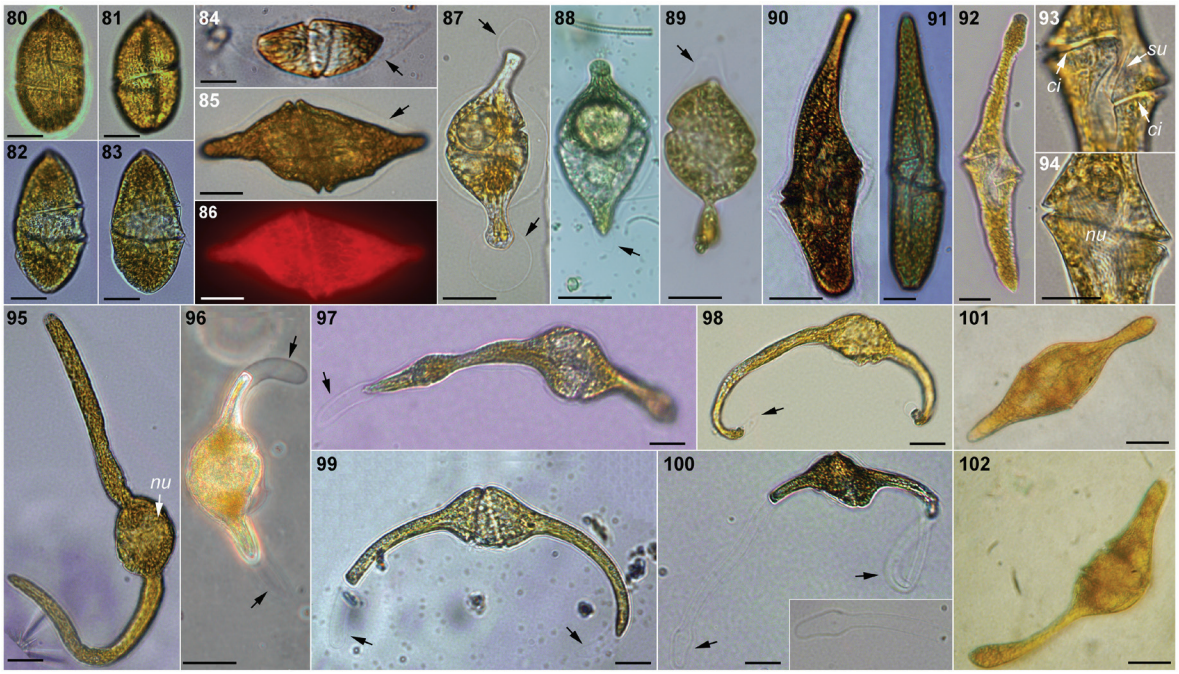
Although in the LSU rRNA gene phylogenies *Ceratoperidinium* does not branch within the clade of the type species, Reñé *et al.* (2013) transferred the species *Gyrodinium falcatum* into the genus *Ceratoperidinium*. The species *G. falcatum*, *C. helix*, and *C. pirum* are closely related species that belong to the same genus. Reñé *et al.* (2013, pp. 682) modified the diagnosis of the genus *Ceratoperidinium* to accommodate *G. fusus* (as *G. falcatum*), and to exclude *C. helix* and *C. convolutum*. They reported in the emended diagnosis: "*Retractile appendices (both apical and antapical) present*". Curiously, the original description of *Ceratoperidinium* (Margalef, 1969) and the cell illustrated by Reñé *et al.* (2013) lacked the apical extension. That definition –based on the extensions– excluded *C. helix* and *C. pirum*. Reñé *et al.* (2013, pp. 682) reported "*Cingulum descending, displaced 2-3 times its own width*". Elbrächter (1979) reported that the cingular displacement of *G. fusus* reached up to 8 times its own width (Figs. 14–16). The emended diagnosis of *Ceratoperidinium* needs to be re-emended to include the morphological variability of *Gymnodinium fusus* (=*Ceratoperidinium falcatum*).

