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Phylogeny and Synonymy of *Gyrodinium heterostriatum* comb. nov. (Dinophyceae), a Common Unarmored Dinoflagellate in the World Oceans

Fernando GÓMEZ[a,b], Luis Felipe ARTIGAS[b], Rebecca J. GAST[c]

[a] **Carmen Campos Panisse 3, E-11500 Puerto de Santa María, Spain**
[b] **Université du Littoral Côte d'Opale, Université de Lille, CNRS, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences, 32 Av. Foch, F-62930 Wimereux, France**
[c] **Woods Hole Oceanographic Institution, Woods Hole, MA 02543-1049, USA**

Abstract. The North Sea and the English Channel are regions with a long tradition of plankton studies, where the colony-forming haptophyte *Phaeocystis globosa* dominates the spring phytoplankton blooms. Among its predators, we investigated an abundant unarmored dinoflagellate (~3000 cells per liter) in the North Sea in May 2019. It has been reported in the literature as *Gymnodinium heterostriatum* or *G. striatissimum*, and often identified as *Gyrodinium spirale*. Phylogenetic analyses using the small-, large subunit- and Internal Transcriber Spacers of the ribosomal RNA (SSU-, LSU-, ITS rRNA) gene sequences indicate that our isolates clustered within the *Gyrodinium* clade. The new sequences formed a sister group with sequences of the freshwater taxon *Gyrodinium helveticum*, being one of the infrequent marine-freshwater transitions in the microbial world. This isolate is the first characterized member of a clade of numerous environmental sequences widely distributed from cold to tropical seas. This common and abundant taxon has received several names due to its morphological plasticity (changes of size and shape, often deformed after engulfing prey) and the difficulty in discerning surface striation. We conclude that the priority is for the species name *Gymnodinium heterostriatum* Kofoid & Swezy 1921, a new name that was proposed for *Gymnodinium spirale* var. *obtusum* sensu Dogiel 1906. The species *Gyrodinium striatissimum* (Hulburt 1957) Gert Hansen & Moestrup 2000 and *Gymnodinium lucidum* D. Ballantine in Parke & Dixon 1964 (=*G. hyalinum* M. Lebour 1925) are posterior synonyms. We propose *Gyrodinium heterostriatum* comb. nov. for *Gymnodinium heterostriatum.*

Keywords: Dinophyta, *Gymnodinium*, new combination, taxonomy, molecular phylogenetics, North Atlantic

INTRODUCTION

The colony-forming haptophyte *Phaeocystis globosa* Scherffel is responsible for massive spring blooms in the southern North Sea and the eastern English Channel (Tillmann and Hesse 1998, Gómez and Souissi 2008). Two unarmored dinoflagellates are mainly reported as predators during these blooms: *Gyrodinium spirale* (Bergh) Kofoid & Swezy, with a fusiform shape, is the most commonly cited in the literature (Stelfox-Widdicombe et al. 2004, Grattepanche et al. 2011), and a second species, often mistaken as *G. spirale* that is smaller and ellipsoidal in shape. It has been identified as *Gymnodinium heterostriatum* Kofoid & Swezy in the English Channel (Lebour 1925, Dodge 1982, Paulmier 1992) and the North Sea (Drebes 1974, Elbrächter 1975,

Address for correspondence: Fernando Gómez, Carmen Campos Panisse 3, E-11500 Puerto de Santa María, Spain; Email: fernando.gomez@fitoplancton.com

Tillmann and Hesse 1998) or *Gymnodinium striatissimum* Hulburt (Elbrächter 1979, Elbrächter & Hoppenrath 2009).

Kofoid and Swezy (1921) proposed the new name *Gymnodinium heterostriatum* for a polymorphic species that Dogiel (1906) identified as *Gymnodinium spirale* var. *obtusum* from his observations in the Gulf of Naples. Kofoid and Swezy (1921) reproduced two of the Dogiel's illustrations, and provided new illustrations from their own observations in the Pacific off La Jolla, California. Without a comparison with *G. heterostriatum*, Hulburt (1957) described *Gymnodinium striatissimum* in the North American Atlantic near Woods Hole. However, his illustrations showed a high similarity with the illustrations of *G. heterostriatum* by Kofoid and Swezy (1921). Elbrächter (1975) reported line drawings of *G. heterostriatum* from the North Sea, and later he reported the same line drawings for *G. striatissimum* from the NW African upwelling (Elbrächter 1979). Elbrächter (1979) considered *Gymnodinium spirale* var. *obtusum* sensu Dogiel (the basionym of *G. heterostriatum*) as a synonym of *G. striatissimum*, while he considered that *G. heterostriatum* and *G. striatissimum* to be distinct species (Elbrächter 1994). Takayama (1998) reported scanning electron microscopy pictures of *G. striatissimum*, citing *Gymnodinium spirale* var. *obtusum* and *G. heterostriatum* as synonyms. The shape of the apical groove was an ellipse bisected by a central line (Takayama 1998). The shape of the apical groove agreed with the redefinition of the genus *Gyrodinium* by Daugbjerg et al. (2000). Based on Takayama's observations and without molecular data, Daugbjerg et al. (2000) proposed the new combination *Gyrodinium striatissimum* (Hulburt) Gert Hansen & Moestrup. Elbrächter and Hoppenrath (2009, p. 123) reported "From light microscopical observations of the path of the acrobase we do not agree with the transfer of *G. striatissimum* into the redefined genus *Gyrodinium* by Hansen and Moestrup in Daugbjerg et al. (2000)". Elbrächter (1975) reported a line drawing of the apical groove of *G. heterostriatum* as an open loop. This is unknown in any other heterotrophic dinoflagellate with longitudinal striae. A micrograph of the apical groove has been never reported despite Elbrächter and Hoppenrath (2009) reported that *G. striatissimum* is common in the English Channel and North Sea.

The species reported as *Gymnodinium heterostriatum* or *G. striatissimum* play an important role as grazers in the *Phaeocystis* blooms in the North Sea and the English Channel, and they have been recorded from coastal plankton studies of famous laboratories (e.g. Helgoland, La Jolla, Naples, Plymouth, Woods Hole). Kofoid and Swezy (1921) and Lebour (1925) remarked that *G. heterostriatum* was the most abundant dinoflagellate in the Pacific off La Jolla and the English Channel off Plymouth. However, molecular data of this common and abundant species is missing, and the correct name for this species is a matter of discussion. This study provides the first molecular information of this dinoflagellate and discusses on its taxonomy and synonymy.

MATERIALS AND METHODS

Source, isolation and microscopy observations

Samples were collected during 158 ship trips at two sampling stations between 1997 and 2005 in the NE English Channel off Boulogne sur Mer (SOMLIT-C and SOMLIT-L stations) as described in Gómez and Souissi (2008). Light micrographs are used here to denote the morphological differences between *Gyrodinium spirale* and *Gymnodinium heterostriatum*/*striatissimum*. Recent data were obtained from seawater samples collected with a Niskin bottle at 2 m depth in the Southern North Sea on-board the R/V 'Simon Stevin' (Vlaamse Institut van der Zee-VLIZ) during the JERICO-NEXT/LifeWatch cruise from May 6–9, 2019 (Fig. 1). Seawater samples were preserved with acid Lugol's iodine solution to a final concentration of 4% (vol:vol), and kept refrigerated (~3 ºC). Subsamples were allowed to settle for 24 h on Utermöhl chambers, examined with an inverted microscope (Nikon Eclipse TE2000-S, Tokyo) and photographed with a Nikon Digital Sight DS-2M camera. The position of the nucleus was studied by using the DNA fluorochrome DAPI (4′,6-diamidino-2-phenylindole) under UV excitation in the same microscope.

DNA extraction, PCR amplification and sequencing

For molecular analyses, two isolates collected off Netherlands at 51° 39' 39" N, 3° 25'47" E on May 9th, 2019 (station 50, Fig. 1). At that sampling station, *Gymnodinium heterostriatum*/*striatissimum* reached an abundance of 3000 cells per liter, associated with a bloom of *Phaeocystis globosa* (>10 millions of cells per liter), and seawater surface temperature and salinity of 11.3 °C and 32.9, respectively. The cells were isolated with a fine capillary and placed into a clean chamber filled with autoclaved Milli-Q ultrapure water and treated with small amounts (150–200 µl) of 10% (weight/volume) sodium thiosulfate for removing the iodine. Finally, 30–40 cells were deposited in a 0.2 ml Eppendorf tube filled with absolute ethanol. The 0.2 ml microcentrifuge tubes were briefly centrifuged and then opened to allow the ethanol to evaporate overnight on the benchtop in a covered container. Cells were resuspended in 20 µl extraction buffer (final concentrations: 1 mg ml^{-1} bovine serum albumin, 10 mM Tris pH 7.4, 100 mM KCl, 1 mM EDTA, 50% glycerol). A negative extraction control was 20 µl of extraction buffer in a sterile 0.2 mL microcentrifuge tube. The tubes were frozen at –80 °C for 20 min followed by rapid warming to room temperature for

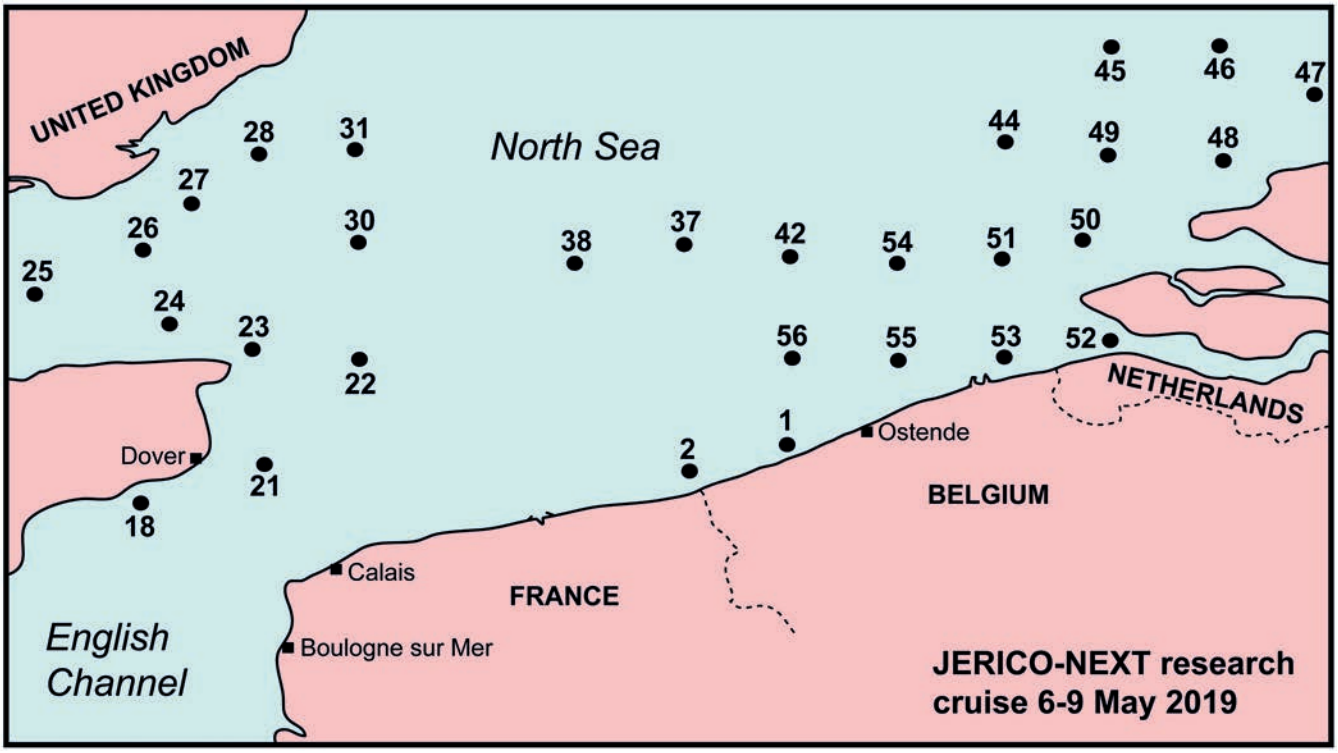

Fig. 1. Map of the sampling stations in the North Sea during the JERICO-NEXT LifeWatch research cruise in May 2019.

