



Taxonomic clarification of the dinophyte *Peridinium acuminatum* Ehrenb., ≡ *Scrippsiella acuminata*, *comb. nov.* (Thoracosphaeraceae, Peridinales)

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Abstract

Peridinium acuminatum (Peridinales, Dinophyceae) was described in the first half of the 19th century, but the name has been rarely adopted since then. It was used as type of *Goniodoma*, *Heteraulacus* and *Yesevius*, providing various sources of nomenclatural and taxonomic confusion. Particularly, several early authors emphasised that the organisms investigated by C.G. Ehrenberg and S.F.N.R. von Stein were not conspecific, but did not perform the necessary taxonomic conclusions. The holotype of *P. acuminatum* is an illustration dating back to 1834, which makes the determination of the species ambiguous. We collected, isolated, and cultivated *Scrippsiella acuminata*, *comb. nov.* (strain GeoB 427) from the type locality off Kiel, Germany (Baltic Sea). We barcoded the species of the Thoracosphaeraceae using rRNA sequences and investigated the morphology of the strain using light and electron microscopy. As taxonomic result, we designate an epitype for *Peridinium acuminatum*, as no conflict with C.G. Ehrenberg's protologue can be stated. It is indistinguishable from *Scrippsiella trochoidea* (likewise described from the Kiel Fjord) that we consider a later heterotypic synonym. Our study contributes to the disentanglement of dinophyte taxonomy in a very challenging case, and we trust that C.G. Ehrenberg and S.F.N.R. von Stein investigated different species under the epithet '*acuminatum*'. The complex nomenclature and taxonomy of *Goniodoma*, and its type species *Goniodoma acuminatum*, is discussed in the Electronic Supplement. We consider *Pyrrhotriadinium*, with the type species *Pyrrhotriadinium polyedricum* (Gonyaulacales), well suited to harbour all gonyaulacalean taxa so far assigned to *Goniodoma* and *Heteraulacus* as well.

Key words: calcareous dinoflagellates; epitypification; *Goniodoma*; molecular systematics; morphology; nomenclature; taxonomy

Introduction

Summarised history of *Peridinium acuminatum*:—*Peridinium acuminatum* Ehrenb. (1836: 541, 575, pl. II 5) is among the first 50 species names ever described in the dinophytes. However, the identity of the species is doubtful because of two major historical pitfalls referring to both its taxonomy and its nomenclature. Confusion arose since Stein (1883) introduced monotypic *Goniodoma* F.Stein (1883: 9, 12, 13, 16, 19, 21), which is nomenclaturally based on the name of C.G. Ehrenberg's species. Stein (1883) investigated heterogeneous material from the type locality of *P. acuminatum* in the Kiel Fjord (Germany) and from the Atlantic Ocean as well (see Electronic Supplement for details), but many early authors such as Jørgensen (1899) emphasised the distinctiveness between S.F.N.R. von Stein's species and C.G. Ehrenberg's species. The second (nomenclatural) imprudence was done by Loeblich Jr & Loeblich III. (1966) when they used *P. acuminatum* to designate the type species of *Heteraulacus* Diesing (1850: 9, 100), a name older than *Goniodoma* (delicately citing in their index the same reference for the type of *Goniodoma*). Previous authors were

in fact aware of the resulting multiple problems for taxonomy and nomenclature, but never performed the necessary taxonomic conclusions.

Peridinium acuminatum was firstly described by Ehrenberg (1836), who observed it in water tow samples from the Kiel Fjord (Baltic Sea, Germany), collected by the amateur naturalist G.A. Michaelis in August 1834. No original specimen could be relocated in the Ehrenberg collection held at the Museum for Natural History in Berlin (Germany), and pl. II 5 in Ehrenberg (1836) (Fig. 1) is thus the type of *P. acuminatum*. It shows dinophyte cells with a length of approximately 45 µm and exhibiting chloroplasts, and Ehrenberg (1836, 1838) was unsure whether the species was bioluminescent. The cells' outline is spherical or ovate (noted in description) through obtusely polygonal (illustrated in drawings: Fig. 1), and Ehrenberg (1836: 541) emphasised that the algae died during observation and drafting. The most distinctive trait of the species, however, is the pointed apex of the cells that is characteristically hyaline in light microscopy (German, 'wasserhell': Jørgensen 1899), and to which the descriptive epithet '*acuminatum*' refers to.



FIGURE 1. Ehrenberg's original material of *Peridinium acuminatum* (note slight deviations between the illustrations regarding cell shape and internal colouring). A. water-coloured drawing (sheet 938, deposited in the Museum for Natural History, Berlin), B. from which the type pl. II 5 (engraver: B. Wienker) in Ehrenberg (1836) as well as C. pl. XXII (engraver: C.E. Weber) in Ehrenberg (1838) was derived.

