Excessive proliferation of new dinoflagellate generic names: the case of
"Torquentidium" (Ceratoperidiniaceae, Dinophyceae)

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ABSTRACT

New genera of unarmoured dinoflagellates represented by a single or very few species have largely increased in the last two decades. An example is the new genus name *Torquentidium* H.H. Shin, Z. Li, K.W. Lee & Matsuoka 2019 (Shin et al., *Eur. J. Phycol*. 54: 249-262) recently proposed for species that were transferred into *Pseliodinium* in 2018. The SSU- and LSU rRNA gene sequences of the type species of *Pseliodinium* and *Torquentidium* only differed by 0.3% and 2%, respectively, and they clustered together as a monophyletic group with high support. Based on these tree topologies and/or the sequence divergences, each dinoflagellate species would be classified in its own genus. The morphological character proposed to distinguish *Pseliodinium* and *Torquentidium* is that the cingulum encircled the cell 1 and 1.5 times, respectively. This kind of arbitrary numeric morphometric character, proposed one century ago, is currently considered invalid for the generic split of unarmoured dinoflagellates. For example, *Polykrikos geminatum* (with ~1.5 cingular turns) clusters between species of *Polykrikos* (1 turn).

Within the Ceratoperidiniaceae, the arrangement of the amphiesmal vesicles in apical structure complex was used for distinction at the genus level (i.e., *Kirithra*), while this character is identical for *Pseliodinium* and *Torquentidium*. For the first time, an unarmoured dinoflagellate genus contains species with smooth cell covering (*T. convolutum, T. helix*) and species with longitudinal striae (*T. pirum*). However, the original description as *Gymnodinium pirum* in 1895 erroneously illustrated two distinct species, and since then nobody has ever reported surface markings in *T. pirum*. The morphological and molecular criteria used for the split of *Torquentidium* from *Pseliodinium* are unsupported, contributing to the excessive proliferation of monotypic genera. *Torquentidium pirum* and *T. convolutum* are synonyms, and *Torquentidium* is a superfluous generic name and junior synonym of *Pseliodinium*.

**Key words:** Cochlodinium; classification; Dinoflagellata; Gymnodinium; Gyrodinium; molecular phylogenetics; naked Dinophyta; new genus; *Pseliodinium*; taxonomy

**Abbreviations:** ASC, apical structure complex; BP, Bootstrap support or Bootstrap Probability; PP, Bayesian Posterior Probability
Introduction

The dinokaryotic dinoflagellates have been traditionally divided into armoured (thecate) and unarmoured (naked or athecate) dinoflagellates. The robust cell covering of the armoured dinoflagellates have facilitated the studies, and the arrangement of the thecal plates is a useful diagnostic character for the classification at the genus level. The study and classification of the unarmoured dinoflagellates is more difficult due to the cell delicacy, the lack of thecal plates, and the polymorphism of some species. The classical generic classification was based on morphometric characters such as the degree of cingular displacement (the distance between both ends of the cingulum) used for the classical macro-genera Gymnodinium F. Stein and Gyrodinium Kofoid & Swezy. However, this character varies intraspecifically (Gymnodinium fusus F. Schütt/Gyrodinium falcatum Kofoid & Swezy), and the molecular data have revealed that other morphological characters (i.e., the shape of the apical groove) are more useful for the classification at the genus level (Daugbjerg et al., 2000). The type of cell covering is other diagnostic character supported by the molecular data, and species with smooth and striate cell surface never cluster together (i.e., Gymnodinium and Gyrodinium). That character is easier to observe during the routine light microscopy observations than the apical groove. Cochlodinium F. Schüt, other classical macro-genus, was a pool of species where the cingulum forms a descending left spiral of 1.5–4 turns around the cell (Kofoid & Swezy, 1921). The value of cingulum encircling the cell ≥1.5 times is arbitrary, and other species characterized by 1 and 1.5 cingular turns were placed in Gyrodinium (G. flavescens Kofoid & Swezy, G. melo Kofoid & Swezy). More than one turn of the cingulum is also a character of the warnowiid dinoflagellates (Erythropsidinium P.C. Silva, Warnowia Er. Lindemann, etc.), but this character is not used for the generic classification in that family (Kofoid & Swezy, 1921). Molecular data confirmed that the genus Cochlodinium pooled unrelated species that shared more than one cingular turn around the cell. Cochlodinium geminatum (F. Schütt) F. Schütt characterized by 1.5 cingular turns was transferred into Polykrikos Buetschli (Qiu et al., 2013). Consequently, the number of turns of the cingulum appear as an invalid diagnostic character at the genus level as this trait is variable among the species of a single genus. Reñé et al. (2013, their figure 5) reported that the sequences of the taxon formerly known as Gyrodinium fusus or Gyrodinium falcatum (with a single turn of the cingulum around the cell) clustered
between species with ~1.5 turn (*Cochlodinium* cf. *helix*, *C*. cf. *convolutum*, *Cochlodinium* sp.1) as a monophyletic group with strong support (bootstrap support, BP 99%; posterior probability, PP 1). Again, one or more turns of the cingulum around the cell is not a valid diagnostic character for the generic split.