20 min. A 2 µl aliquot of the extracted product was used as DNA template for polymerase chain reaction (PCR) amplification. To amplify SSU rRNA gene fragments from the isolate FG1, the primers EukA1 and EukB2 (Table 1) were used in a reaction with GoTaq polymerase (Promega Corp., Madison, WI, USA). For this reaction, the following thermocycler program was performed: initial denaturation at 94 °C for 5 min; 40 cycles of denaturation at 94 °C for 30 s, annealing at 54 °C for 30 s, and extension at 72 °C for 2 min; then final extension at 72 °C for 7 min. For the isolate FG2, the A1/B2 amplification was unsuccessful so a nested approach was taken. An initial PCR was carried out using 2 µl of the extracted DNA and the primer set EukA1/TW14 (Table 1). Conditions for this PCR were the same as before, except that the cycling extension time was lengthened to 3 min. This was followed by nested amplification using 1 µl of the reaction as template and primer set EukA1/B2 (Table 1), using the same cycling conditions with 2 min extension.

To amplify the ITS/5'-LSU rRNA gene region of the isolate FG1, primers ITS1F and TW14 (Table 1) were used with the same conditions as the SSU rRNA gene amplification, with a 2 min extension. For the isolate FG2, 1 µl of the EukA1/TW14 reaction above was re-amplified with the primer set 1200F/TW14. PCR products were cleaned up using the MinElute PCR Purification Kit (Qiagen Inc., Germantown, MD, USA) and directly sequenced at GENEWIZ Inc. (South Plainfield, NJ, USA). Chromatograms were checked and assembled using Sequencher v.5.4.6 (Gene Codes Corp., Ann Arbor, MI, USA), and the contig exported as a FASTA file. While SSU, ITS and LSU rRNA gene sequences were obtained for the isolate FG1, only the SSU rRNA gene sequence was obtained for the isolate FG2. The sequences were deposited in DDBJ/EMBL/GenBank under accession numbers MT67910.2–MT677911.2 and MW000332.

Phylogenetic analyses

The ribosomal RNA gene sequences (small and large subunit rRNA and ITS) of *Gymnodinium heterostriatum*/*striatissimum* were analyzed using Basic Local Search Tool (BLAST, http://blast.ncbi.nlm.nih.gov/Blast.cgi) against the GenBank database. The first 80 closest matches of the complete SSU rRNA gene sequence were environmental sequences, and the first identified sequence belonged to the freshwater species *Gyrodinium helveticum* (GenBank accession number AB120004) with a percentage of similarity of 97.8%. When using a partial sequence, the number of environmental sequences was even higher, and the closest first identified sequence was another sequence (FJ024299) of *G. helveticum* with a percentage of similarity of 99.0%. Based on these results, SSU rRNA gene sequence alignments were constructed from a short selection of the closest environmental sequences and sequence representatives of all the species of the *Gyrodinium* and other dinoflagellates.

The closest matches of the D1–D2 region of the recovered LSU rRNA gene sequence were two environmental sequences misidentified in GenBank as '*Gyrodinium rubrum*' (KT389947, KT389953) from the South China Sea with percentages of similarity of 93.9% and 92.3%, respectively. Although labelled as '18S, ITS and 28S ribosomal RNA gene', the sequences KT389953 and KT389947 only contained 1591 and 589 base pairs (bp), respectively, and they were

Table 1. List of primers used for initial amplification, nested PCR, and sequencing of the isolates of *Gymnodinium heterostriatum*/*striatissimum* from the Dutch North Sea.

Primer name	Sequence (5´-3´)	Use	Reference
EukA1	AAY CTG GTT GAT YCT GCC AG	Initial amplification, sequencing	Modified from Medlin et al. (1988)
EukB2	GAT CCT KCT GCA GG TTC ACC TA	Initial amplification, sequencing	Modified from Medlin et al. (1988)
373F	GAT TCC GGA GAG GGA GCC T	Sequencing	Weekers et al. (1994)
570F	GTA ATT CCA GCT CCA ATA GC	Sequencing	Weekers et al. (1994)
570R	GCT ATT GGA GCT GGA ATT AC	Sequencing	Weekers et al. (1994)
892R	CCA AGA ATT TCA CCT CTG AC	Sequencing	Gast et al. (1994; reverse of 892C)
1200F	CAG GTC TGT GAT GCC C	Nested amplification, sequencing	Weekers et al. (1994)
ITS1F	TCC GTA GGT GAA CCT GCG G	Initial amplification, sequencing	https://nature.berkeley.edu/brunslab/tour/primers.html
TW14	GCT ATC CTG AGG GAA ACT TC	Initial amplification, sequencing	https://nature.berkeley.edu/brunslab/tour/primers.html

not useful for the SSU rRNA gene phylogeny. The misidentified environmental sequences KT389947 and KT389953 are included because they are closely related to our new sequences. In contrast, other misidentified environmental sequences from the same study (KT390093, KY399897, KT390002) are excluded because they are distantly related to our new sequences and their misidentified names induce confusion. The first documented sequences were *Gyrodinium helveticum* (MG255302–3) with a percentage of similarity of 91.5%. Based on these results, LSU rRNA gene sequence alignments were constructed with sequences representatives of all the available species of the genus *Gyrodinium*, and other dinoflagellates.

A phylogenetic tree based on the Internal Transcriber Spacer (ITS) marker was not useful due to the small number of available sequences, and all corresponded to the same isolates already included in the LSU rRNA gene phylogeny. SSU- and LSU rRNA gene sequence alignments were accomplished by ClustalW (Larkin et al. 2007) and the evolutionary history was inferred by using the Maximum Likelihood method using the General Time Reversible substitution model with Gamma distributed rate variation among sites (GTR+G) in MEGA7 software (Kumar et al. 2016). Bootstrap values were obtained after 1000 replications. The sequences of the syndinean *Syndinium turbo* and the perkinsid *Perkinsus marinus* were used for rooting the SSU- and LSU rRNA gene phylogenetic trees, respectively.

RESULTS

Morphological observations

The blooms of *Phaeocystis globosa* dominated the spring phytoplankton during the routine phytoplankton monitoring surveys in the NE English Channel off Boulogne sur Mer from 1997 to 2004. A large fusiform dinoflagellate, *Gyrodinium spirale*, was occasionally found feeding on colonies of *Phaeocystis* (Fig. 2A–B). However, *G. spirale* reached higher abundances in early summer, after the *Phaeocystis* bloom, and it fed preferentially on diatoms. A second unarmored dinoflagellate, often mistaken with deformed cells of *G. spirale*, was more commonly found associated with the *Phaeocystis* blooms. It fed on individual cells of *Phaeocystis*, and occasionally on diatoms (Fig. 2C–F). It is abundant in the preserved samples, but few cells were observed when live plankton replicates are examined and they easily lysed (Fig. 2G–H). This evidences that the cells were lost due to the transport and sample treatment. In addition, the observations are difficult due to

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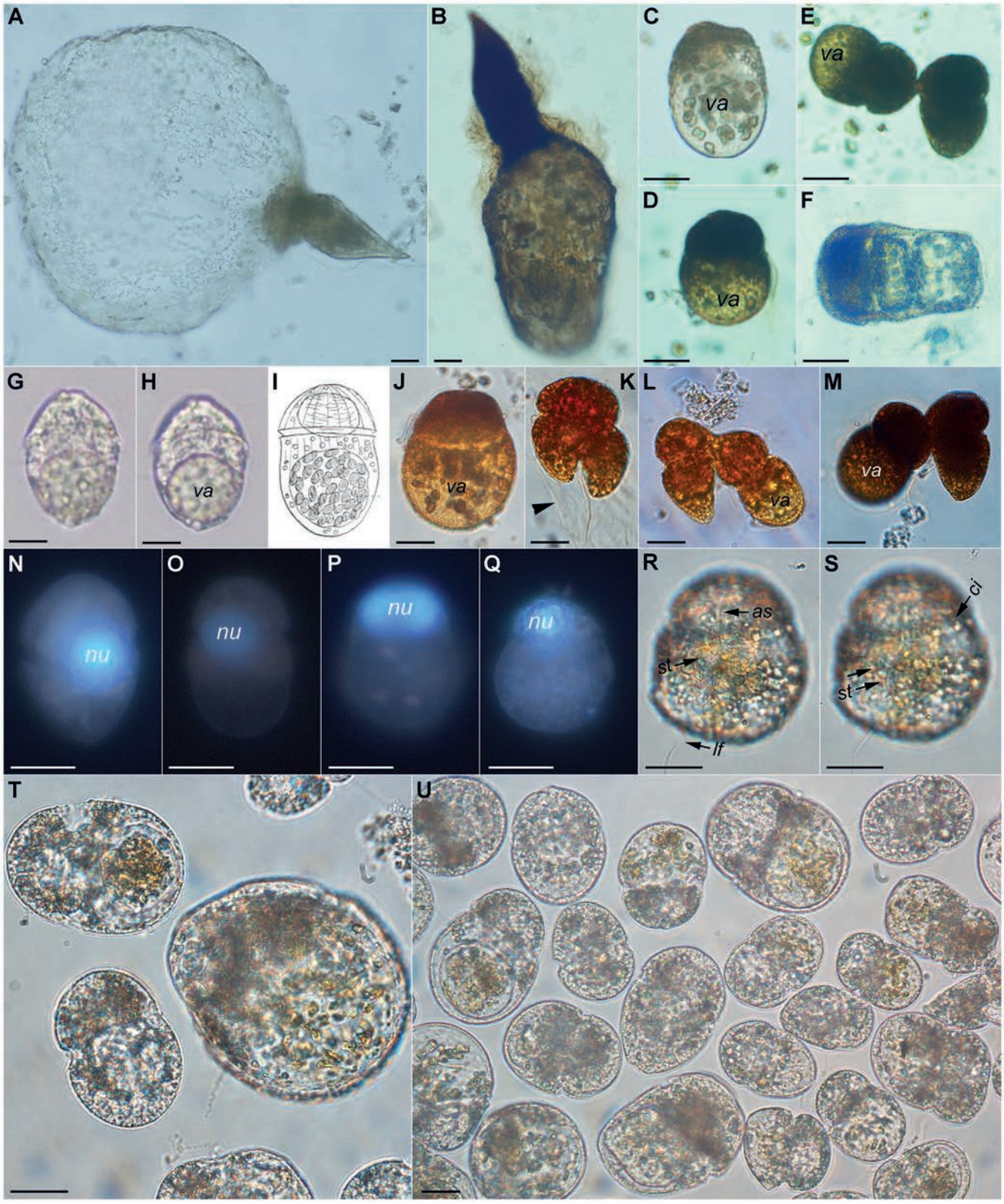
Fig. 2. Images of *Gyrodinium spirale* (A–B) and *Gymnodinium heterostriatum* (C–U). (A–F, J–U) Lugol's solution preserved cells. (G–H). Live cells. (A–B) *Gyrodinium spirale* feeding on colonies of *Phaeocystis globosa* from the NE English Channel in spring of 2004. (C–H) *Gymnodinium heterostriatum* from the NE English Channel. (C–D) Individuals feeding on individual cells of *Phaeocystis*. (E) Recently divided individual. (F) Individual feeding on the diatom *Detonula pumila*. (G–H) Two views of a live cell. (I) *Gymnodinium heterostriatum* reproduced from Lebour (1917, 1925). (J–U) *Gymnodinium heterostriatum* from the North Sea in May 2019. (J) Note the large vacuole in the hyposome. (K) The arrowheads indicate filaments that emerged from hyposome. (K–M) Dividing cells. (N–Q) Epifluorescence micrographs showing the position of the nucleus stained with DAPI. (R–S) Ventral view. The arrow indicates the sulcus that extended into the apex. Longitudinal striae were hardly visible in the preserved individuals. (T–U) Note the differences in size and shape. These individuals were isolated for molecular analyses. *as* = anterior extension of the sulcus in the episome; *ci* = cingulum; *lf* = longitudinal flagellum; *nu* = nucleus; *va* = food vacuole; *st* = longitudinal striae. Scale bar = 20 µm.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the high abundance of the surrounding cells of *Phaeocystis*. The live cells showed a more pointed apex than the preserved cells (Fig. 2G–H). This dinoflagellate identified as *Gymnodinium heterostriatum*/*striatissimum* since the earlier studies in the region (Fig. 2I). It can be distinguished from *G. spirale* because its episome is smaller than the hyposome, it has a smaller cell size (30–70 µm long, 25–60 µm wide), very low cingular displacement and the absence of pointed apices. The hyposome was almost spherical when a large vacuole was present (Fig. 2C–D). During the cruise in the southern North Sea in May 6–9th, 2019, this dinoflagellate was associated with a bloom of *Phaeocystis globosa*. *Gymnodinium heterostriatum*/*striatissimum* reached the highest abundances off the Dutch estuaries (Rhine, Westerschelde) and off northern Belgium (sampling stations 49–56, Fig. 1) with abundances ranging from 500 to 3000 cells per liter.