Nomenclature of *Peridinium acuminatum* and associated names:—The nomenclature of *P. acuminatum* is complex and was controversially in the past (e.g., Jørgensen 1899, Loeblich Jr & Loeblich III 1966, Balech 1979, 1988, Dodge 1981, Sournia 1984, Özdikmen 2009, Nakada 2010). It was designated as type of three generic names, namely *Goniodoma* F.Stein (1883: 9, 12, 13, 16, 19, 21), *Heteraulacus* Diesing (1850: 9, 100) and *Yesevius* Özdikmen (2009: 235). In his epochal work, Stein (1883) introduced the generic name *Goniodoma*, with the only (and subsequently type) species *Goniodoma acuminatum* (Ehrenb.) F.Stein (1883: 12–13, pls VII 1–16, VIII 1–2) included, a combination of *P. acuminatum* (Ehrenberg 1836). *Goniodoma* is not available for nomenclatural purposes under the *International Code of Zoological Nomenclature* (ICZN Art. 52.2; Ride *et al.* 1999), since it is a later homonym of a lepidopteran (Zeller 1849). However, the name is in fact validly published under the *International Code of Nomenclature for algae, fungi, and plants* (ICN Arts 45.1, 54.1; McNeill *et al.* 2012) since its usage by Schütt (1887) in a botanical journal.

Diesing (1850) created the generic name *Heteraulacus* (orthographical variant *Heteroaulax* Diesing 1866: 381) for four already described species assigned earlier to *Peridinium* Ehrenb. (1832: 38) without personal observations or providing figures of the species. The scientific motives of K.M. Diesing to establish the name *Heteraulacus* remain obscure, as the delimitation from other dinophytes is not precisely worked out: The taxon may combine dinophytes that can be assigned to the Gymnodiniales, Peridiniales and Gonyaulacales as well. Moreover, Diesing (1850, 1866) failed to designate a type for *Heteraulacus*, but the name is available under the ICZN since 1850 (ICZN Arts 12.2.5., 13.3.) and therefore also available if regarded as alga (ICN Art. 45.). *Heteraulacus* was neglected more than a century until Loeblich Jr and Loeblich III. (1966) designated *Heteraulacus acuminatus* (Ehrenb.) Diesing (1850: 100–101)—a combination of *P. acuminatum* (Ehrenberg, 1836)—as type. This procedure reflects their taxonomical view in the mid-sixties of the last century and is formally acceptable, as ‘an originally included nominal species is eligible for subsequent fixation as type species, even if it is the type species of another genus-group taxon’ (ICZN Arts 67.11, 69.2.). However, it made *Heteraulacus* and *Goniodoma* objective synonyms (ICZN Art. 61.3.3.), with *Heteraulacus* having nomenclatural priority.

Yesevius is also based on *P. acuminatum* (Özdikmen 2009), but it is a later homotypic and therefore superfluous, illegitimate replacement name for *Heteraulacus* (under ICZN as well as under ICN) and for *Goniodoma* (under ICN). Apparently, H. Özdikmen does not have personal experience with *P. acuminatum* when he does not provide any figure or descriptive detail. Further, the generic name *Triadinium* J.D.Dodge (1981: 278) was introduced to include the species described as *Peridinium polyedricum* C.H.G.Pouchet (1883: 440, pl. XX 34), which is regarded as heterotypic synonym of *Goniodoma acuminatum* sensu Stein (1883) since Bütschli (1885: 1004). J.D. Dodge’s combination *Triadinium polyedricum* (C.H.G.Pouchet) J.D.Dodge (1981: 279) was incorrect (though valid) when he included *P. acuminatum* in the synonymy. Anyway, the generic name is a later homonym of the ciliate *Triadinium* Fiorentini (1890: 16) (Sournia 1984, Nakada 2010).

TABLE 1. Original literature data comparison between *Glenodinium trochoideum* (Stein 1883), *Peridinium acuminatum* (Ehrenberg 1836, 1838) and *Gonyaulax polyedra* (Stein 1883), all of which were described from Kiel Fjord. Note that of all species listed in Hällfors (2004), only *Scrippsiella* (\equiv *Glenodinium*) *trochoidea* and *Lingulodinium* (\equiv *Gonyaulax*) *polyedrum* show similarity to C.G. Ehrenberg’s species. Diagnostic morphological characters reject conspecificity of *Go. polyedra* and *P. acuminatum*, whereas *Gl. trochoideum* and *P. acuminatum* are regarded as conspecific, lacking differentiating characters. Already previous authors such as Jørgensen (1899), Lemmermann (1910b) and Schiller (1937) identified *Gl. trochoideum* as synonymous with *P. acuminatum*, although none of them drew the correct nomenclatural conclusion.

trait	<i>Gl. trochoideum</i>	<i>P. acuminatum</i>	<i>Go. polyedra</i>
cell apex	mucronate	with spine	obtuse
cell outline	ovate through slightly polygonal	ovate through obtusely polygonal	polygonal
cell surface	smooth	smooth	punctulate
thecal plates	inconspicuous	not differentiated	prominent
cingulum displacement	< ½ width	none	> 1 width
adcingular lists	absent	absent	present
bioluminescence	absent	doubtful	present

Identification of *Peridinium acuminatum*:—The name *P. acuminatum* was otherwise rarely adopted since its description (Ehrenberg 1838, Claparède & Lachmann 1859, 1868, Schütt 1887, Pouchet 1893). Irrespective of the generic name used (*i.e.*, *Goniodoma*, *Heteraulacus* or *Yesevius*), *P. acuminatum* in the sense of Stein (1883) is currently considered an element of the Gonyaulacales (Drugg & Loeblich Jr 1967, Loeblich Jr & Drugg 1968, Fensome *et al.* 1993). However, a number of morphological discrepancies can be stated between C.G. Ehrenberg’s species and