When the molecular data of the type species of *Cochlodinium*, *C*. *strangulatum* F. Schütt, was available (Gómez et al., 2017), the sequences of *Cochlodinium* species were dispersed into four distinct clades. This supported that a cingulum with more one turn appeared repeatedly in the evolution. The type species of the genus *Pseliodinium* Sournia, *P. vaubanii* Sournia, is a junior synonym of *Gymnodinium fusus/Gyrodinium falcatum*, and *Pseliodinium* appears as the earlier available genus name for the members of this monophyletic group. New combinations in the genus *Pseliodinium* were proposed for *Cochlodinium helix* (C.H.G. Pouchet) Er. Lemmermann and *Cochlodinium pirum* (F. Schütt) Er. Lemmermann (the latter considered a synonym of *C. convolutum* Kofoed & Swezy) (Gómez, 2018). Hu et al. (2019) provided molecular data of a Chinese strain identified as *Pseliodinium pirum* (F. Schütt) F. Gómez, and considered it as a junior synonym of *C. convolutum*. The new sequence clusters with *P. fusus* and other former *Cochlodinium* species (*C*. cf. *helix*, *C*. cf. *convolutum*, *Cochlodinium* sp.1) as a monophyletic group with strong support (BP 100%, PP 1; Hu et al., 2019, their figures 5 and 6). Shin et al. (2019) disagreed with this classification and revived the use of the cingular turns as a diagnostic character for the generic split of unarmoured dinoflagellates, and they considered *Cochlodinium pirum* and *C. convolutum* as independent species. With the proposal of *Torquentidium* H.H. Shin, Z. Li, K.W. Lee & Matsuoka, the genus *Pseliodinium* remains exclusively for its type species, contributing to the excessive proliferation of monotypic genera.