The most common morphology was an ellipsoidal cell, with an almost spherical hyposome occupied by a vacuole containing individual cells of *Phaeocystis globosa* (Fig. 2J). Some individuals showed long thin filaments that emerged from the hyposome (Fig. 2K). Cell division began in the hyposome and the daughter cells remained attached by the episome before the split. One of the daughter cells received the round hyposome of the mother cell often still containing the prey, and the other daughter cell regenerated a new hyposome that showed a conical shape (Fig. 2K–M). The nucleus was located at the level of the cingulum (Fig. 2N–O), or in the episome due to the displacement by the large food vacuole in the hyposome (Fig. 2R–U). In ventral view, the cells showed very low cingular displacement, and the sulcus extended towards the apex (Fig. 2R). Longitudinal striae were present, but they were hardly visible in these preserved individuals (Fig. 2S). The cell shape and size were highly variable, but generally, the cell shape was ellipsoidal when the vacuole was empty, while almost spherical when a large vacuole was formed (Fig. 2T–U).

Molecular phylogeny

The two SSU rRNA gene sequences from the two isolates were identical (100%) and closely related to more than 100 environmental sequences available in GenBank. These environmental sequences were from samples collected off Los Angeles (California), South China Sea, Sargasso Sea, off NW Africa upwelling, Atlantic coasts of North America at North Carolina or Nova Scotia, among other locations, and they clustered together with the sequence of *Gymnodinium heterostriatum*/*striatissimum* with full support (100%) (Fig. 3). This clade formed a sister group with sequences of the freshwater species *Gyrodinium helveticum* (Penard) Y. Takano & Horiguchi isolated from lakes in Japan and Russia, and environmental sequences from North American lakes (Fig. 3).

In the LSU rRNA gene sequence phylogeny, the sequence of *Gymnodinium heterostriatum*/*striatissimum* clustered with two environmental sequences from the South China Sea (KT389947, KT389953) mislabeled as '*Gyrodinium rubrum*' and documented sequences of *Gyrodinium helveticum* from the lake Baikal in a more basal position. This clade formed a sister group of a clade of marine species of *Gyrodinium* Kofoid & Swezy (*G. jinhaense* S.H. Jang & H.J. Jeong, *G. moestrupii* E.Y. Yoon, N.S. Kang & H.J. Jeong, and *G. dominans* Hulburt) (Fig. 4). In the SSU- and LSU rRNA gene phylogenies, the sequences of *Gymnodinium heterostriatum*/*striatissimum* clustered within the clade of type species of *Gyrodinium*, *G. spirale*, and distantly related to the type species *Gymnodinium* F. Stein, *G. fuscum* F. Stein (Figs. 3–4).

DISCUSSION

Environmental sequencing and barcoding surveys reveal that species of the genus *Gyrodinium* are abundant and widespread in the world oceans, but numerous sequences cannot be assigned at the species level due to the lack of molecular data for identified species (Terrado et al. 2009, Christaki et al. 2017). The numerous environmental sequences similar to the sequences of *Gymnodinium heterostriatum*/*striatissimum* reveal that this species is ubiquitous, and potentially abundant, in the world oceans (Fig. 3). For example, several tens of environmental sequences are from the coasts of Southern California, where Kofoid and Swezy (1921: 222) reported that this species was the most abundant unarmored dinoflagellate. Despite being a common and abundant species, accessible near the specialized laboratories, this species has received little attention, and until now, molecular data were not available. The closer relative of *Gymnodinium heterostriatum*/*striatissimum* is *Gyrodinium helveticum*, a species first described from Switzerland (Penard 1891), with documented DNA sequences from a lake in Japan (Takano and Horiguchi 2004), from Lake Baikal (Annenkova et al. 2009, Annenkova 2018) and environmental sequences from

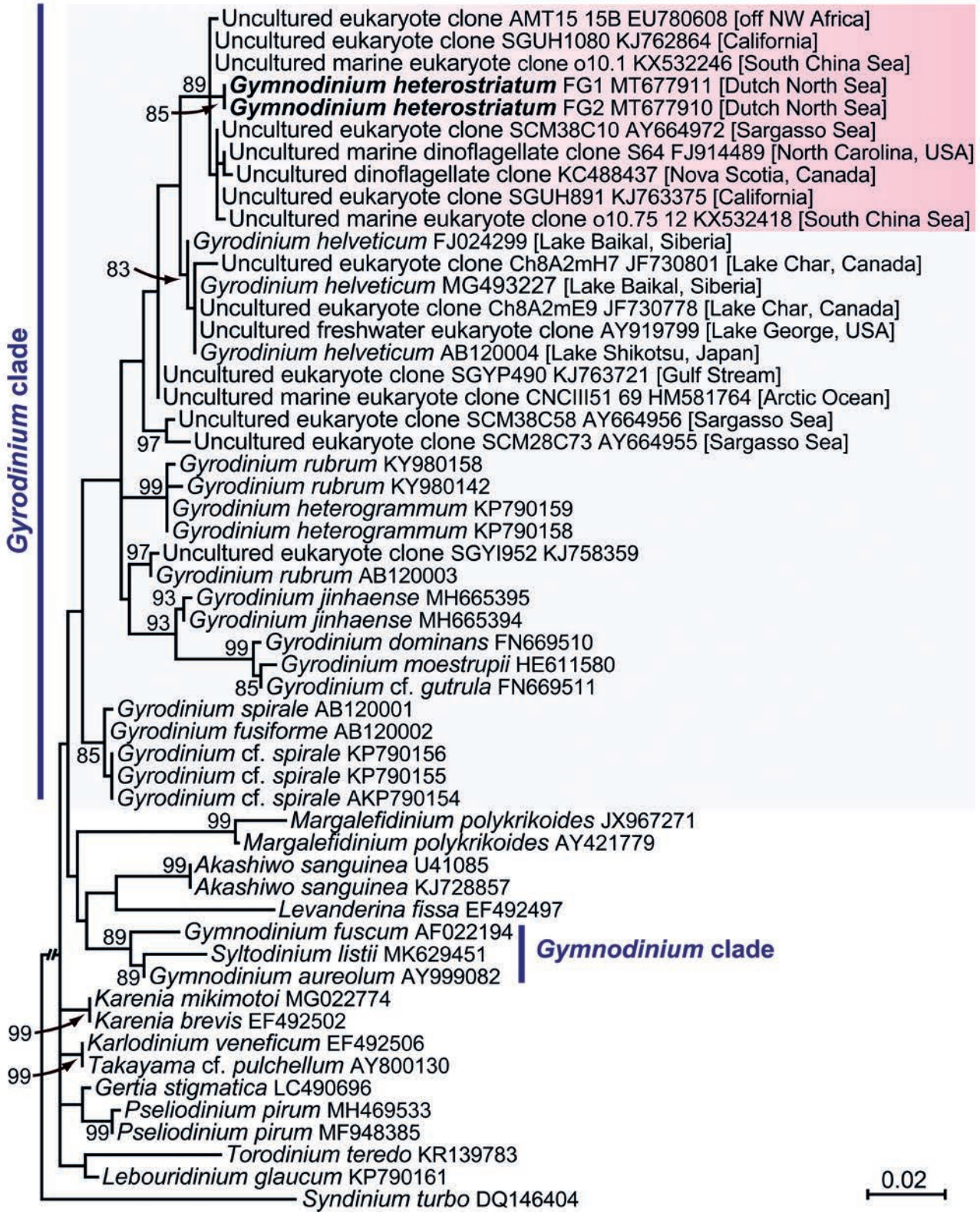

Fig. 3. Phylogenetic tree based on SSU rRNA gene sequences, showing the position of the sequences of *Gymnodinium heterostriatum/striatissimum* by Maximum Likelihood (ML). The new sequences are indicated in bold face. Numbers near branches denote ML bootstrap probability value. Bootstrap values <70 are omitted. The geographic origin is placed between brackets. Scale bar denotes 0.02 substitutions per site.

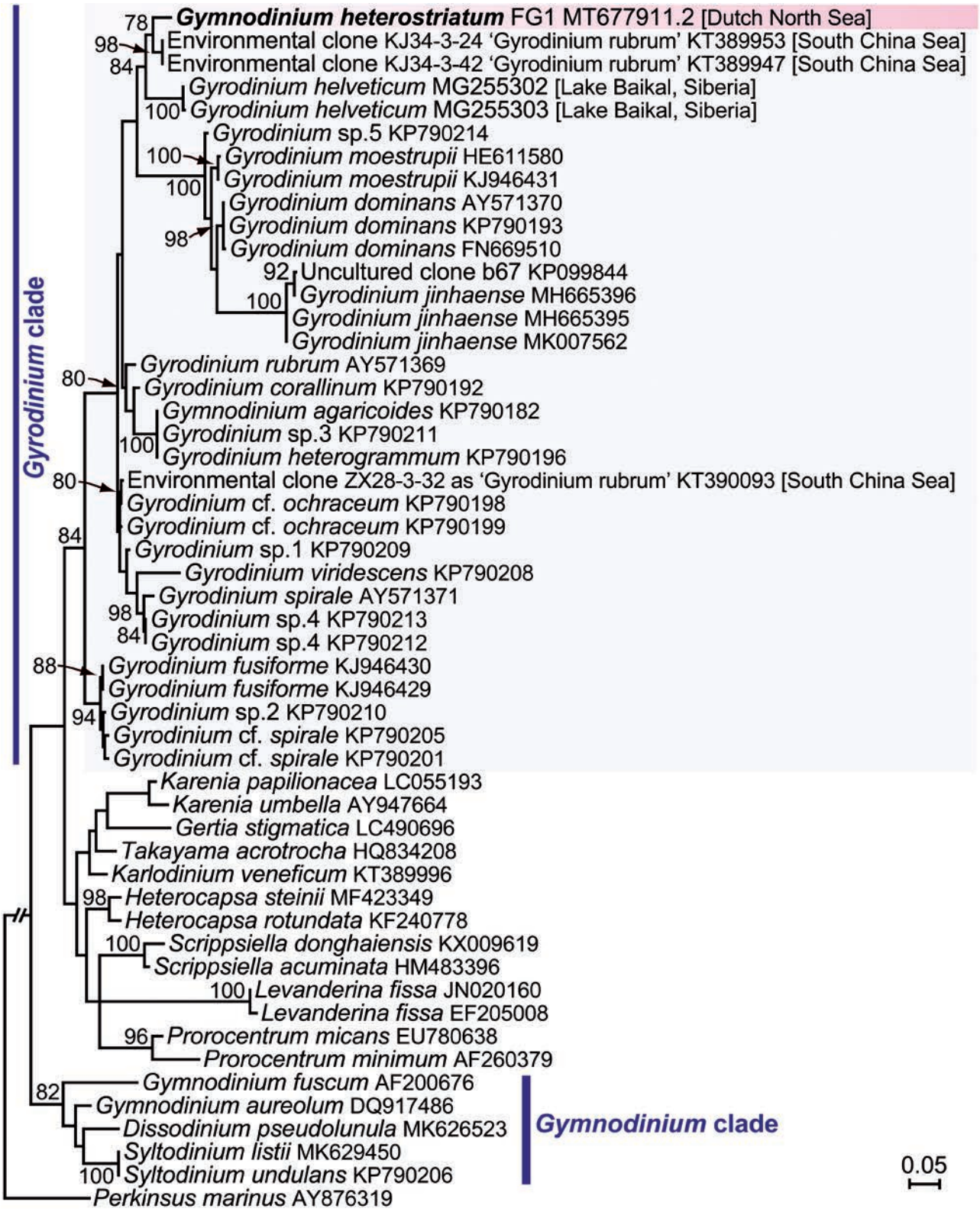

Fig. 4. Phylogenetic tree based on LSU rRNA gene sequences, showing the position of the sequence of *Gymnodinium heterostriatum/striatissimum* by Maximum Likelihood (ML). The new sequence is indicated in bold face. Numbers near branches denote ML bootstrap probability value. The geographic origin is placed between brackets. Bootstrap values <70 are omitted. Scale bar denotes 0.05 substitutions per site.

lakes in North America (Fig. 3). This is an example of the infrequent marine-freshwater transitions in the microbial world (Logares et al. 2009).