S.F.N.R. von Stein's species that are outlined in the Discussion section in detail. The protologue of *P. acuminatum* and pl. II 5 in Ehrenberg (1836) (Fig. 1) does not conflict with a species that is known as *Scrippsiella trochoidea* (F.Stein) A.R.Loeb. (1976: 25) (Tab. 1), likewise described from the Kiel Fjord and whose taxonomic identity was recently clarified (Zinssmeister *et al.* 2011). Today, *S. trochoidea* is considered to belong to the Thoracosphaeraceae (Peridiniales) comprising mostly marine dinophytes that produce calcified shells during the coccoid stage of their life history (Elbrächter *et al.* 2008; Gottschling & Soehner 2013). The immotile calcareous cells (commonly termed a 'cyst') have a mostly ovoid shape, with numerous processes developed at the cell surface. In the thecate cells, species of *Scrippsiella* Balech (1959: 199–200) can morphologically be distinguished from other phototrophic peridinoid marine dinophytes based on the presence of six (*versus* less) cingular plates (three of which seen in mid-dorsal view of motile cells: Fine & Loeblich III. 1976, Dale 1977, 1978: Fig. 1, Zinssmeister *et al.* 2012). Molecular data indicate the existence of a large sequence diversity of molecular ribotypes, particularly of the Internal Transcribed Spacer (ITS) (Montresor *et al.* 2003, Gottschling *et al.* 2005, Gu *et al.* 2011, Soehner *et al.* 2012), that is not reflected in morphological differentiation and that may correspond to numerous 'cryptic species' within the *S. trochoidea* species complex.

Jørgensen (1899) was first to recognise the link between *P. acuminatum* and *Glenodinium trochoideum* F.Stein (1883: pl. III 27–29) (and who also emphasised that *P. acuminatum* and *Go. acuminatum* in the sense of Stein 1883 are not conspecific: see Electronic Supplement). He subsequently transferred *P. acuminatum* to *Glenodinium* Ehrenb. (1837: 147), under which *S. trochoidea* initially was described. After examination of material collected at the Kiel Fjord, Lemmermann (1910b) confirmed the synonymy between *P. acuminatum* and *Gl. trochoideum*. He had the key in his hand to remediate S.F.N.R. von Stein's misinterpretation early in history, but his combination *Peridinium trochoideum* (F.Stein) Lemmerm. (1910b: 336–338, figs 33–36) was incorrect (though valid) when he included *P. acuminatum* in the synonymy under the name. It is explicit aim of our study to disentangle the desperate taxonomic situation and to test the hypothesis of conspecificity between *P. acuminatum* and *Gl. trochoideum*.

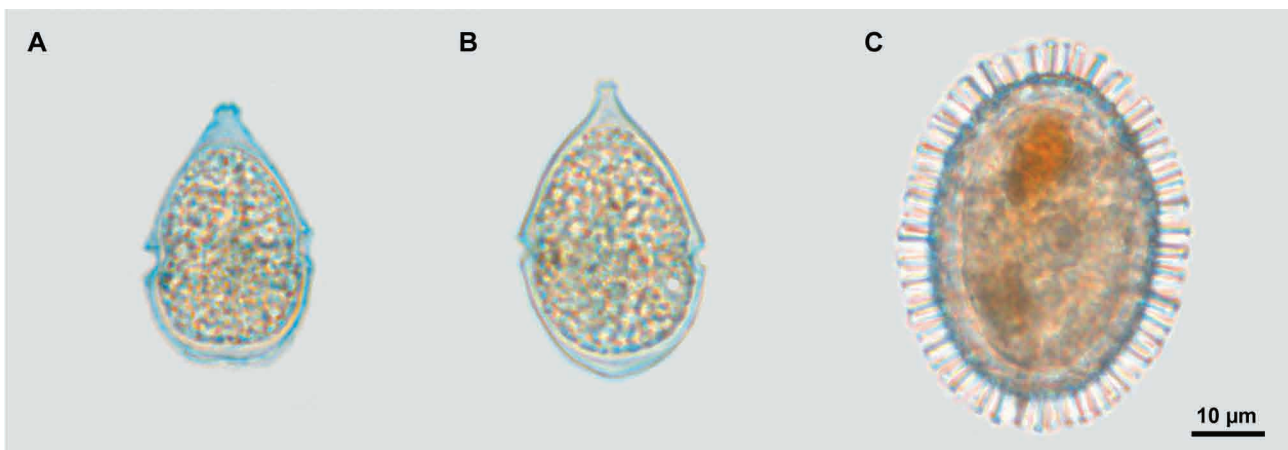


FIGURE 2. Single cells from the epitype (or copies) of *Scrippsiella acuminata*, *comb. nov.* (light microscopy; GeoB 427). A, B. Motile thecate cells. C. Calcareous coccoid cell with processes.

Primarily because of the limited type material available, the taxonomic identity of *P. acuminatum* is presently uncertain (and the history of the name complex). Among all taxa that have been assigned to *P. acuminatum* in the literature, *S. trochoidea* is the only dinophyte from the Kiel Fjord with a characteristically acuminate theca (Hällfors 2004; Tab. 1). In such cases of taxonomic uncertainty, an important innovation in the application of the type concept was brought into the ICBN in form of the epitype (Greuter *et al.* 1994). This is 'a specimen or illustration selected to serve as an interpretative type when [...] all original material associated with a validly published name is demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name of a taxon' (ICN Art. 9.8.). To avoid further confusion with the name *P. acuminatum*, we designate an epitype in this study (Fig. 2). It was prepared from cells of a strain established from the type locality in the Kiel Fjord and is in accordance with the protologue. It is, moreover, morphologically indistinguishable from epitype material of *Gl. trochoideum* (Zinssmeister *et al.*, 2011) and exhibits the identical sequence of the Internal Transcribed Spacer (GenBank Acc. No. JN982383). Thus, we agree with Jørgensen (1899), Lemmermann (1910b) and Schiller (1937) that *Gl. trochoideum* is a later heterotypic synonym of *P. acuminatum*.