**Molecular data support**

Shin et al. (2019) reported in the abstract “Phylogeny based on SSU and LSU rDNA sequences revealed that the Korean isolate (*Torquentidium convolutum*) forms a clade independent from *Pseliodinium fusus*”. However, there is no support to consider *Torquentidium* and *Pseliodinium* as independent genera based on the topology of the SSU- and LSU rRNA gene phylogenies (Shin et al., 2019; their figures 52–53; See also
Figs 1–2). Shin et al. transferred three species into *Torquentidium*, but only one species is represented in the molecular phylogenies as member of *Torquentidium*. In the LSU rRNA gene phylogeny, Shin et al. (2019, their figure 53) did not highlight the sequences of *Cochlodinium* cf. *convolutum* (GenBank ascension number KF245460) and *Cochlodinium* sp.1 (KF245461) as belonging to *Torquentidium*. It is uncertain why these species with the cingulum encircling the cell 1.5 times are excluded as members of *Torquentidium*, when this is the main diagnostic character of that genus. Finally, if we follow the criterion by Shin et al. (2019), this strongly supported monophyletic group (BP 100%, PP 1) should be split into three or four monotypic genera. In contrast, Hu et al. (2019) considered that all these species belong to *Pseliodinium* based on the phylogeny of the same sequences. The LSU rRNA gene sequences of *Torquentidium convolutum* (Kofoid & Swezy) H.H. Shin, Z. Li, K.W. Lee & Matsuoka (MF948386) from Korea is not available yet, but it is probably identical with the sequence of *Pseliodinium pirum* from northern China (MH469535).
Fig. 1. Maximum-likelihood phylogenetic tree of sequences of the SSU rRNA gene using the same sequences in Shin et al. (2019), two additional environmental sequences and the sequence of *Pseliodinium pirum* (MH469533) by Hu et al. (2019). Molecular phylogenetic methods are similar than in Gómez et al. (2019, https://doi.org/10.1016/j.ejop.2019.125636). Supports at internal nodes are bootstrap support higher than 50%. *Oxyrrhis marina* was used as outgroup. The scale bar represents the number of substitutions for a unit branch length.
Shin et al. (2019, their Table 2) also supported the generic split of *Torquentidium* and *Pseliodinium* based on the divergence of the LSU rRNA gene sequences. As the sequence of *T. convolutum* (MF948386) is not available yet, for comparative purposes we use the sequence identified as *Cochlodinium cf. helix* (KF245459) that Shin et al. considered co-specific with *T. convolutum*. The sequence of the type species of *Torquentidium, T. convolutum*, differed by 2% from that of the type species of *Pseliodinium*. In Shin’s et al.’s phylogenetic tree, the sequences of the unarmoured dinoflagellate *Akashiwo sanguinea* (K. Hirasaka) Gert Hansen & Moestrup are represented near the Ceratoperidiniaceae. The sequence divergence of strains of *A. sanguinea* (MK236590, KY817605) are higher than 5%. Shin et al. (2019, their figure 53) reported sequences of other former *Cochlodinium* species, *Margalefidinium polykrikoides* (Margalef) F. Gómez, Richlen & D.M. Anderson and *M. fulvescens* (M. Iwataki, H. Kawami & Matsuoka) F. Gómez, Richlen & D.M. Anderson that clustered together within the genus *Margalefidinium*. The sequences of these congeneric species (AB288382, KC577592) diverged by 14%. The sequences of the SSU rRNA gene is the most extended molecular marker to support the classification of the dinoflagellates at the genus level. As an example of the intraspecific variability, the SSU rRNA sequences of two isolates of *Pseliodinium fusus* (F. Schütt) F. Gómez collected from the same localization diverged by 0.3% (KP790150–1). In contrast, the sequences of *Pseliodinium fusus* (KP790151) and *Torquentidium convolutum* (MF948385) that also diverged by 0.3% are considered as belonging to independent genera. The SSU rRNA gene sequences of the strains of *Akashiwo sanguinea* (AF276818, KP976596) diverged by 2.1%, and *Margalefidinium polykrikoides* and *M. fulvescens* diverged by 11% (AB288380, EU418971).
Fig. 2. Maximum-likelihood phylogenetic tree of sequences of the LSU rRNA gene using the same sequences in Shin et al. (2019), except the sequence MF948386 of Torquentidium convolutum by Shin et al. that is not available yet. The sequence of Pseliodinium pirum (MH469535) by Hu et al. (2019) is also included. Molecular phylogenetic methods are similar than in Gómez et al. (2019, https://doi.org/10.1016/j.ejop.2019.125636). Supports at internal nodes are bootstrap support higher than 50%. Oxyrrhis marina was used as outgroup. The scale bar represents the number of substitutions for a unit branch length.

There is no unique number of sequence difference indicating that two DNA sequences belong to the same or distinct taxa. However, we can expect some coherency.
especially when the topology of the phylogenetic trees shows a monophyletic group for *Pseliodinium* and *Torquentidium* with strong support (Reñe et al., 2013; Gómez et al. 2017; Gómez, 2018; Hu et al., 2019; Shin et al., 2019). A recurrent criticism is that each organism has a distinct evolutionary rate, but at least we can assume similarities between the members of the Ceratoperidiniaceae. The LSU rRNA gene sequences of *Gymnodinium* sp.1 (KF245462), *Gymnodinium* sp.2 (KF245463) and *Kirithra asteri* Boutrup, Tillmann, Daugbjerg & Moestrup (MF666674) diverged among them for more than 7%. Shin *et al.* considered that a sequence divergence of 2% supports the placement of *Pseliodinium fusus* and *Torquentidium convolutum* in independent genera. Then, each species of the Ceratoperidiniaceae will belong to an independent genus. In fact, if Shin *et al.*’s practice extends to other dinoflagellates, the concept of genus will disappear and each dinoflagellate species will belong to an independent genus.