The shape of the groove of *Gymnodinium heterostriatum*/*striatissimum* is an ellipse bisected by a central line that together to the surface longitudinal striae (Takayama 1998). This is a diagnostic characteristic of the type species of the genus *Gyrodinium*, *G. spirale*, and other congeners. Based on these morphological observations, Daugbjerg et al. (2000) proposed the new combination *Gyrodinium striatissimum* (Hulburt) Gert Hansen & Moestrup. The generic assignation of this species in the genus *Gyrodinium* is clear based on the morphology, and confirmed by the molecular data (Figs. 3, 4). However, the discrepancies are in the priority for the use of the species epithet 'heterostriatum' or 'striatissimum'.

When using the species epithet 'striatissimum', we are attributing the species name to a relatively recent description (Hulburt 1957), while this taxon was probably already described in earlier studies (Dogiel 1906; Lebour 1917, 1925; Kofoid and Swezy 1921, Kofoid 1931, Wailes 1939). This taxon is prone to be described with distinct species names because it shows important differences in size and shape, often deformed by a large vacuole, and the nucleus is located in different positions. In addition, the information on the longitudinal striae vary among the authors because they are hardly visible, depending on the optical resources available and whether observations are made of healthy live cells or preserved material. An extended account of the taxonomy and illustrations of *G. heterostriatum*/*striatissimum* in the literature is reported the Appendix S1 as Supplementary Material.

There is an agreement among authors that the first record of this taxon corresponded to the species identified as *Gymnodinium spirale* var. *obtusum* in Dogiel (1906). Dogiel already noted the morphological variability, and he reported the species with different shapes and sizes. Kofoid was a splitter taxonomist, admitting little intraspecific variability, often describing new species from the observations of one or few individuals, and proposing new species based on the illustrations by other authors (Kofoid and Swezy 1921, Kofoid 1931). However, in this case Kofoid admitted that all Dogiel's illustrations corresponded to a single species. Kofoid and Swezy (1921: 222) remarked that Dogiel's *Gymnodinium spirale* var. *obtusum* was the most abundant species in their samples, and consequently they had the opportunity to realize of the intraspecific morphological variability. Kofoid and Swezy (1921) noted that Dogiel's illustrations did not correspond to *Gymnodinium spirale* var. *obtusum* as originally described in Schütt (1895), and they proposed two distinct species: *Gyrodinium obtusum* (F. Schütt) Kofoid & Swezy for *G. spirale* var. *obtusum* F. Schütt, and the new name *Gymnodinium heterostriatum* Kofoid & Swezy, citing as basionym *Gymnodinium spirale* var. *obtusum* in Dogiel (1906). Beyond a reproduction of two Dogiel's illustrations as '*Gymnodinium heterostriatum* nom. sp. nov.', Kofoid and Swezy (1921) reported original illustrations showing the morphological variability of this taxon: a line drawing in the main text and two colored pictures (see Appendix S1 as Supplementary Material). When in the earlier descriptions, an author illustrated the morphological variability of a taxon, other authors may interpret that the illustrations belong to distinct species. The article 7.3 of I.C.N. states: 'A new combination or a name at new rank (Art. 6.10) is typified by the type of the basionym even though it may have been applied erroneously to a taxon now considered not to include that type (but see Art. 48.1)'. This means that independently of the identity of the species illustrated as *G. heterostriatum* in Kofoid and Swezy (1921), the species reported as *G. spirale* var. *obtusum* in Dogiel (1906) is, in fact, *Gymnodinium heterostriatum* Kofoid & Swezy.

Hulburt (1957) described the new species *Gymnodinium striatissimum* in the Atlantic near Woods Hole. Hulburt's figure 5 shows a high similarity to the figure 56 of *G. heterostriatum* in Kofoid and Swezy (1921, plate 4). The only significant difference is the positon of the nucleus, which is variable in this species because it can be displaced by the food vacuole (Fig. 2N–Q). Hulburt (1957) did not compare his new species with *G. heterostriatum.*

Elbrächter (1979) reported *Gymnodinium spirale* var. *obtusum* in Dogiel (1906) as a synonym of *Gymnodinium striatissimum*. However, Elbrächter (1979, 1994) and Elbrächter and Hoppenrath (2009) considered that *Gymnodinium heterostriatum* and *G. striatissimum* were distinct species. This is incoherent because if *G. spirale* var. *obtusum* sensu Dogiel is a synonym of *G. striatissimum*, then *G. striatissimum* and *G. heterostriatum* are forced to be synonyms because *G. spirale* var. *obtusum* sensu Dogiel is the basionym of *G. heterostriatum*. Elbrächter (1994) reported micrographs of a taxon identified as *Gymnodinium heterostriatum*. Kofoid reported that *G. heterostriatum* is a common unarmored dinoflagellate, and consequently it should

be expected that other authors would find it. In contrast, Elbrächter (1994) reported that *G. heterostriatum* is a rare species only previously known from Kofoid's records (Kofoid and Swezy 1921, Kofoid 1931). However, the individuals illustrated by Elbrächter (1994) were larger (106 µm long) than *G. heterostriatum* (< 70 µm long), and they showed a more elongated shape and acute hyposome. The morphology of Elbrächter's *G. heterostriatum* is closer *Gymnodinium multilineatum* Kofoid & Swezy that is a rare species.

The synonymy proposed by Elbrächter (1979) influenced further authors. For example, Takayama (1998: 121) identified the species as *G. striatissimum*, and he cited *G. spirale* var. *obtusum* in Dogiel 1906 and *G. heterostriatum* as synonyms. The principle of priority was not followed when the name *G. heterostriatum* proposed in 1921 is a posterior synonym of *G. striatissimum* Hulburt 1957. Based on Takayama's observations, Daugbjerg et al. (2000) transferred *G. striatissimum* into *Gyrodinium*. This means that Daugbjerg et al. were giving the priority to *G. striatissimum* over *G. heterostriatum*, or accepting two independent species.

The taxon that we have observed and sequenced from the North Sea is most probably the same taxon first reported as *G. spirale* var. *obtusum* in the Gulf of Naples (Dogiel 1906), reported as *G. heterostriatum* in the English Channel (Lebour 1925, Dodge 1982, Paulmier 1992) and the North Sea (Drebes 1974, Elbrächter 1975), *Gymnodinium striatissimum* (Elbrächter 1979, Elbrächter and Hoppenrath 2009) or *Gyrodinium striatissimum* (Daugbjerg et al. 2000). If *G. heterostriatum* Kofoid & Swezy 1921 and *G. striatissimum* Hulburt 1957 are synonyms, the priority is for *G. heterostriatum*, and a new combination in the genus *Gyrodinium* with the epithet 'heterostriatum' is needed. Even, if *G. heterostriatum* and *G. striatissimum* are not considered synonyms, the species that we have observed and sequenced from the North Sea is the taxon first described as *G. spirale* var. *obtusum* in Dogiel (1906) that is the basionym of *G. heterostriatum*. In any case, *Gymnodinium heterostriatum* needs to be placed into the genus *Gyrodinium*.

Gyrodinium heterostriatum (Kofoid & Swezy 1921) F. Gómez, Artigas & Gast, comb. nov.

Basionym: *Gymnodinium spirale* var. *obtusum* in Dogiel (1906, *Mitt. Zool. Sta. Neapel* 18: 38–43, plate 2, figs. 50–56).

Synonyms: *Gymnodinium rhomboides* F. Schütt 1895 in Lebour (1917, figure 6c, e); *Gymnodinium heterostriatum* Kofoid & Swezy (1921, nom. nov. pro *Gymnodinium spirale* var. *obtusum* in Dogiel 1906; text-fig. M; text-fig. Y7; plate 2, figure 24; plate 5, figure 56); *Gymnodinium hyalinum* M. Lebour 1925; *Gymnodinium striatissimum* Hulburt 1957; *Gyrodinium striatissimum* (Hulburt) Gert Hansen & Moestrup 2000; *Gymnodinium lucidum* D. Ballantine in Parke & Dixon 1964 (nom. nov. pro *G. hyalinum* M. Lebour 1925).

Non *Gymnodinium hyalinum* A.J. Schilling 1891; nec *Gymnodinium obtusum* var. *spirale* F. Schütt 1895; nec *Gyrodinium obtusum* (F. Schütt 1895) Kofoid & Swezy 1921; nec *Gymnodinium rhomboides* Schütt sensu Lebour 1917, figs. 6a–b, d; nec *Gymnodinium heterostriatum* Kofoid & Swezy 1921 sensu Elbrächter 1994 (=*Gymnodinium multilineatum* Kofoid & Swezy).

Supporting information

Appendix S1. Historical account of *Gymnodinium heterostriatum* and allied species names available on the journal's website.

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Supplementary Material

Phylogeny and synonymy of *Gyrodinium heterostriatum* comb. nov. (Dinophyceae), a common unarmored dinoflagellate in the world oceans

F. Gómez, L.F. Artigas, R.J. Gast

Appendix S1. Historical account of *Gymnodinium heterostriatum* and allied species names

Schütt (1895) described *Gymnodinium rhomboides* without diagnosis and lacking information on the geographical origin of the species. In most of the cases, the information on the taxa reported by Schütt was restricted to illustrations and figure legends. He reported two illustrations. The line drawing of the figure 63.1 illustrated the dorsal view of a biconical -rhomboidal-cell, with a median cingulum and a similar number of longitudinal striae in the episome and hyposome. The line drawing of the figure 63.2 showed same individual in ventral view. The cell is ovate, with a slight cingular displacement. In the figure legend, Schütt (1895, p. 163) explained that the illustration corresponded to the same individual inflated before the cell lysis. Later, Paulsen (1907, 1908) reproduced the Schütt's illustration 63.1 and he added a cell length of 47 µm.

From the North American Atlantic Ocean at Woods Hole, Calkins (1901, p. 429) described *Gymnodinium gracile* var. *sphaericum*. He illustrated a spherical cell (68 µm long, 55 µm wide) with a premedian cingulum, low cingular displacement, with an extension of the sulcus in the episome, smooth cell surface, nucleus in the episome and food vacuoles in the hyposome. Kofoid and Swezy (1921, p. 258–9) ranked the variety at the species level as *G. sphaericum* (Calkins) Kofoid & Swezy. They also reported their own observations and they remarked that the species lacked surface striation. They reported similar characters that the original description, and other colored pictures of the cell enclosed in a hyaline membrane, and with red corpuscles. Despite Calkins (1901, p. 429) reported that *G. sphaericum* is common, the species has almost disappeared from the literature, even in further studies of the unarmored dinoflagellate near Woods Hole (Hulburt 1957). Wood (1963) reported a very sketchy illustration of a cell with a median cingulum identified as *G. sphaericum*. The relationship with *Gymnodinium heterostriatum* is discarded because there is no evidence of longitudinal striae.