Material and Methods

Fine sediment was collected using a self-made rocket-like bore probe (Gottschling & Kirsch 2009) at the Kiel Fjord (Germany; 54° 22' 08" N, 10° 09' 10" E, water depth: 5 m) on March 18th, 2009. The sediment samples were washed through sieves with different mesh sizes (125 µm, 75 µm and 20 µm). Single calcareous coccoid cells were isolated from sediment fractions between 20 and 75 µm and were transferred to six-well microplates (Zefa; Munich, Germany) supplied with K-media without silicate (Keller *et al.* 1987) prepared from filtered sea water. After successful growth, substrains were established (preferably from single cells) and were cultivated in a climate chamber WKS 3200 (Liebherr; Bulle, Switzerland) at 18 °C, 80 µmol photons m⁻²s⁻¹ and a 12:12 h light:dark photoperiod. The established strains are currently held in the culture collections at the Institute of Systematic Botany and Mycology (University of Munich) and are available upon request. They are equivalent with the substrain CCAC4748B from the Culture Collection of Algae at the University of Cologne. Cells were observed, documented and measured with a CKX41 inverse microscope (Olympus; Hamburg, Germany) equipped with a DP73 digital camera (Olympus).

For the preparation of the epitype, cells of the strain GeoB 427 were stained with astra blue (Fluka; Buchs, Switzerland) and eosin (Merck; Darmstadt, Germany) as described in detail previously (Zinssmeister *et al.* 2011, Kretschmann *et al.* 2014). The epitype is deposited at the Centre of Excellence for Dinophyte Taxonomy (CEDiT; Wilhelmshaven, Germany), and copies are held in Botanischer Garten und Botanisches Museum Berlin-Dahlem (B) and Botanische Staatssammlung München (M; see below). The preparative techniques for light (LM) and scanning electron microscopy (SEM) followed standard protocols (Janofske 2000) and were basically the same as described in Gottschling *et al.* (2012). Briefly, SEM samples were either air-dried or dehydrated in a graded acetone series and critical point dried, followed by sputter-coating with platinum. The Kofoidian system (Taylor 1980, Fensome *et al.* 1993) was used to designate the plate formula.

Ribosomal RNA (rRNA) sequences including the Internal Transcribed Spacers (ITSs) were generated for strain GeoB 427 (isolate D430, GenBank No JN982383) already in a previous of our studies (Zinssmeister *et al.* 2012; and subject of molecular phylogenetics: Gottschling & Soehner 2013, Kretschmann *et al.* 2014). In the alignment editor 'Se-Al' (Rambaut 2001), the ITS sequence of GeoB 427 was visually compared to other ITS sequences assigned to *Scrippsiella*, including those obtained from strain GeoB*185 (isolate D319, GenBank No HQ729493).

Results

The strain GeoB 427 exhibited both motile thecate cells (Figs 2A–B, 3A–C, H–I, 4F) and immotile calcareous coccoid cells (Figs 2C, 3F–G, J–K). The motile cells were predominant, whereas the coccoid cells were rare. The epitheca was conical (the outline sometimes slightly polygonal) and had a slightly acuminate, hyaline apex, while the hypotheca's outline was polygonal through hemispheric. In apical view (Fig. 4A, E), the cingular outline was nearly circular through slightly polygonal. The cingular girdle was excavated and slightly descendent (Figs 3H, 4B), the displacement comprised always less than 50% of the cingulum width. The sulcus was likewise excavated and extended from the cingulum to the antapex.

The thecate cells were variable in size and could be classified into three different dimension types (Fig. 3A–C). The cells of the small-sized type ranged from 17–23 µm in length (mean: 21 µm; median: 22 µm; SD: 2 µm; n=17) and 14–20 µm in width (mean: 17 µm; median: 16 µm; SD: 2 µm; n=17) and were light yellow in colour. The majority of the motile cells in the cultivation plates represented the mid-sized dimension type. Such cells ranged from 25–37 µm in length (mean: 32 µm; median: 32 µm; SD: 3 µm; n=101) and 17–27 µm in width (mean: 22 µm; median: 22 µm; SD: 2 µm; n=101). The colour of this cell type was yellowish through golden. The cells of the large dimension type ranged from 39–44 µm in length (mean: 40 µm; median: 40 µm; SD: 2 µm; n=18) and 23–29 µm in width (mean: 25 µm; median: 25 µm; SD: 2 µm; n=18). The colour of the large-sized cells did not differ from the colour of the mid-sized cells.

The phototrophic motile cells of all dimension types were covered by a theca constituting of cellulosic plates. The basic thecal plate arrangement was Po, cp, X, 4', 3a, 7'', 6c, 5s, 5''', 2'''' (Figs 4A–D, 5A–E). Aberrant formulas were frequently observed (examples are given in Fig. 4E–F). The deviation consisted mostly of plates, which were divided by additionally sutures. Occasionally, cells with the same kind of deviation could be observed. In addition, the outlines of the thecal plates varied between individuals. The cell surface was smooth and did not show any ornamentation. Small circular pores were irregularly scattered over the thecal plates or rarely linearly arranged near the plate boundaries.