**Morphological support**

There is no molecular support for the generic split, and the morphological character used for the distinction of *Pseliodinium* and *Torquentidium* based on a numeric morphometric value is a step back to the past. In the classical classifications, Kofoid & Swezy (1921) used arbitrary morphometric values for the generic split. For example, a cingular displacement lower or higher than 20% of the cell length for *Gymnodinium* and *Gyrodinium*, respectively; the relative height of the episome (*Amphidinium* Claparède & J. Lachmann); or the number of turns of the cingulum (*Cochlodinium*) that were later demonstrated to be unsupported by the molecular data (Daugbjerg *et al.*, 2000; Gómez *et al.*, 2017). Shin *et al.* (2019) have revived the use of a morphometric value as the cingulum encircling the cell 1.5 times for a generic diagnosis. The use of morphometric values is always arbitrary as there is no a clear cut among the species. There are intermediate forms between *Pseliodinium fusus* and *Torquentidium convolutum* such as *Gyrodinium melo* Kofoid & Swezy or *Gyrodinium flavescens* Kofoid & Swezy ranging between 1 and 1.5 cingular turns. Incoherently, Shin *et al.* did not accept this diagnostic character for the generic split of other former *Cochlodinium* species. Shin *et al.* (2019, their figure 52) reported the sequence of *Polykrikos geminatum* D. Qiu & Senjie Lin placed among other species of *Polykrikos*. *Polykrikos geminatum* is a former *Cochlodinium* species which cingulum encircles 1.5 times the cell, while the other species
of *Polykrikos* has one cingular turn (Qiu et al., 2013). If the criterion by Shin et al. (2019) is followed, *Polykrikos geminatum* should be placed into an independent monotypic genus, and the genus *Polykrikos* split into at least four genera.

For most of the dinoflagellates, the cingulum that harbours the transversal flagellum encircles the cell with one turn. The transversal flagellum is responsible for the locomotion, and species with a longer cingulum have higher swimming speeds (Jeong et al., 1999; Sohn et al., 2011). A longer cingulum results when both ends of the cingulum are more distant (higher cingular displacement), and/or the cingulum describes more than one turn around the cell. In coastal waters, bloom-forming species have developed different strategies to increase the swimming speed for predator avoidance or migrations such as the formation of colonies and/or the increase of the length of the cingulum with more than one turn (i.e., species formerly classified in *Cochlodinium* such as *Margalefidinium polykrikoides*). Coastal blooming species such as those currently placed in *Torquentidium* do not form colonies, but they have developed a longer cingulum with ~1.5 turns. In the stratified open ocean, the presence of photosynthetic unarmoured dinoflagellates forming colonies or more than one cingular turns is uncommon. The swimming speed is not a priory and other strategies appear such as the projection of body extensions (i.e. *Ceratoperidinium margalefii* A.R. Loeblich, *Pseliodinium fusus*). As its relatives, *Torquentidium convolutum* is also able to project body extensions under culture conditions (Shin et al., 2019; their figures 22–23), but this is not a useful adaptation in turbulent coastal waters. An increase of the number of cingular turns or the projection of body extensions are just recent adaptations to particular environmental conditions.

Within the family Ceratoperidiniaceae, Boutrup et al. (2017) proposed the genus *Kirithra* Boutrup, Tillmann, Daugbjerg & Moestrup using as a generic diagnostic character the morphology of amphiesmal vesicles comprised between the apical groove and the apex [known as apical structure complex (ASC)]. Shin et al. (2019, p. 12) reported: “In *K. asteri*, the amphiesmal vesicles within the ASC are arranged with one central vesicle encircled by approximately eight vesicles and the upper row in the three parallel rows is located within ASC, whereas…the upper row of *T. convolutum* is located outside of ASC”. Shin et al. (2019, p. 11) reported: “The ASC of *T. convolutum* is consistent with that of…*Pseliodinium fusus*”. Shin et al. used the apical structure complex as a diagnostic character for the generic split between *Kirithra* and *Torquentidium*, while
this is invariable for *Pseliodinium* and *Torquentidium*. The differences in the apical structure complex used for the generic classification in the Ceratoperidiniaceae do not support the split of *Torquentidium* and *Pseliodinium*. When splitting the genus *Torquentidium* from *Pseliodinium*, Shin et al. (2019) forgot to re-define *Pseliodinium* with an emended diagnosis.