From the Gulf of Naples, Dogiel (1906) reported several illustrations of a species identified as *Gymnodinium spirale* var. *obtusum*, a variety name proposed by Schütt (1895). Dogiel (1906) illustrated the intraspecific morphological variability with the cell shape that changed from conical to hemispherical. The cingulum was median or premedian with a low cingular displacement. The nucleus was located in the center, or anterior in the episome when displaced by a large vacuole. The cell showed more longitudinal striae in the hyposome than in the episome. Schütt (1895) described the variety *Gymnodinium spirale* var. *obtusum* for a cell with a high cingular displacement. Unequivocally, Dogiel's species does not correspond to Schütt's *Gymnodinium spirale* var. *obtusum*. Kofoid and Swezy (1921) ranked the Schütt's variety at the species level as *Gyrodinium obtusum* (F. Schütt) Kofoid & Swezy, and they considered that *Gymnodinium spirale* var. *obtusum* sensu Dogiel (1906) as an distinct species, proposing the new species name *Gymnodinium heterostriatum* Kofoid & Swezy and citing Dogiel's species as basionym.

In the English Channel off Plymouth, Lebour (1917) reported several illustrations of a species identified as *Gymnodinium rhomboides* F. Schütt. Lebour (1917, p. 190) reported "Dogiel's species probably belongs to

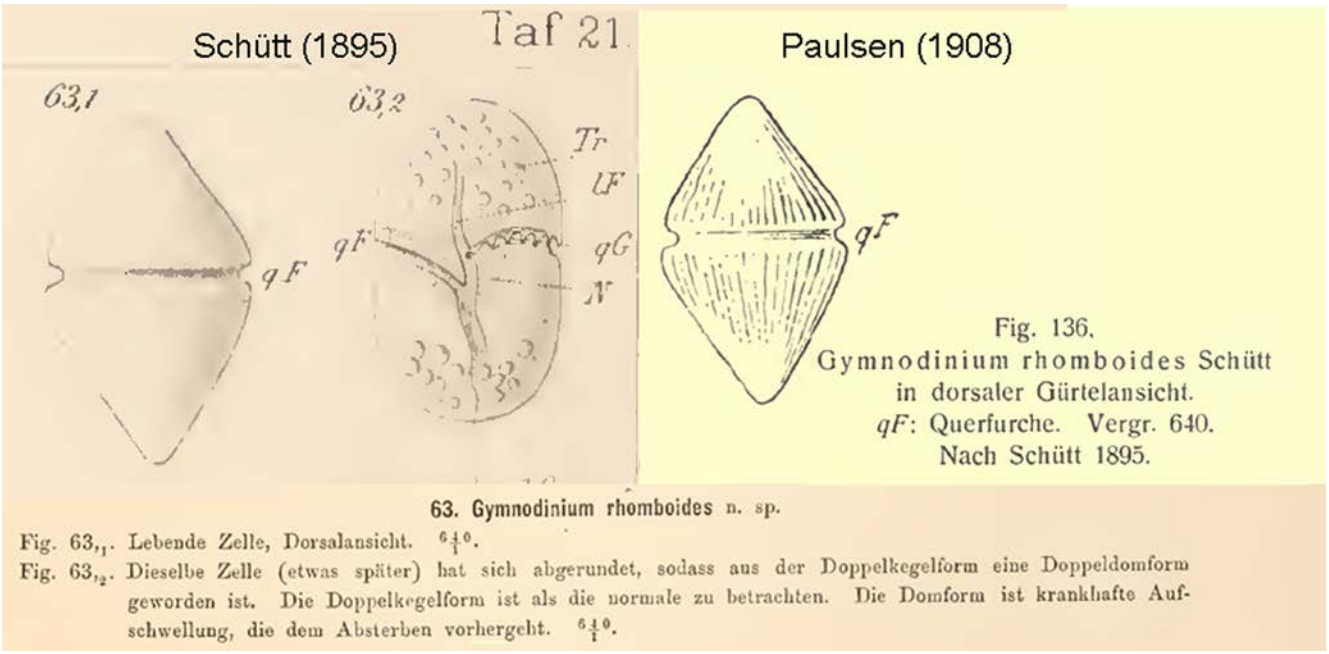

Fig. 1.

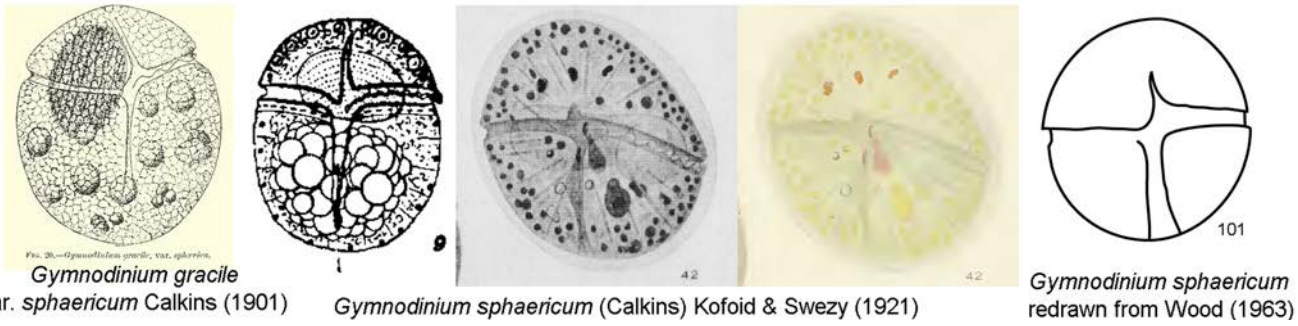

Fig. 2.

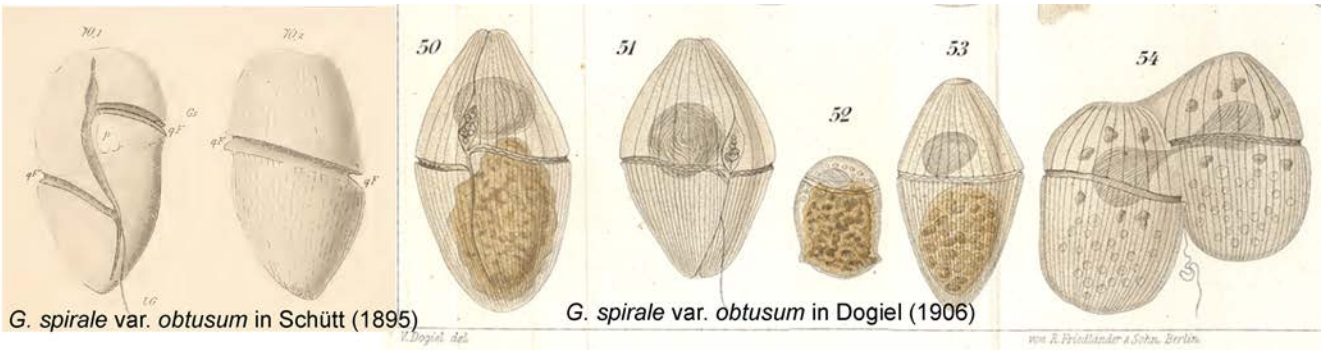

Fig. 3.

G. rhomboides or else some closely related form". She reported five illustrations (her figures 6a–e). In the figures 6a–b, the cells were bi-conical, with acute apices, a median cingulum with undulated cingular lists and more or less similar number of striae in the episome and hyposome. In the figure 6d, the individual ingested a centric diatom and the hyposome was rounded. The individuals of the figures 6a,b,d fit well with Schütt's figure 63.1 of *G. rhomboides*. In contrast, Lebour's figures 6c and 6e showed individuals with an ellipsoidal shape, rounded apices, premedian cingulum, anterior nucleus, and more longitudinal striae in the hyposome than in the episome. Her individuals showed a large vacuole with cells of *Phaeocystis* in the hyposome. Lebour (1917, p. 190, 192) reported for *Gymnodinium rhomboides* "one of the commonest in this area appears to be the species figured by Schütt (1895)...Certain aspects of my specimens agree very closely with Schütt's figures, I have therefore taken the name given by him rather than create a new one… This is perhaps the commonest gymnodinian...".

Lebour (1917) described *Gymnodinium triangulare* M. Lebour from the observation of a single individual. It fed on *Phaeocystis* as her *Gymnodinium rhomboides* (her figure 6c, e), but the hyposome was deformed giving a triangular appearance, while the cells ellipsoidal in the view of other illustration. Kofoid and Swezy (1921, p. 263) reported: "The form figured by Lebour (1917b) as *G. triangulare* is evidently a mutilated specimen. The posterior part of the body is frequently deformed... This is often the result of the extrusion of a large food mass... This process was often followed by us, particularly in *Gymnodinium heterostriatum*". The assumption of Kofoid and Swezy is based on that these unarmored dinoflagellates largely deformed with the ingestion or egestion of the contents of the large vacuoles. This suggests that Lebour observed many individuals of this common dinoflagellate feeding on *Phaeocystis*, and she described a new species from a single individual that was deformed. The species name *Gymnodinium triangulare* appears as an alternative name for the species illustrated as *G. rhomboides* in Lebour's figure 6c, e. However, it is difficult to assure that *G. triangulare* corresponded to *G. heterostriatum* because morphological data such as the presence of longitudinal striae was unreported.

Lebour (1925) modified some of the identifications that she did in 1917. She maintained the name *Gymnodinium rhomboides* for the biconical cells with a median cingulum in her plate 6, figures 1a–c. In the figure 1a, Lebour added the nucleus is the middle of the cell. In the figure 1c, she illustrated a more robust cell inside a hyaline membrane. Lebour (1925) copied the figure 6c in Lebour (1917), but then she replaced the identification as *G. rhomboides* by the name *G. heterostriatum* that Kofoid & Swezy (1921) proposed for *G. spirale* var. *obtusum* sensu Dogiel (1906).

In the plate 6, figure 3, Lebour (1925) illustrated the new species *Gymnodinium hyalinum* M. Lebour 1925. It strongly resembles the individuals of *G. heterostria-*

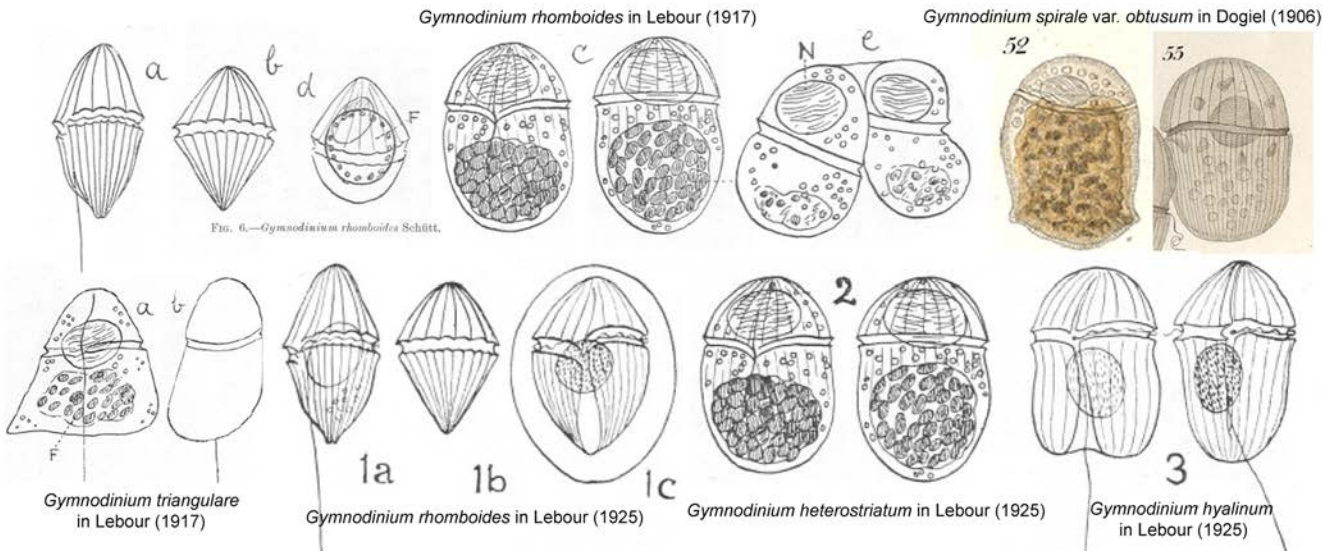

Fig. 4.

tum in her figure 2, but missing the large food vacuole. The cingulum is premedian, the nucleus is now located in the hyposome. The species name *Gymnodinium hyalinum* A.J. Schilling 1891 was already used for a freshwater dinoflagellate. Despite Lebour (1925) reported Schilling (1913) and Kofoid and Swezy (1921) in the cited literature, apparently, she did not realize about the homonymy. Years later, the new name *Gymnodinium lucidum* D. Ballantine was proposed for *Gymnodinium hyalinum* M. Lebour 1925 to solve the homonymy (Parke and Dixon 1964).