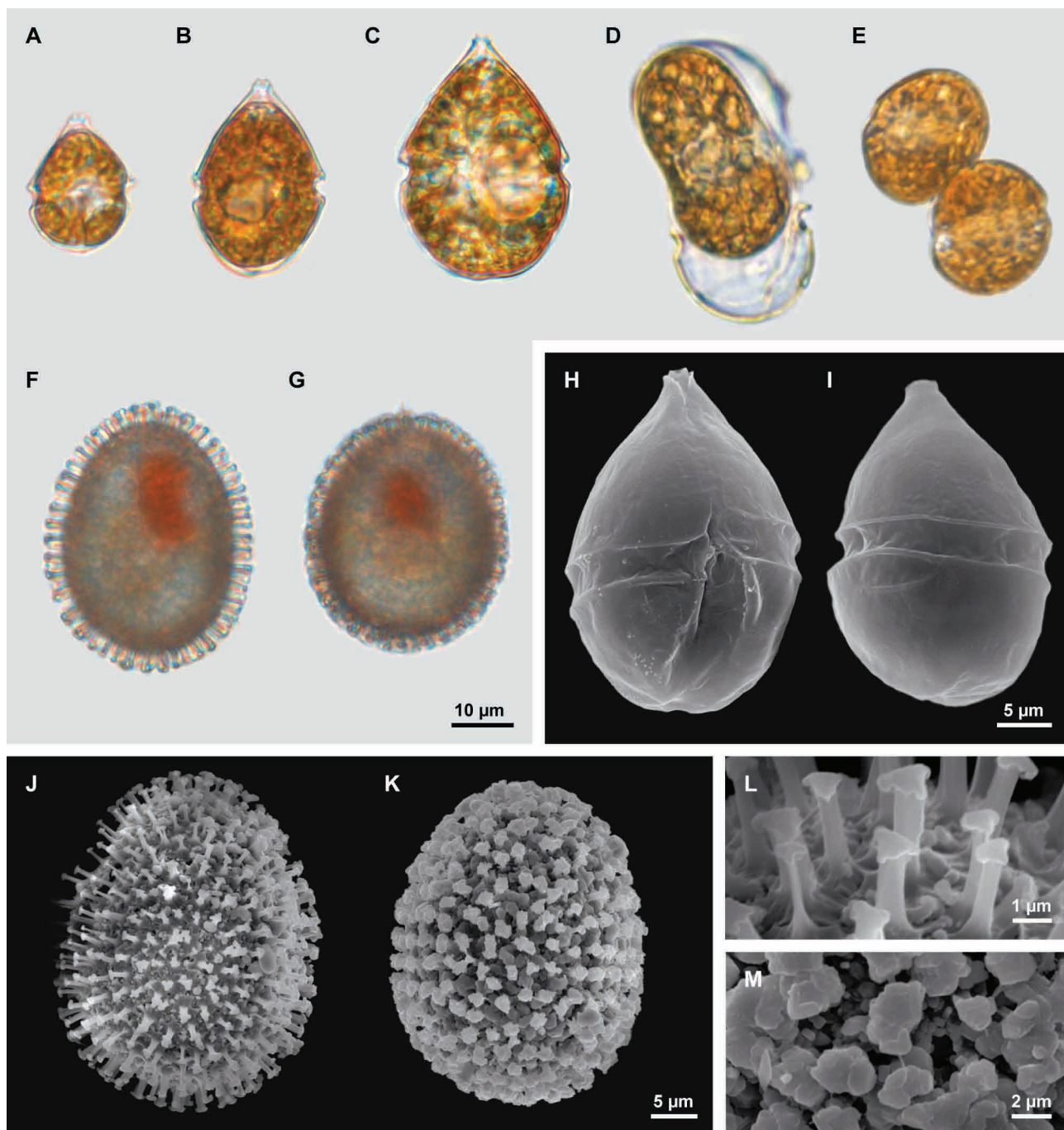


FIGURE 3. Motile and immotile stages during life history of *Scripsiella acuminata*, *comb. nov.* (GeoB 427; A–G: light microscopy, all at the same scale; H–M: scanning electron microscopy). A. Thecate cell of the small-sized morphotype. B. Thecate cell of mid-sized morphotype. C. Thecate cell of large-sized morphotype. D. Immotile cell of the mid-sized morphotype with thecal remnant. E. Two attached mid-sized thecate cells at the bottom of the cultivation plate. F. Coccoid cell with long thin processes. G. Coccoid cell with short thick processes. H. Ventral view of mid-sized thecate cell. I. Dorso-lateral view of mid-sized thecate cell. J. Coccoid cell with long thin processes. K. Coccoid cell with short, thick processes. L. Close-up view of long and thin processes. M. Close-up view of short and thick processes.

The apical pore complex was elongated. The apical pore consisted of a circular apical pore plate and was shielded by a cover plate. A canal (or X or preapical) plate was also present (Fig. 4D). Partitions of the apical collar were not observed. The sulcal region was composed of five plates (Fig. 4B), which varied slightly among individuals in size and shape. The smaller sulcal plates, Sa and Sm, were mostly covered by the larger plates, Sd and Ss.