**Synonymy of *Pseliodinium pirum* and *Cochlodinium convolutum***

The molecular data support the markings in the cell covering as a generic diagnostic character in unarmoured dinoflagellates. For example, the clades of *Gyrodinium* or *Cucumeridinium* F. Gómez, P. López-García, H. Takayama & D. Moreira exclusively contain species with longitudinal striae. These taxa are heterotrophic and the longitudinal striae or ridges are re-enforcements helping with the cell deformation after engulfing large preys. In order to avoid internal damages, the nucleus, an important internal organelle, is also protected by a capsule. The smooth cell covering is more commonly found in photosynthetic taxa such as the members of the Ceratoperidiniaceae. Shin et al. (2019) for the first time placed species with a smooth cell surface (*T. convolutum*) and longitudinal striae [*T. pirum* (F. Schütt) H.H. Shin, Z. Li, K.W. Lee & Matsuoka] within the same genus. In the genus diagnosis, Shin et al. (2019) reported: “Cell surface with amphiesma of small polygonal and rectangular vesicles”. They forgot to comment that *Torquentidium* also contains species with longitudinal striae. The truth is that nobody has ever observed a photosynthetic unarmoured dinoflagellate with longitudinal striae enclosed in a hyaline membrane. There are records in the literature of cells identified as *Cochlodinium/Pseliodinium pirum*, but they are illustrated with a smooth surface (Kofoid & Swezy, 1921; Gárate-Lizárraga, 2014; Gómez, 2018; Hu et al., 2019). Shin et al. (2019, Table 2) compared the morphological characters of *T. convolutum* and *T. pirum*. The only remarkable difference was that *T. pirum* is covered by longitudinal striae, citing Schütt (1895) and Kofoid & Swezy (1921) as data sources. However, Kofoid & Swezy (1921, p. 375) clearly stated for their records of *Cochlodinium pirum*: “We find no striae on our specimens on close examination”. Kofoid & Swezy (1921, their figure 101) illustrated of *C. pirum* with a smooth surface (see the original illustrations in the Fig. 3).
Fig. 3. Line drawings and light microscopy photographs of *Pseliodinium pirum*. (A) *Gymnodinium pirum* in Schütt (1895, his figure 76.2). (B) *Gymnodinium pirum* in Schütt (1895, his figure 76.1). (C) *Cochlodinium pirum* in Schiller (1933). (D) *Cochlodinium pirum* in Kofoid & Swezy (1921). (E–F) *Cochlodinium convolutum* in Kofoid & Swezy (1921). (G–I) Cells of *Pseliodinium pirum* from Ubatuba, Brazil. Note the different morphology of the cells and the shape of the surrounding hyaline membranes.

Schütt (1895) was one of the pioneers in the difficult study of the unarmoured dinoflagellates. In his publication, there are no species diagnoses, and even the geographical origin of the specimens is missing. There are illustrations with legends, and dispersed comments in the main text. At that time, little was known of the intraspecific morphological variability. Schütt (1895) reported distinct genera for a single species
(Monaster F. Schütt, Amphitholus F. Schütt nom. rej.) and illustrations of distinct species under the same species name (Gymnodinium cucumis F. Schütt, G. lunula F. Schütt, G. teredo C.H.G. Pouchet). Schütt (1895) illustrated Gymnodinium pirum with two illustrations of the whole cell. His illustration 76.2 showed a typical cell of the Ceratoperidiniaceae, similar to Gymnodinium helix C.H.G. Pouchet or Gymnodinium fusus: a photosynthetic solitary cell with smooth cell surface enclosed in a hyaline membrane. In contrast, Schütt’s figure 76.1 illustrated a Gyrodinium-related species: a heterotrophic cell with food vacuoles, and the cell surface with longitudinal striae. These striae in Schütt’s figure 76.1 were even more evident than those in other Gyrodinium species in the same publication. Schütt’s figure 76.1 illustrated the cell with an almost spherical nucleus, while it is typically ellipsoidal or reniform in Gymnodinium pirum. In this case, the size of the food vacuole do not justify the deformation of the nucleus shape. The individual of Schütt’s figure 76.1 also illustrated an anterior sack-shaped pusule near the pore of the transverse flagellum and a cluster of twisted rodlets near the apex. Schütt (1895) illustrated these morphological features in heterotrophic species with longitudinal striae such as Gyrodinium spirale (his figures 66.1, 70.1), and a similar pusule was also illustrated in Cochlodinium strangulatum F. Schütt (his figure 72.1). This supported that Schütt’s figures 76.1 and 76.2 illustrated distinct species. Influenced by Schütt (1895), Kofoid & Swezy (1921) reproduced the pusule in their illustrations. However, this character has not been observed in the Ceratoperidiniaceae. Shin et al. (2019) considered that Torquentidium convolutum and T. pirum are independent taxa because the latter possesses longitudinal striae, but nobody has ever observed a photosynthetic gymnodioid cell with longitudinal striae enclosed in a hyaline membrane. Contrary to Shin et al., there is no any clade of unarmoured dinoflagellate combining DNA sequences of species with smooth and striate cell surface.