Kofoid and Swezy (1921, p. 173) reported *Gymnodinium triangulare* in the list of *incertae sedis* due to the lack of sufficient data, and later reported in page 263 "The form figured by Lebour (1917b) as *G. triangularis* is evidently a mutilated specimen". Later, Lebour (1925, p. 50) reported for *Gymnodinium triangulare* M. Lebour 1917: "A triangular species supposed by Kofoid and Swezy to be malformed. Not sufficiently defined".

Kofoid and Swezy (1921) reported *Gymnodinium rhomboides*, the new name *G. heterostriatum* for *G. spirale* var. *obtusum* sensu Dogiel (1906), and several related species with longitudinal striae and low cingular displacement such as *G. multistriatum* Kofoid & Swezy and *G. multilineatum* Kofoid & Swezy. Kofoid and Swezy (1921) reported *G. rhomboides* without own observations. Kofoid and Swezy (1921, p. 249) reported: "*G. rhomboides*, Lebour (1917b), pp. 183, 190, 191, fig. 6. In part, includes *G. fissum*". This is confusing because the Lebour's figure 6 does not resemble *Gymnodinium fissum*. Kofoid and Swezy (1921, p. 170) reported that the species *G. spirale* var. *striatum*, Pouchet 1883 described from Brittany is *Gyrodinium fissum* Kofoid & Swezy, while in page 300 they proposed *Gyrodinium fissum* (Levander 1894) Kofoid & Swezy and they cited as an earlier description *Gymnodinium spirale* var. D by Pouchet (1883, fig. K). The illustrations of Lebour (1917) are not related to the species described by Levander (1894) as *Gymnodinium fissum* neither *Gymnodinium spirale* var. D Pouchet (1883, fig. K). Pouchet (1883) did not illustrate *G. spirale* var. *striatum*.

Kofoid and Swezy (1921) described the new species *Gymnodinium multilineatum* as an elongated cell, with low cingular displacement, and more striae in the hyposome than in the episome. The larger size (108 µm long, Table 1), cell elongation and the pointed apices are important differences with *G. heterostriatum*, which suggest two distinct species. The other species, *G. multistriatum*, has a higher cingular displacement and acute apices.

As reported above, Kofoid and Swezy (1921) proposed the new species name *Gymnodinium heterostriatum* for *Gymnodinium spirale* var. *obtusum* in Dogiel (1906, figs. 50–56). Kofoid and Swezy (1921, p. 222) reported: "It was the most abundant species of the Gymnodinioidae in plankton examined by us". They provided four illustrations in different locations of their monograph of the unarmored dinoflagellates. Kofoid and Swezy (1921, p. 70) reproduced Dogiel's figures 54 and 55 of *G. spirale* var. *obtusum* under the name *G. heterostriatum* nom. sp. nov. The other three illustrations were original (text-fig. Y7; plate 2, figure 24; plate 5, figure 56).

In the Atlantic near Woods Hole, Hulburt (1957) studied the unarmored dinoflagellates. He did not report the species *Gymnodinium sphaericum* (Calkins) Kofoid & Swezy that Calkins (1901) described as common in the region. Hulburt (1957) described the new species *G. striatissimum* for species with a median cingulum and the nucleus in the hyposome. Hulburt reported: "*Gymnodinium striatissimum* is similar in different number of striations on epicone and hypocone to the much larger *G. multistriatum*, *G. rubrum*, and *G. translucens* (Kofoid and Swezy 1921)". Hulburt did not compare his new species with the original illustrations of *G. heterostriatum* in Kofoid and Swezy (1921). Hulburt's figures 5 and 6 showed a high similarity with *G. heterostriatum* in the figures 56 and 24 in Kofoid and Swezy (1921), respectively. The only significant difference is the position of the nucleus, but it often changed the position displaced by the food vacuole. This evidences that *Gymnodinium heterostriatum* as illustrated by Kofoid and Swezy (1921) is co-specific with *G. striatissimum* Hulburt 1957.

Schiller (1933, p. 371) reproduced one of the illustrations of *G. heterostriatum* in Kofoid and Swezy (1921), and the two Lebour's illustrations of *G. heterostriatum*. Wailes (1939) illustrated *G. multistriatum* and *G. heterostriatum* from the Canadian Pacific. Wood (1963, 1968) reported line illustrations of cells from Australia and Caribbean Sea, but his line drawings are very sketchy. His illustration of *G. heterostriatum* showed a cell with some cingular displacement and a more acute hyposome.

Elbrächter (1975) reported line drawings of *Gymnodinium heterostriatum* from the North Sea, including a view of the apical groove as an open loop. Elbrächter (1975) reported as basionym *Gymnodinium spirale* var.

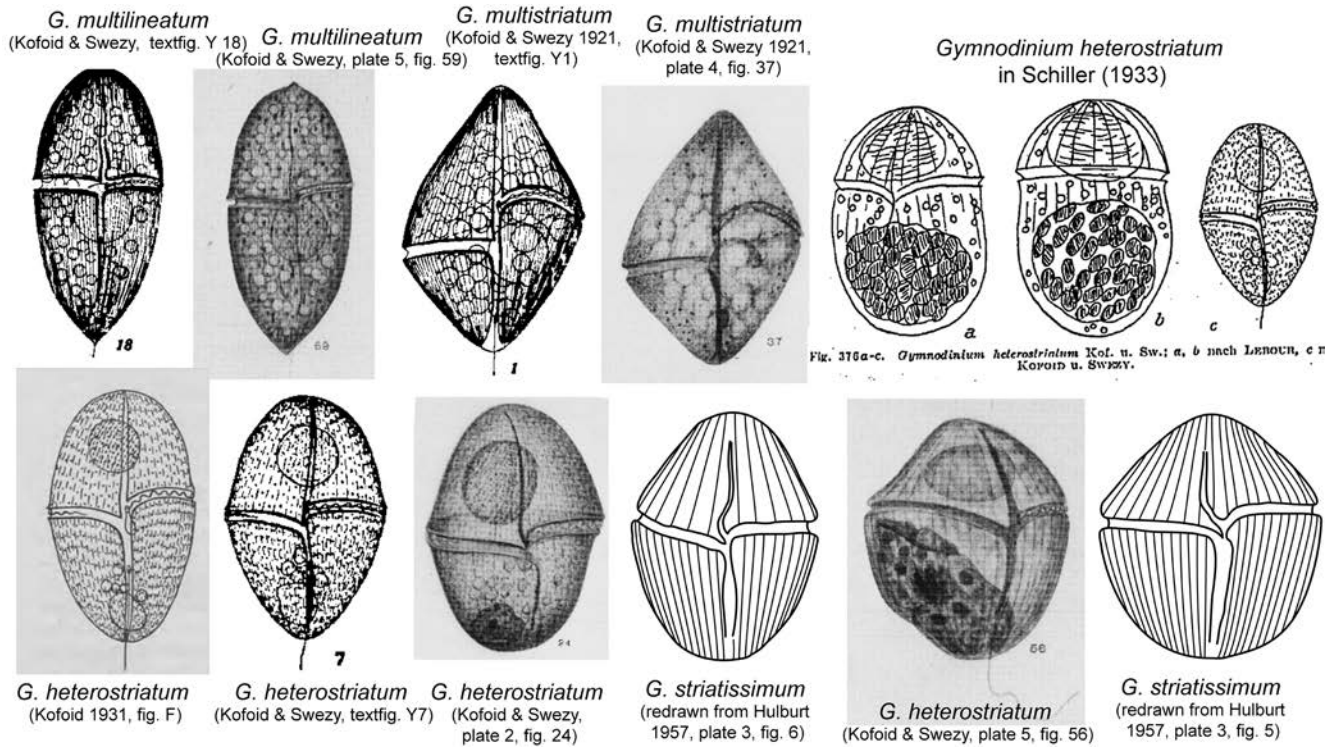
G. multilineatum
(Kofoid & Swezy, textfig. Y 18)
G. multilineatum
(Kofoid & Swezy, plate 5, fig. 59)
G. multistriatum
(Kofoid & Swezy 1921, textfig. Y1)
G. multistriatum
(Kofoid & Swezy 1921, plate 4, fig. 37)
Gymnodinium heterostriatum
in Schiller (1933)
Fig. 376a-c. Gymnodinium heterostriatum Kof. u. Sw.; a, b nach Lebour, c n
Kofoid u. Swezy.
G. heterostriatum
(Kofoid 1931, fig. F)
G. heterostriatum
(Kofoid & Swezy, textfig. Y7)
G. heterostriatum
(Kofoid & Swezy, plate 2, fig. 24)
G. striatissimum
(redrawn from Hulburt 1957, plate 3, fig. 6)
G. heterostriatum
(Kofoid & Swezy, plate 5, fig. 56)
G. striatissimum
(redrawn from Hulburt 1957, plate 3, fig. 5)

Fig. 5.

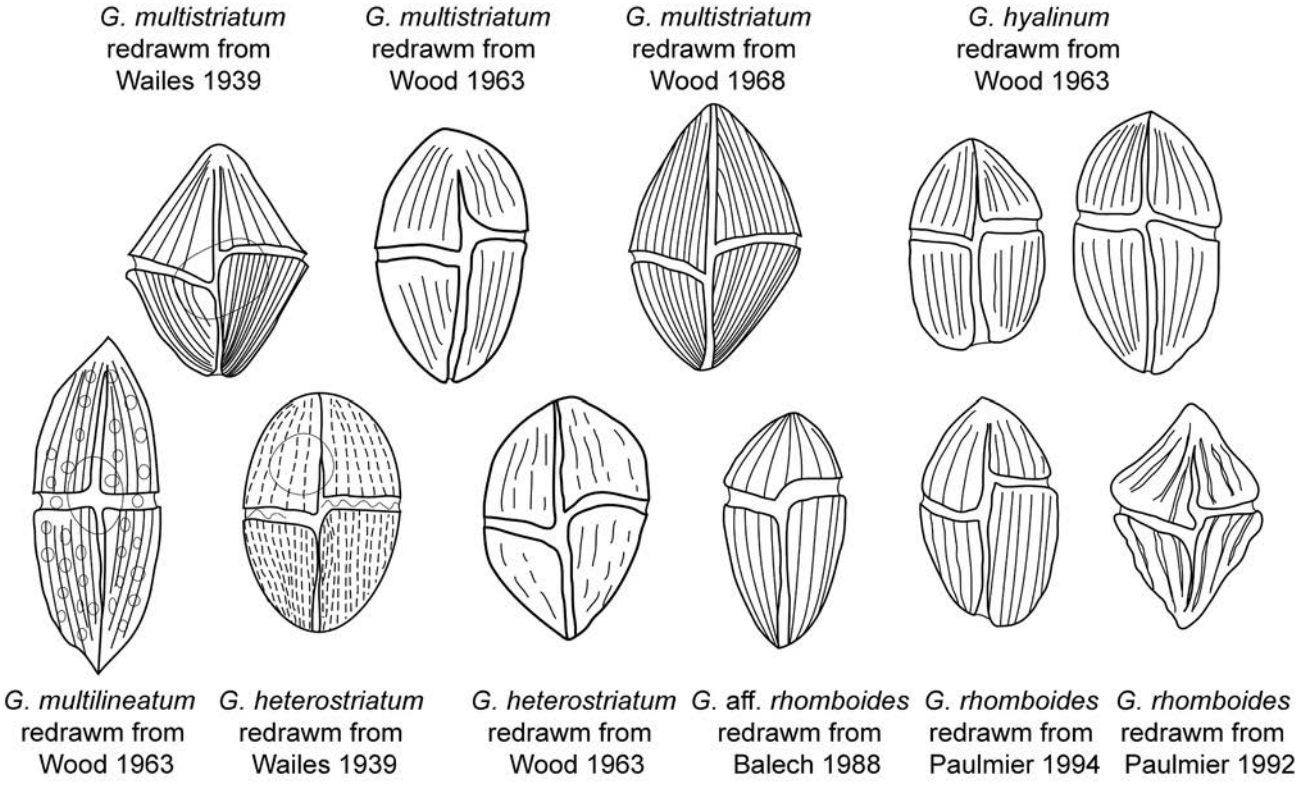
G. multistriatum
redrawm from
Wailes 1939
G. multistriatum
redrawm from
Wood 1963
G. multistriatum
redrawm from
Wood 1968
G. hyalinum
redrawm from
Wood 1963
G. multilineatum
redrawm from
Wood 1963
G. heterostriatum
redrawm from
Wailes 1939
G. heterostriatum
redrawm from
Wood 1963
G. aff. rhomboides
redrawm from
Balech 1988
G. rhomboides
redrawm from
Paulmier 1994
G. rhomboides
redrawm from
Paulmier 1992

Fig. 6.