Along the boundaries of the thecal plates, the overlap of adjacent plates was visible occasionally by growth bands (Figs 4A–C, 5C–D). Generally, it followed an imbricate pattern from dorsal to ventral: In the epitheca, the dorsal

precingular plate 4'' was the keystone plate, as was plate 4C in the cingulum. The keystone plate of the hypotheca was postcingular plate 3''', and the antapical plates laid under the postcingular plates. The large sulcal plate Sp was overlapped by all adjacent plates (Fig. 4B).

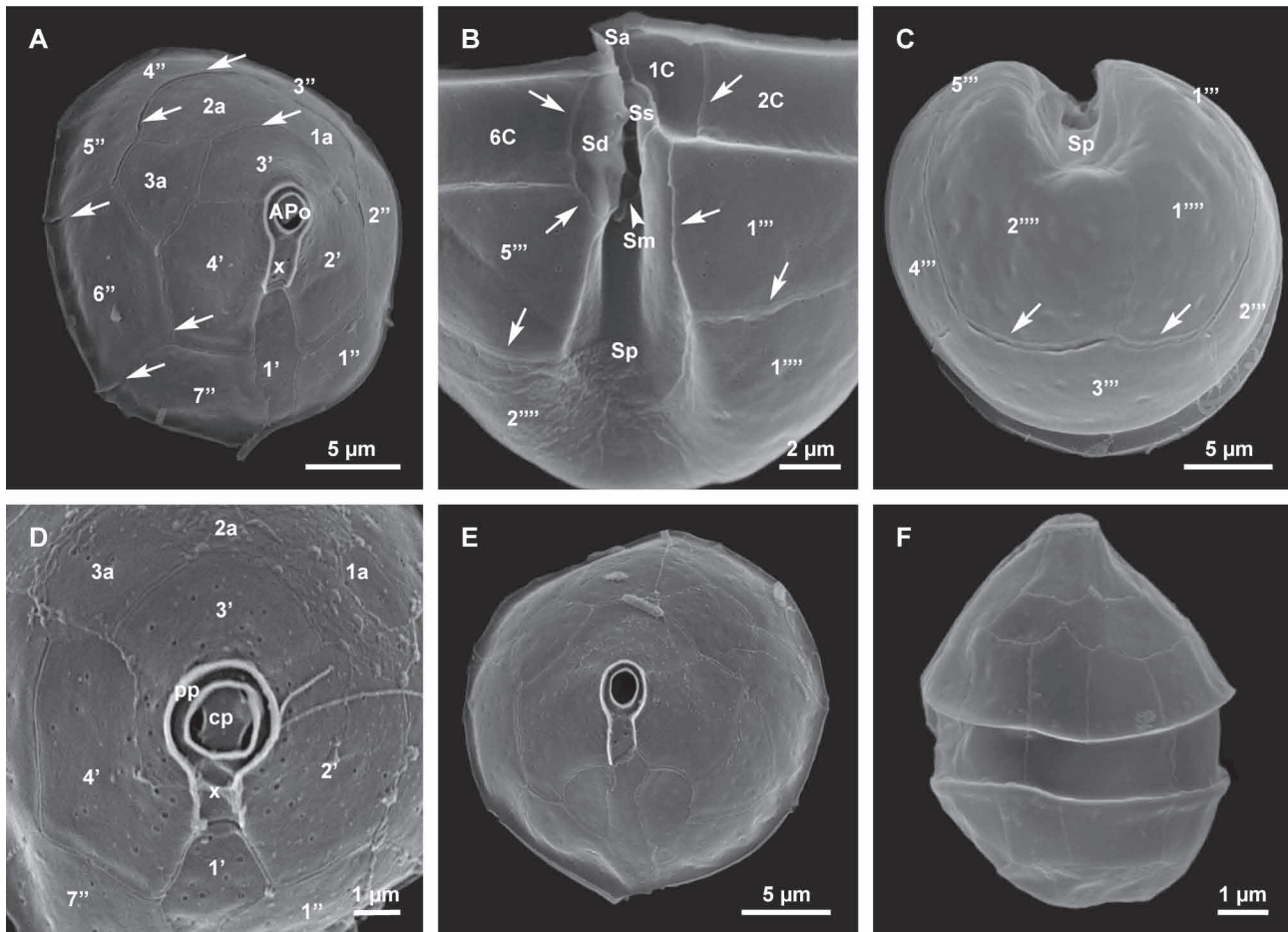


FIGURE 4. Tabulation pattern of the thecate cells of *Scrippsiella acuminata*, *comb. nov.* A. Apical view of epitheca. B. Ventral view of hypotheca with cingulum and sulcal region. C. Antapical view of hypotheca. D. Apical view of the apical pore complex. E. Apical view of epitheca with unusual additional plates. F. Small-sized thecate cell with unusual additional plates (as homologies to the typical conformation is dubious, plates are not indicated). Abbreviations: Apo: apical pore plate. cp: closing plate. n': apical plate. n'': precingular plate. n''': postcingular plate. n''': antapical plate. na: anterior intercalary plate. nC: cingular plate. pp: pore plate. Sa: anterior sulcal plate. Sd: right sulcal plate. Sm: median sulcal plate. Sp: posterior sulcal plate. Ss: left sulcal plate. x: preapical plate. Arrows in A–C indicate plate overlap pattern.