The type species of *Ceratoperidinium*, *C. margalefii*, showed important morphological differences when compared to the members of the clade of *G. fusus/C. helix*. *Cochlodinium margalefii* is a hi-



Figures 65–79. Light micrographs of *Cochlodinium* spp. **65–67**. *Cochlodinium helix*. **68–69**. *Cochlodinium* cf. *helix.***70–79**. *Cochlodinium pirum* from the Mediterranean Sea and South Atlantic Ocean. See methods in Gómez *et al.* (2017). nu = nucleus. Scale bar 20 µm.

ghly dorso-ventrally compressed species with two antapical extensions (Gómez *et al.*, 2004) while *G. fusus* is not compressed or shows slight lateral compression, and a single retractile antapical extension (Figs. 80–102). The sulcus of *C. margalefii* is displaced toward the right side, while it is centrally located in *G. fusus*. The anterior and posterior sulcus of *C.margalefii* is shallow and hardly visible, while deep and conspicuous in *G. fusus*. Illustrations by Reñé *et al.* (2013, pp. 77) depicted the sulcus extending into one of the antapical extensions, a feature unreported in any other unarmored dinoflagellate. In



Figures 80–102. Light micrographs of *Gymnodinium fusus* from the Mediterranean Sea and the South Atlantic Ocean. See methods in Gómez *et al.* (2017). **80–86**. Form *Gymnodinium fusus*. **87–88**. Form *Gymnodinium caudatum*. **89**. Form resembling *Pavillardia*. **90–94**. Form *Gyrodinium falcatum*. **95–100**. Form *Pseliodinium vaubanii*. Arrows point to the hyaline membrane. **101–102**. Form *Gyrodinium falcatum* in culture. ci = cingulum; nu = nucleus; su = sulcus. Scale bar 20 µm.

contrast, the posterior extension of the sulcus of *G. fusus*/*C. helix* was deep and did not reach the antapex. *Ceratoperidinium* is morphologically different from *Gymnodinium fusus*/*Cochlodinium helix*. The morphological and molecular data suggest the placement of the members of the clade of *G. fusus*/*C. helix* in a different genus, other than *Ceratoperidinium* or *Kirithra* (Fig. 103).

Alternative generic names for the clade of *Gymnodinium fusus*/*Cochlodinium helix*:

Pavillardia Kofoid & Swezy

The scarcely known genus *Pavillardia* is characterized by a single antapical extension (Fig. 23). The shape resembles *Gymnodinium fusus* with an incompletely retracted antapical extension as illustrated here (Fig. 89) or in Steidinger and Williams (1970, their fig. 73b). Kofoid and Swezy (1921) reported some longitudinal striae in their illustration of *Pavillardia*, while the cell surface of *G. fusus* is smooth. They also described *Gyrodinium rubricaudatum* Kofoid & Swezy with surface striae and a short antapical extension (Fig. 24). Takayama (1998) illustrated a cell assigned to *Pavillardia* by SEM. His cell showed a lateral compression, an anterior cingulum, and rugose cell surface lacking striae that does not fit with the description of *Pavillardia.* Gómez (2009) reported *Pavillardia* with a smooth surface and a circular cell shape. Kofoid and Swezy (1921) described the antapical extension as a tentacle that "*jerked back with a convulsive jerk*". The epithet of the species is "*tentaculifera*" and Kofoid and Swezy (1921) placed *Pavillardia* in the Noctilucales based on the resemblance of the antapical extension and the motile tentacle of the noctilucoid dinoflagellates. Curiously, Jacques and Soyer (1977) proposed a relationship between *Pseliodinium* and the Noctilucales. Cachon *et al.* (1989) described the motility of the extensions of *Gymnodinium fusus* (as *Gyrodinium sugashimanii*) and the movement does not correspond to a tentacle. The identity of *Pavillardia* remains mysterious, and if it is strictly followed the original description by Kofoid and Swezy (1921), a cell with a tentacle and striae in the cell surface does not fit with the characteristics of the members of the clade of *G. fusus/C. helix*.

Glyphodinium Kofoid & Swezy

Kofoid and Swezy (1921) proposed the subgenus *Glyphodinium* for species such as *Cochlodinium helix*, *C. schuettii*,and *C. convolutum*. The name *Glyphodinium* was proposed as subgenus, and it will need to be ranked at the genus level. Article 11.2 of the I.C.N. states: "*A name has no priority outside the rank in which it is published*" and Article 11.3 "*For any taxon from family to genus, inclusive, the correct name is the earliest legitimate one with the same rank…*". Consequently, even if *Glyphodinium* is raised at the generic rank, it does not have priority over the older generic names.