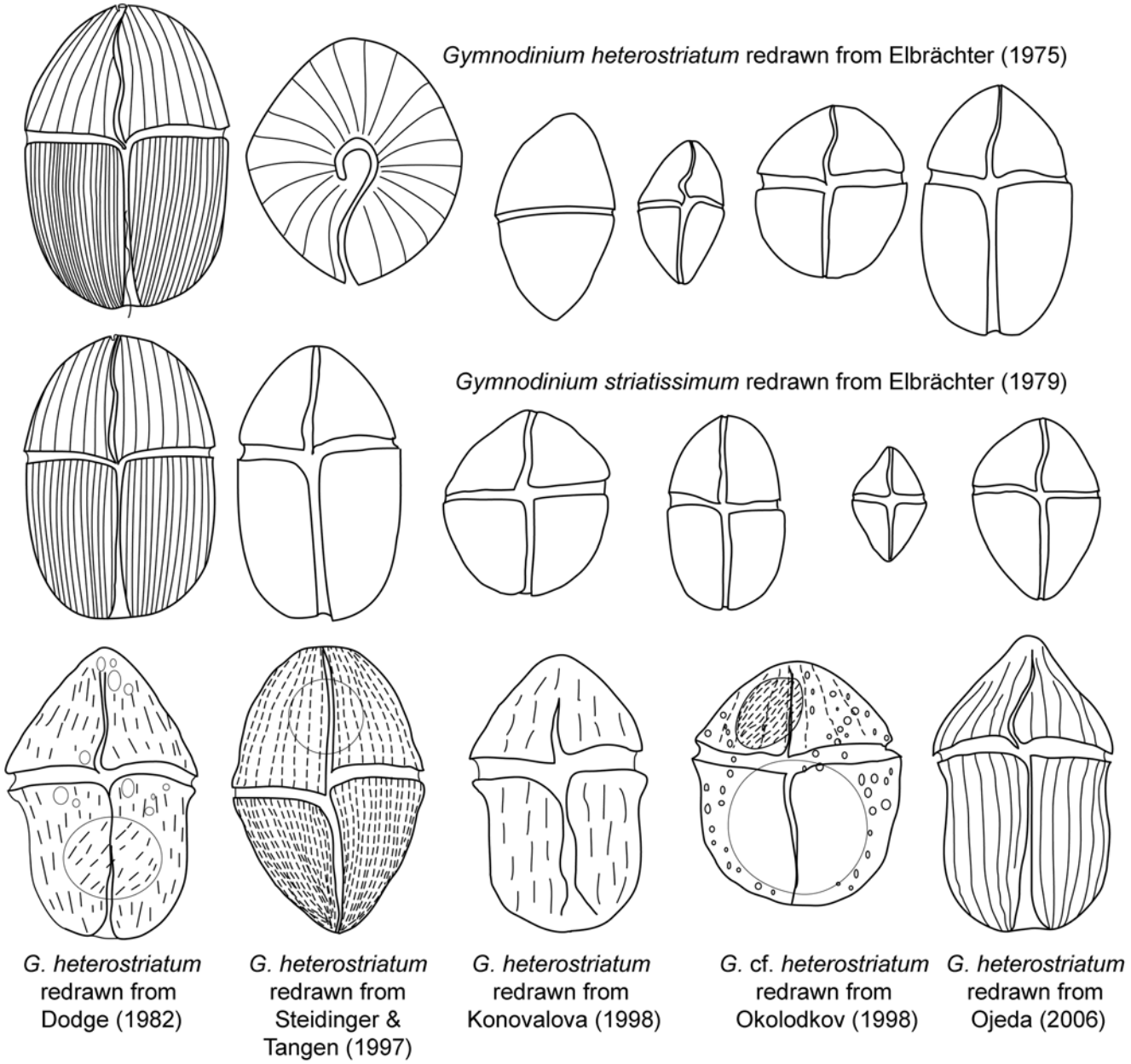

Fig. 7.

obtusum sensu Dogiel (1906) and considered *G. striatissimum* as a posterior synonym of *G. heterostriatum*. Later, Elbrächter (1979) reported observations of the same taxon from the NW African upwelling and he reported the similar line drawings in Elbrächter (1975), excluding apical groove view. This time, Elbrächter (1979) named the taxon as *Gymnodinium striatissimum*, and again reporting as basionym *Gymnodinium spirale* var. *obtusum* sensu Dogiel (1906). Without reporting observations of *G. heterostriatum*, he reported that *Gymnodinium striatissimum* and *G. heterostriatum* are distinct species. According to Elbrächter (1975, 1979) these two species shared the same basionym. Elbrächter (1979) reported the following synonymy for *Gymnodinium striatissimum*: "Synonyms: *Gymnodinium spirale* var. *obtusum* Dogiel 1906, figs 50–56, non *Gymnodinium spirale* var. *obtusum* Schütt 1895; *Gymnodinium rhomboides* Schütt sensu Lebour 1917, figs. 6a–6e; Lebour

1925, plate 6, figs 1a–1c, auct. nonnull., non *G. rhomboides* Schütt 1895, non Schiller 1928; *Gymnodinium heterostriatum* Kofoid & Swezy 1921 pro parte: pl. 5, fig. 56, non p. 221-223. pl. 2 fig. 24, textfig. Y, 7, non Kofoid 1931, fig. F, non auct. nonnull.; *Gymnodinium hyalinum* Lebour 1925, pl. 16 figs 3–4, non *Gymnodinium hyalinum* Schilling 1891; *Gymnodinium lucidum* Ballantine in Parke & Dixon 1964, p. 518".

Elbrächter (1979) considered all the illustrations identified as *G. rhomboides* in the figure 6a–d by Lebour (1917) corresponded to *G. striatissimum*. However, these figures illustrated two distinct species: the typical biconical cells with the morphology of *G. rhomboides* (fig. 6a, b, d), and the ellipsoidal cells of the figures 6c and 6e. Later Lebour (1925) reproduced the figure 6c under the name *G. heterostriatum* in her figure 2. However, Elbrächter (1979) considered the figure 1a–c in Lebour (1925) as a synonym of *G. striatissimum* that corresponded to the truly *G. rhomboides*, and he omitted the figure 2 in Lebour (1925) that corresponded to *G. heterostriatum*. This is incoherent because the figure 2 in Lebour (1925) is a copy of the figure 6c in Lebour (1917) that Elbrächter considered as a synonym of *G. striatissimum.* Elbrächter (1979) also reported that *Gymnodinium hyalinum* as a synonym of *G. striatissimum*. That species is very similar to *G. heterostriatum* in the figure 2 by Lebour (1925) that Elbrächter did not consider it as a synonym of *G. striatissimum*. Elbrächter (1979) considered that the figure 56 in the plate 5 identified as *G. heterostriatum* in Kofoid and Swezy (1921) corresponded to *G. striatissimum*, but not the individual of the figure 24 in the plate 2. However, that individual in figure 24 of the plate 2 also resembled the figure 6 of the original description of *G. striatissimum* in Hulburt (1957).

Elbrächter (1979) reported *Gymnodinium spirale* var. *obtusum* Dogiel 1906 as synonym of *G. striatissimum*. *Gymnodinium spirale* var. *obtusum* sensu Dogiel (1906) is the basionym of *G. heterostriatum*, independently of that Kofoid and Swezy (1921) could report pictures of distinct species under the name *G. heterostriatum*. Kofoid and Swezy (1921, p. 223) reported: "Dogiel (1906) described, as *Gymnodinium spirale* var. *obtusum* Schütt, a form identical with our species. Schütt's organism (1895) of that name, however, is a *Gyrodinium*, and not the same as Dogiel's form. We therefore place the latter with our species as *Gymnodinium heterostriatum* nom. sp. nov.". The article 7.3 of I.C.N. states: 'A new combination or a name at new rank (Art. 6.10) is typified by the type of the basionym even though it may have been applied erroneously to a taxon now considered not to include that type (but see Art. 48.1)'. If we accept that *Gymnodinium spirale* var. *obtusum* sensu Dogiel (1906) is a synonym of *G. striatissimum*, then *G. heterostriatum* Kofoid & Swezy 1921 is also a synonym because it is the new name for *Gymnodinium spirale* var. *obtusum* sensu Dogiel. When Elbrächter (1979, 1994) considered that *Gymnodinium spirale* var. *obtusum* in Dogiel 1906 is a synonym of *G. striatissimum*, he is implicitly reporting that *G. heterostriatum* and *G. striatissimum* are synonyms. If *Gymnodinium spirale* var. *obtusum* sensu Dogiel is considered a synonym of *G. striatissimum* as reported Elbrächter (1979, 1994), then *G. heterostriatum* Kofoid & Swezy 1921 and *G. striatissimum* Hulburt 1957 are synonyms, and the priority is for *G. heterostriatum*. Other discussion is to which species correspond the individuals in the original illustrations of *G. heterostriatum* by Kofoid and Swezy (1921).

Dodge (1982) and Okolodkov (1998) reported illustrations of a species identified as *Gymnodinium heterostriatum*. Dodge (1982) reported *G. spirale* var. *obtusum* in Dogiel 1906 as a synonym of *G. heterostriatum*. Okolodkov (1998, p. 214) reported the same synonymy that Dodge (1982), and he commented "Note. -*G. heterostriatum* is probably conspecific with *G. rhomboides* Schütt, 1985 (Dodge 1985)". Okolodkov (1998) did not cite Dodge 1985 in the reference list.

As *Gymnodinium heterostriatum*, Elbrächter (1994, figs 1–9) reported micrographs of elongated cells with a pointed hyposome and a length of 106 µm. It is atypical to find cells of *G. striatissimum* or *G. heterostriatum* with a pointed episome, and they are always smaller than 70 µm long. The individuals in Elbrächter (1994, figs 1–9) looks more like *Gymnodinium multilineatum* Kofoid & Swezy that is significantly larger (100–120 µm long) than *G. heterostriatum*.

Elbrächter (1994) discussed on the diagnostic characters to distinguish between *G. heterostriatum* and *G. striatissimum*. He reported: "1) The antapex is clearly pointed in *G. heterostriatum* but is rounded in *G. striatissimum*; (2) *G. heterostriatum* always has a sack-like pusule at the junction of sulcus and cingulum and may also have a second one; *G. striatissimum* never has a pusule: (3) *G. heterostriatum* is larger than *G. striatissimum.* Only following a change of cell shape, due to unfavourable conditions, may the smallest cells of *G. heterostriatum* reach the size of the largest cells of *G. striatissimum*; (4) The cytoplasm of *G. heterostriatum* is always either a pale chalcedony yellow or pinkish cinnamon colour, whereas the clear cytoplasm

of *G. striatissimum* is greenish or greyish, and the cells appear refractive under the dissecting microscope".