Cell division is normally by eleutheroschisis (Fig. 3D): Many epi- and hypothecae were observed empty at the bottom of the cultivation plates. Thecate cells opened along the upper ridge of the cingulum (*i.e.*, the cingulum was attached to the hypotheca) for releasing dividing or ecdysing cells. It was further observed that an elongated immotile cell laid at the bottom of the cultivation plate with the shed thecate cell next to it (Fig. 3D). In addition, a mid-sized thecate cell (see below) was occasionally attached with its apex to the cingulum of another mid-sized thecate cell (Fig. 3E). Such cell pair swam slowly, and after a few minutes of observation the cells sank down to the bottom of the cultivation plate.

The immotile coccoid cells were spherical to mostly ovoid (Figs 2C, 3F–G, J–K). They were variable in size ranging from (including the processes) 34–56 µm in length (mean: 46 µm; median: 46 µm; SD: 5 µm; n=86) and 30–44 µm in width (mean: 37; median: 38 µm; SD: 3 µm; n=86). During the coccoid stage, a red accumulation body was visible. The outer calcareous layer of the cells was composed of numerous processes. The processes were styliform and narrowly conoid through narrowly pyramidal with a triangular base and varied in length (ranging from 2–5 µm), width and shape (Fig. 3F–G, J–M). The apex of the processes was obtuse or capitate and varied in the same strain at the same moment in time.

The ITS sequence obtained from the strain GeoB 427 (JN982383) was identical to GenBank entry HQ729493 obtained from GeoB*185 (*i.e.*, the strain, from which epitype material of *Gl. trochoideum* was prepared).

Discussion

In a recent review, De Clerck *et al.* (2013) describe how old names of species may become ineffective at fulfilling their 'unique identifier' function, and the possible shift to a rather informal naming system in algae. We trust that it is more respectful when we continuously acknowledge the work of previous researcher generations, and we taxonomists are encouraged to give the clarification also and particularly of old scientific names at least a try. We have all necessary tools at hand, and it appears as the most sensible approach to collect living material from the type locality (and preferable during the same season) for morphological and molecular re-investigations. Material preserved from corresponding cultivated material can then serve for reliable determination after the application of the epitype concept (Greuter *et al.* 1994) available under the ICN. We realise such philosophy in this study by epitypification of *P. acuminatum* (Ehrenberg 1836, 1838) with newly collected material at the type locality in the Kiel Fjord.

Dinophytes have been rarely investigated under the name *P. acuminatum* since its description (Ehrenberg 1836, 1838). Claparède & Lachmann (1859, 1868) observed small (30–40 µm), ovoid cells with a tapered rump (apex, as we know today) from Norway (Bergen Fjord, Sandefjord). They emphasised the high degree of similarity to C.G. Ehrenberg's species, also concerning the rather smooth surface of the cells without any ornamentation. Later, Schütt (1887) reported from the reproduction of a taxon collected at the Kiel Fjord, which he identified as '*Peridinium acuminatum* Ehrenb. = *Goniodoma acuminatum*, Stein'. Because of the punctulate surface and the clear delimitation of thecal plates, we consider this species determination as misidentification probably of gonyaulacalean *Lingulodinium polyedrum* (F.Stein 1883: 13, pl. IV 7–9) J.D.Dodge (1989: 291) firstly described also from the Kiel Fjord (Fig. S1; Tab. 1). Further, Pouchet (1893) investigated material from the Bay of Biscay and reported eight morphologically distinct stages of life history that he assigned to *P. acuminatum*. This would be partly in accordance with our observations of different dimension types of thecate cells, but no dinophyte species is known at present that would include all of C.H.G. Pouchet's morphotypes. He was uncertain himself whether in fact all such stages would represent a single species, and doubts are allowed that he investigated conspecific material.

The information Ehrenberg (1836, 1838) provides is not even sufficient to decide whether *P. acuminatum* is an element of the Peridinales or of the Gonyaulacales (*i.e.*, diagnostic traits of tabulation wanting). Superficially, C.G. Ehrenberg's drawings may resemble *L. polyedrum*, but he observed thecal plates (that are very distinct in *L. polyedrum*) only in other species, but not in *P. acuminatum*. Moreover, *L. polyedrum* has an obtuse apex and a cingulum displaced for (at least) its width (Fig. S1), which conflicts once more with C.G. Ehrenberg's illustrations and descriptions (Tab. 1). The current taxonomic assignment of *P. acuminatum* to the Gonyaulacales, but not to the Peridinales (Drugg & Loeblich Jr 1967, Loeblich Jr & Drugg 1968, Fensome *et al.* 1993), is based on S.F.N.R. von Stein's scientific authority. However, this classification goes back to a misinterpretation of C.G. Ehrenberg's species because of multiple diagnostic reasons:

i) Ehrenberg (1836, 1838) described and drew very explicitly a dinophyte with a tapered epitheca, to which also the epithet '*acuminatum*' refers to. Such structure is not shown by any of the thorough (though heterogeneous: see Electronic Supplement) figures Stein (1883) provides for his species. This was firstly noted by Jørgensen (1899) six years after the introduction of *Goniodoma*, and a number of authors taxonomically excluded *P. acuminatum* from *Goniodoma* (Paulsen 1908, Lemmermann 1910b, Lindemann 1928, Schiller 1937, Balech 1979, Dodge 1981, Sournia 1984).

ii) The distinctly porous surface is a crucial trait of S.F.N.R. von Stein's species (Stein 1883: 12–13); if C.G. Ehrenberg would have investigated that species, then he certainly would have depicted and described such trait, as he did for other species such as *Peridinium cinctum* (O.F.Müll. 1773: 98–99) Ehrenb. (1832: 38).