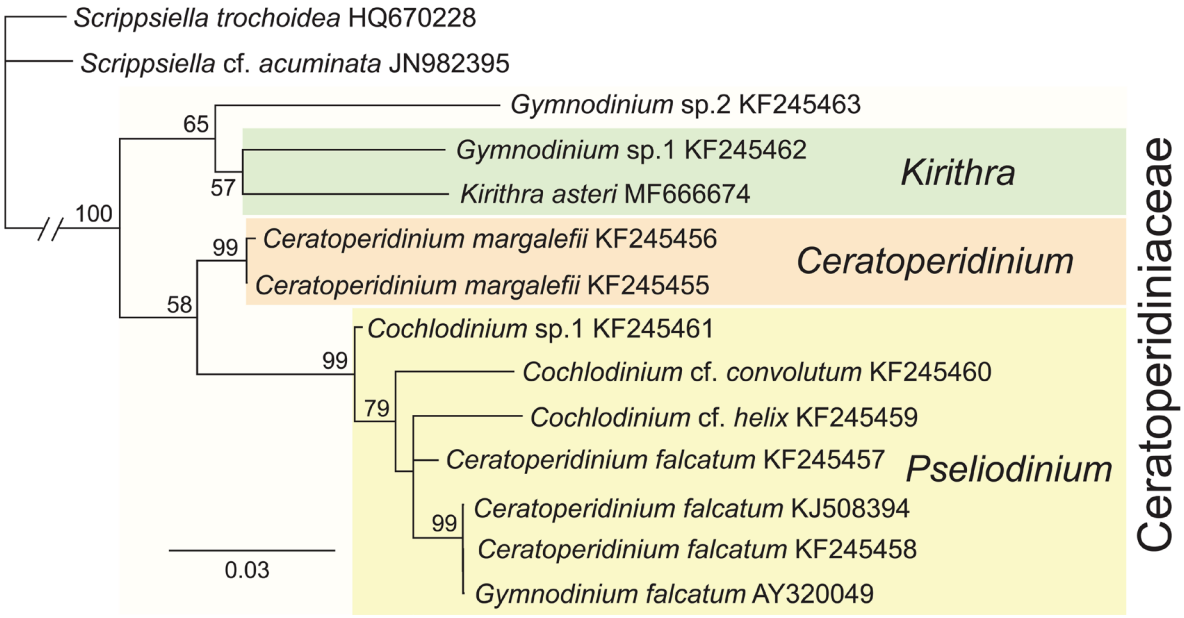


Figure 103. Neighbor-Joining phylogenetic tree of the D1-D2 LSU rRNA gene sequences of the family Ceratoperidiniaceae, using *Scrippsiella* spp. as outgroup. Numbers at nodes are bootstrap proportions. Accession numbers are provided. The scale bar represents the number of substitutions for a unit branch length.

Gynogonadinium F. Gómez

This genus is characterized by antapical and apical extensions and a circular apical groove (Figs. 25–26; Gómez, 2007a). It resembles the illustration of *Gyrodinium falcatum* by Kofoid (1931) (Fig. 12) and swelling of the apical extension is often found in *Gymnodinium fusus* (Fig. 100). *Gynogonadinium* is a candidate for membership in the family Ceratoperidiniaceae. It also exhibits important differences compared with the clade *G. fusus/C. helix*. The type species is highly laterally compressed, with a triangular cell body, and has a cingular list that is absent in other members of Ceratoperidiniaceae. In any case, *Gynogonadinium* does not hold priority over oldest generic names.

Pseliodinium Sournia (Figs. 80–102)

Previous studies have reported *Pseliodinium vaubanii* as a morphotype of *Gymnodinium fusus* (Konovalova, 2003; Gómez, 2007b). In recently collected live plankton, it is possible to observe how the retraction of the extensions leaves behind a hyaline membrane with the shape of *Pseliodinium* (Figs. 96–100). In cultures, cells do not develop the long extensions as those observed in wild cells (Figs. 101–102). The species *Pseliodinium vaubanii* is a synonym of *G. fusus*. The genus *Pseliodinium* is legitimate and its type species is a member of the clade of *G. fusus/C. helix*. The earliest available generic name for the species of this clade is *Pseliodinium*.

Taxonomical considerations

Family Ceratoperidiniaceae A.R. Loeblich 1980 *emend.* F. Gómez

Emended diagnosis: Unarmored dinoflagellates. The apical groove is circular, encircling the apex and connecting with the anterior sulcus. The cell surface is smooth, lacking ridges or striae, and with a hyaline amphiesma comprising polygonal vesicles. The cytoplasm may retract leaving behind a hyaline membrane. The dinokaryotic nucleus lacks the perinuclear capsule. A reddish-orange pigmented body or eyespot is absent. Cells are solitary, or sometimes forming a two-celled colony.