According to Elbrächter (1994), *Gymnodinium heterostriatum* is present in the NW African upwelling, and the only previous records were by Kofoid in California and Japan (Kofoid and Swezy 1921, Kofoid 1931). Kofoid and Swezy (1921, p. 222) reported for *Gymnodinium heterostriatum* "It was the most abundant species of the Gymnodinioidae in plankton examined by us". Consequently, this abundant species disappeared, and only Elbrächter (1994) have observed it after Kofoid. The micrographs of *G. heterostriatum* in Elbrächter (1994) showed an elongated cell with a more or less acute antapex that resembled the illustrations of original illustrations of *G. multilineatum*, a rare species described from the observation of three individuals. Kofoid and Swezy (1921) reported a length of 66–85 µm and 108 µm for *G. heterostriatum* and *G. multilineatum*, respectively. Elbrächter (1994) reported a length of 93–106 µm for *G. heterostriatum*. These features suggested that Elbrächter (1994) misidentified *G. heterostriatum* with *G. multilineatum*. Elbrächter (1994) insisted that "Erroneously, Kofoid & Swezy (1921) regarded the species that Dogiel (1906) had illustrated as *Gymnodinium spirale* var. *obtusum* (see Dogiel's plate 2, figs 50–56) as conspecific with *G. heterostriatum*. Elbrächter (1979) identified the species Dogiel had described and depicted in 1906 as *Gymnodinium striatissimum* Hulburt 1957".

Takayama (1998, p. 121) cited Elbrächter (1979) and he reported *Gymnodinium spirale* var. *obtusum* Dogiel 1906 and *Gymnodinium heterostriatum* Kofoid & Swezy 1921 as a synonym of *G. striatissimum* Hulburt 1957. This is not coherent because the name *G. heterostriatum* should have the priority. Takayama (1998, plate 18, figs 7–9) reported light and scanning electron microscopy pictures of *G. striatissimum*. The apical groove is an ellipse bisected by a central line similar to the type species of *Gyrodinium*. Without molecular data, Daugbjerg et al. (2000) transferred *Gymnodinium striatissimum* into *Gyrodinium*. Daugbjerg et al. did not report if they considered *Gymnodinium heterostriatum* and *G. striatissimum* as independent species, or the reason to give the priority to *G. striatissimum* over *G. heterostriatum* in case of synonymy.

Elbrächter and Hoppenrath in Hoppenrath et al. (2009, p. 123) reported for *G. striatissimum*: "Similar species: Confused with *Gymnodinium heterostriatum* Kofoid et Swezy by many authors (e.g., Drebes 1974, Dodge 1982). In addition, the records of *Gymnodinium rhomboides* of Lebour (1925), *Gymnodinium hyalinum* M. Lebour (= *Gymnodinium lucidum* D. Ballantine; non *G. hyalinum* A.J. Schilling) apparently apply to *Gymnodinium striatissimum*, for a detailed discussion see Elbrächter (1979), for the delimitation from *Gymnodinium heterostriatum* see Elbrächter 1994). From light microscopical observations of the path of the acrobase we do not agree with the transfer of *G. striatissimum* into the redefined genus *Gyrodinium* by Hansen and Moestrup in Daugbjerg et al. (2000). Therefore we retain the species in the genus *Gymnodinium* awaiting further detailed microscopical and molecular genetic investigations".

Elbrächter (1975) reported a line drawing of the apical groove of *G. striatissimum* with the shape of an open loop. Despite this is common species in the North Sea, this author or others have never reported LM or SEM pictures of the apical groove. This is anomalous because an open loop-shaped apical groove is unknown in any heterotrophic dinoflagellate with longitudinal striae.

Elbrächter and Hoppenrath in Hoppenrath et al. (2009, p. 123) reported for *G. striatissimum*: "very variable species, due to differences in nutritional conditions. The nucleus is spherical and can be found in various locations, partially due to displacement by food vacuoles...feds voraciously on *Phaeocystis globosa*...Widespread in the northern hemisphere, recorded from the North Sea, Baltic Sea, Mediterranean, North Atlantic Ocean, off California, Pacific Ocean...Recorded in the German Bight all year round, most abundant from April to July, often associated with blooms of *Phaeocystis*, on which it feeds". Curiously, this common species has disappeared from the German North Sea. Kraberg et al. (2019, p. 12) reported that "*Gymnodinium striatissimum* Hulburt (syn. *Gymnodinium heterostriatum*)" is absent 2009 onwards in the Helgoland Roads time series. In this study, we found that *Gymnodinium heterostriatum*/*striatissimum* is the most abundant dinoflagellate in the Dutch North Sea in May 2019 reaching abundances of 3000 cells per liter, while it apparently disappeared from the German North Sea since 2009 (Kraberg et al. 2019). Individuals of *Gymnodinium heterostriatum*/*striatissimum* are very likely misidentified as *Gyrodinium spirale*.

What is the name for this common taxon? We are dealing with common dinoflagellates in the world ocean. There is a tradition of plankton studies in the North Sea and the English Channel for over 150 years. This species reaches high abundance in the southern North Sea and the English Channel. Is the name of this species the relatively recently described *Gymnodinium striatissimum* Hulburt 1957?

It is not evident that this taxon was illustrated in the XIX century (Bergh 1881; Pouchet 1883, 1885; Levander 1894, Schütt 1895). Calkins (1901) described *Gymnodinium gracile* var. *sphaericum*, later reported as *G. sphaericum*, but the illustrations did not show longitudinal striae. The taxon illustrated as *G. rhomboides* in Schütt (1895) is a distinct species. The first illustration of *Gymnodinium heterostriatum*/*striatissimum* corresponded to Dogiel (1906, figs 50–56) that reported the morphological variability with several illustrations from the Gulf of Naples under the name *Gymnodinium spirale* var. *obtusum* F. Schütt 1895. Lebour (1917) in her figure 6 illustrated two distinct species, but she named both species as *G. rhomboides*. She refrained to describe a new species and she reported "Certain aspects of my specimens agree very closely with Schütt's figures, I have therefore taken the name given by him rather than create a new one".

Kofoid and Swezy (1921) proposed the new name *Gymnodinium heterostriatum* nom. nov. for the species identified as *Gymnodinium spirale* var. *obtusum* in Dogiel (1906) and *Gyrodinium obtusum* (F. Schütt) Kofoid & Swezy for *Gymnodinium spirale* var. *obtusum* F. Schütt 1895. Independently of what species Kofoid and Swezy observed and illustrated in Californian waters, the new name for *Gymnodinium spirale* var. *obtusum* in Dogiel (1906) is *Gymnodinium heterostriatum* Kofoid & Swezy 1921.

The species of figure 6c initially identified as *G. rhomboides* in Lebour (1917) is later reproduced as the figure 2 in plate 6 as *G. heterostriatum* in Lebour (1925). Unequivocally, this species is the abundant taxon that fed on *Phaeocystis* in the English Channel and North Sea, and first reported as *Gymnodinium spirale* var. *obtusum* in Dogiel (1906). *Gymnodinium triangulare* described in Lebour (1917) could be co-specific, but the illustration and description from a single individual is incomplete. There is no information on the longitudinal striae, and it could be other heterotrophic unarmored dinoflagellate. We cannot assure that *G. triangulare* is an earlier description of *G. heterostriatum*.

Are *Gymnodinium heterostriatum* Kofoid & Swezy 1921 and *Gymnodinium striatissimum* Hulburt 1957 synonyms? Taken into account that *Gymnodinium heterostriatum* Kofoid & Swezy 1921 is the name for the species described as *G. spirale* var. *obtusum* in Dogiel (1906), the individuals of *Gymnodinium striatissimum* in the figure 5 and 6 of Hulburt 1957 are in the range of variability of *G. spirale* var. *obtusum* sensu Dogiel. We can consider that they are synonyms. This agrees with Elbrächter (1979, 1994) that considered *G. spirale* var. *obtusum* sensu Dogiel as a synonym of *G. striatissimum*. The confusion is due to that Elbrächter (1994) probably mistook cells of *G. multilineatum* as *G. heterostriatum*.

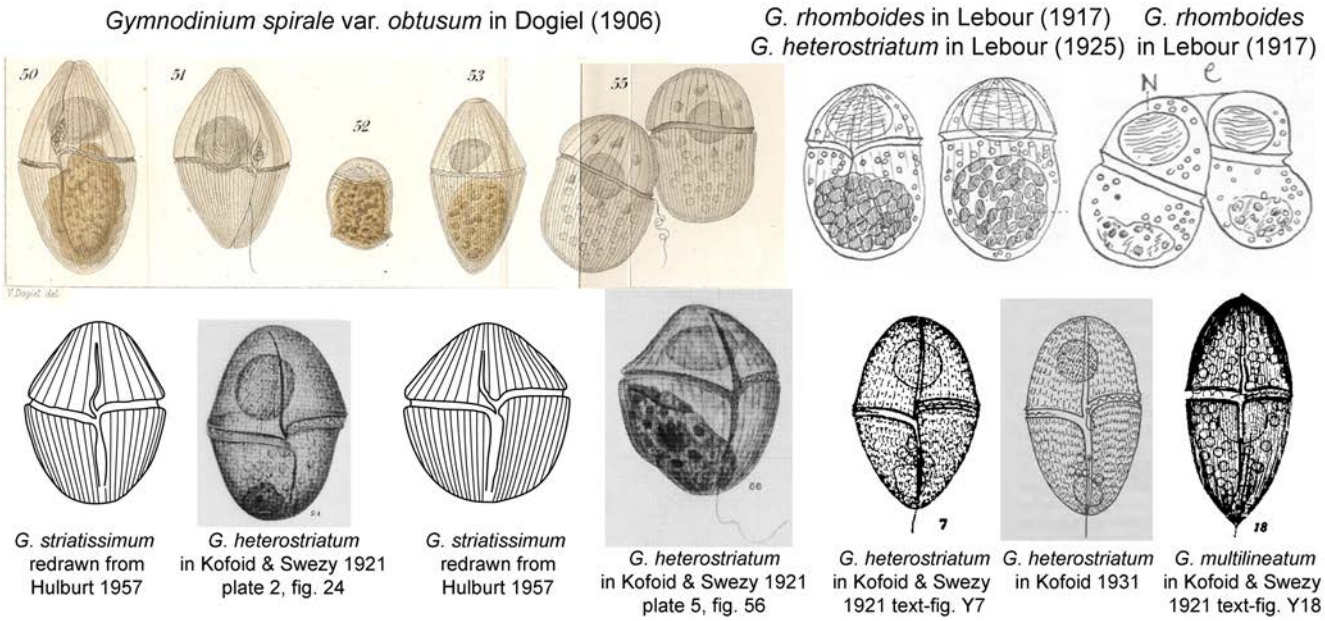

Fig. 8.

Table 1. Dimensions of *Gymnodinium heterostriatum* and allied taxa.

Taxon	Length/width (in μm)	Reference
G. gracile var. *sphaericum*	68/55	Calkins (1901)
G. sphaericum	47–68/40–47	Kofoid and Swezy (1921)
G. rhomboides	47	Paulsen (1908)
G. rhomboides	46	Kofoid and Swezy (1921)
G. rhomboides	40–50	Lebour (1917)
G. rhomboides	30–46	Lebour (1925)
G. rhomboides	30–46 /20–26	Schiller (1933)
G. triangulare	45	Lebour (1917)
G. hyalinum	39	Lebour (1925)
G. hyalinum	40	Wood (1963)
G. heterostriatum	60–85/48–72	Kofoid and Swezy (1921)
G. heterostriatum	60–85/48–72	Kofoid (1931)
G. heterostriatum	40	Lebour (1925)
G. heterostriatum	66–85/48–72	Schiller (1933)
G. heterostriatum	60–70	Wood (1963)
G. heterostriatum	40–85	Dodge (1982)
G. cf. *heterostriatum*	40–48/33–42	Okolodkov (1998)
G. heterostriatum	93–106/50–56	Elbrächter (1994)
G. multilineatum	108/50	Kofoid and Swezy (1921)
G. multilineatum	100–120	Wood (1963)
G. multistriatum	100/68	Kofoid and Swezy (1921)
G. multistriatum	100	Wood (1963)
G. multistriatum	100	Wood (1968)
G. striatissimum	29–43/23–31	Hulburt (1957)
G. striatissimum	29–66/23–48	Elbrächter (1979)
G. striatissimum	29–66/24–48	Elbrächter and Hoppenrath (2009)

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