Kofoid was a splitter taxonomist that described the species ignoring the intraspecific variability and using morphometric numeric values as a diagnostic character based on the measurements of a single or very few individuals. For example, Kofoid & Swezy (1921) used in their dichotomous key used criteria such as “Displacement of girdle 0.82 transdiameter” for the split of Cochlodinium convolutum and other species, while their measurements were restricted to four individuals that co-occurred with their observations of C. pirum. Kofoid & Swezy (1921, p. 376) reported for C. pirum: “It is
very near *C. convolutum*, but has less torsion, 0.5 instead of 0.6, and less displacement of the girdle, 0.5–0.6 instead of 0.6 total length, and is more ochraceous and less greenish in color”. Obviously, the colour is a poor diagnostic character, especially when you are observing moribund cells after net sampling and transport to the lab, and a difference of torsion (0.5 versus 0.6) is even difficult to note in this polymorphic taxon. The data evidence that there are no morphological differences between *C. pirum* and *C. convolutum*, and both species are synonyms. Cells of *C. pirum* with a surface striation do not exist. The molecular data do not evidence a high species richness in this monophyletic group. At the present, sequences from different geographical origins identified as *Cochlodinium cf. helix* (Reñé et al., 2013), *Pseliodinium pirum* (Hu et al., 2019) and *Torquentidium convolutum* (Shin et al., 2019) correspond to a single species, and the topology of this monophyletic group remains invariable since Reñé et al. (2013).

In the etymology of the genus name *Torquentidium*, one of the accepted meanings of the stem -torquêo, torquenti- is torment, torture. In *Torquentidium convolutum*, the meanings of both genus and epithet names are ‘twist’ or ‘turn’. Shin et al. (2019, p. 13) did not report the etymology of the suffix –dium-. It is uncertain whether the aim of the authors was to use –dinium- (meaning again ‘turn around’ or ‘twist’, referring to dinoflagellate) that is the most common suffix for dinoflagellates. Anyway, the genus name will be commonly misspelled as ‘Torquentidinium’. So much ‘twists’ should not disorient us, and the morphological and molecular data in Shin et al. do not justify the placement of these species in new genus name independent of *Pseliodinium*. The proposal of *Torquentidium* sets a negative precedent in the classification of unarmoured dinoflagellates.

Genus *Pseliodinium* Sournia emend. F. Gómez

Synonyms: *Cochlodinium* pro parte, *Gymnodinium* pro parte, *Gyrodinium* pro parte, subgenus *Glyphodinium* Kofoid & Swezy, *Torquentidium* H.H. Shin, Z. Li, K.W. Lee & Matsuoka.

Type species: *Pseliodinium vaubanii* Sournia

Other species:
Pseliodinium fusus (F. Schütt) F. Gómez (=Pselodinium vaubanii Sournia)

Pseliodinium helix (C.H.G. Pouchet) F. Gómez

Pseliodinium pirum (F. Schütt) F. Gómez [=Torquenidium convolutum (Kofoid & Swezy) H.H. Shin, Z. Li, K.W. Lee & Matsuoka]. Basionyn: Gymnodinium pirum F. Schütt (1895, pp. 6, 166, plate 23, fig. 76.2, non 76.1).

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