Genus *Ceratoperidinium* A.R. Loeblich 1980 *emend.* F. Gómez

Emended diagnosis: *Ceratoperidinium* differed from other members of the Ceratoperidiniaceae in the high dorso-ventral flattening and presence of two antapical retractile extensions.

Type species: *Ceratoperidinium margalefii* A.R. Loeblich 1980

Synonyms: *Ceratoperidinium yeye* Margalef 1969, nom. illeg.; *C. mediterraneum* Abboud-Abi Saab.

Genus *Pseliodinium* Sournia 1972 *emend.* F. Gómez

Emended diagnosis: Unarmored free-living dinoflagellates that possess chloroplasts with a yellow-greenish pigmentation. Cell shape globular or slightly compressed, often with outstanding posterior processes or developing single apical and an-

tapical retractile extensions. Cells are solitary, or sometimes forming a two-celled colony. Cells often enclosed in a hyaline membrane.

Synonyms: *Cochlodinium* pro parte, *Gymnodinium* pro parte, *Gyrodinium* pro parte, subgenus *Glyphodinium* Kofoid & Swezy 1921.

Type species: *Pseliodinium vaubanii* Sournia (1972; pp. 156, figs 18–22).

Species:

Pseliodinium fusus (F. Schütt) F. Gómez, *comb. nov.*

Basionym: *Gymnodinium fusus* F. Schütt (1895, Ergeb. Plankton Exped., Humboldt-Stift. IV. M. a. A.: pp. 166, 167, plate 24, fig. 79, plate 25, fig. 81).

Synonyms:"Kyste de...*Gymnodinium*" in Pouchet 1885, plate 2, fig. 4a–d; *Gyrodiniun falcatum* Kofoid & Swezy 1921; *Gyrodinium caudatum* Kofoid & Swezy 1921; ?*Gymnodinium scopulosum* Kofoid & Swezy 1921; ?*Gyrodinium truncatum* Kofoid & Swezy 1921; ?*Gyrodinium citrinum* Kofoid 1931; *Pseliodinium vaubanii* Sournia 1972; *Gyrodinium sugashimanii* J. Cachon, H. Sato, M. Cachon & S. Sato 1989; 'Gymnodinium falcatum' in de Salas *et al.* (2003, pp. 1241); *Ceratoperidinium falcatum* (Kofoid & Swezy) Reñé & de Salas 2013.

Pseliodinium helix (C.H.G. Pouchet) F. Gómez, *comb. nov.*

Basionym: *Gymnodinium helix* C.H.G. Pouchet (1887, *J. Anat. Physiol.* 23: pp. 94–96, tex-fig. in page 95).

Synonyms: *Cochlodinium helix* (C.H.G. Pouchet) Lemmermann 1899; *C. schuettii* Kofoid & Swezy 1921; *C. helicoides* M. Lebour 1925.

Pseliodinium pirum (F. Schütt) F. Gómez, *comb. nov.*

Basionym: *Gymnodinium pirum* F. Schütt (1895, Ergeb. Plankton Exped., Humboldt-Stift. IV. M. a. A.: pp. 6, 166, plate 23, fig. 76.1–4).

Synonyms:*Cochlodinium pirum* (F. Schütt) Lemmermann 1899; *Cochlodinium cavatum* Kofoid & Swezy 1921; *Cochlodinium convolutum* Kofoid & Swezy 1921; ?*Gyrodinium flavescens* Kofoid & Swezy 1921.

Other species that may belong to *Pseliodinium*:

Cochlodinium cereum Kofoid & Swezy (1921, Mem. Univ. Calif. 5: 357; text-fig. GG5) (Fig. 64).

Cochlodinium radiatum Kofoid & Swezy (1921, Mem. Univ. Calif. 5: 377; text-fig. GG12; pl. 6, fig. 67) (Fig. 62).

Cochlodinium rosaceum Kofoid & Swezy (1921, Mem. Univ. Calif. 5: 379; text-fig. HH4; plate 8, fig. 85) (Fig. 61).

Cochlodinium vinctum Kofoid & Swezy (1921, Mem. Univ. Calif. 5: 384; text-fig. HH3; pl. 2, fig. 15) (Fig. 63).

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