iii) All armoured cells Stein (1883) drew show distinctive epithecal and hypothecal adcingular lists. Such lists are neither identifiable in C.G. Ehrenberg's illustrations (Fig. 1), nor noted in the description. The cingular cilia, corresponding to the transverse flagellum as we know today, cannot be interpreted as lists, as they were also depicted for other dinophytes doubtlessly without any lists such as *Gymnodinium fuscum* (Ehrenb.) F.Stein (Ehrenberg 1838).

iv) S.F.N.R. von Stein's intension was to describe a heavily armoured dinophyte species. The most significant of his material originated from the (presumably rather subtropical locality in the) Atlantic Ocean, not from the (more temperate) Baltic Sea (*i.e.*, type locality of *P. acuminatum*). The illustrated Baltic cells can be assigned to *Lingulodinium polyedrum* (see Electronic Supplement with Fig. S1), whose thecate (*obs.* Elbrächter, Peters 1930, Hällfors 2004) and resting cysts are continuously reported from the Kiel Fjord (Nehring 1994, 1997).

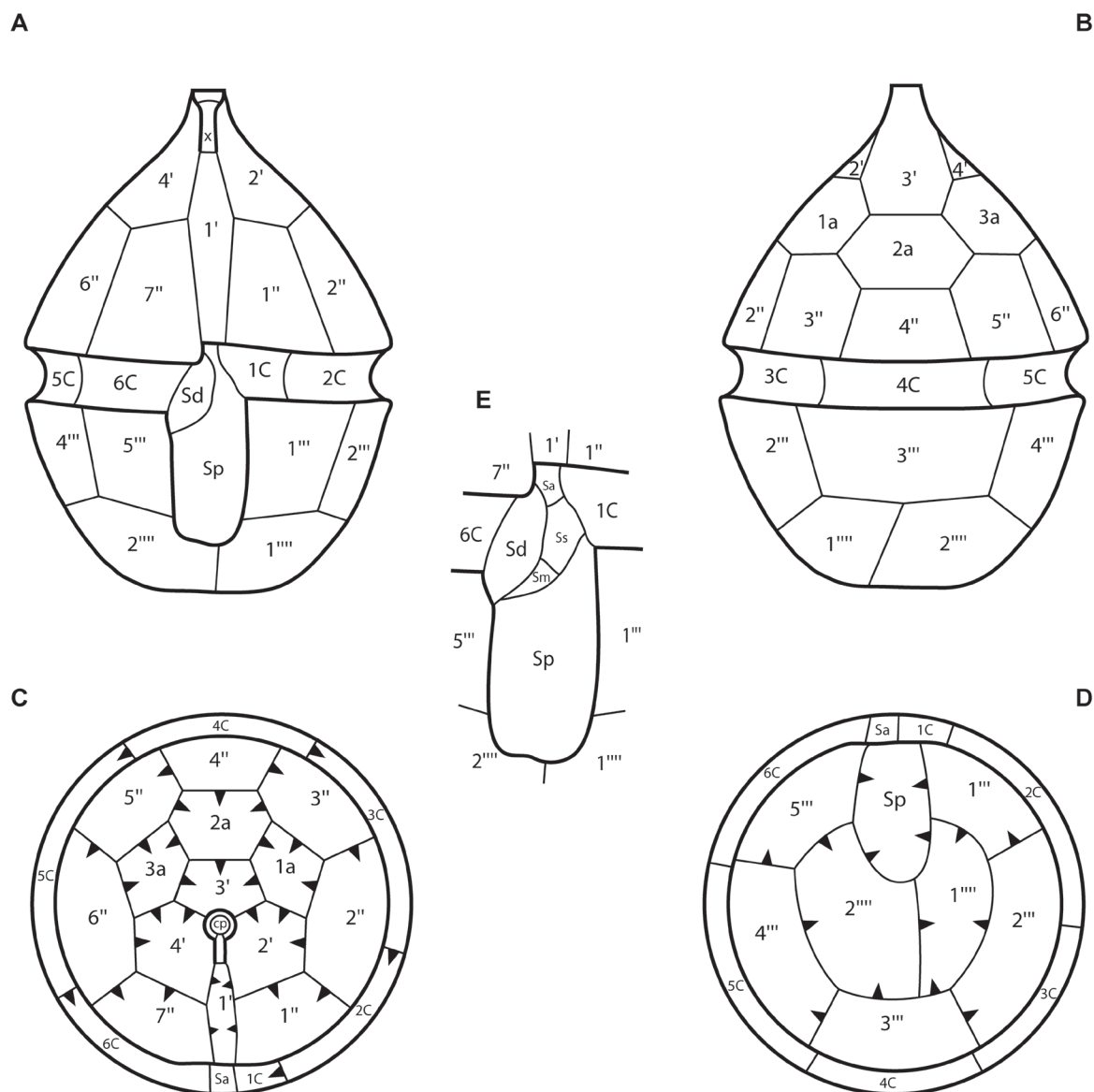


FIGURE 5. Schematic drawing of the thecal plates. A. Ventral view. B. Dorsal view. C. Apical view. D. Antapical view. E. Enlarged sulcal region. Abbreviations: cp: closing plate (graphically surrounded by the pore plate). n': apical plate. n'': precingular plate. n''': postcingular plate. n''': antapical plate. na: anterior intercalary plate. nC: cingular plate. Sa: anterior sulcal plate. Sd: right sulcal plate. Sm: median sulcal plate. Sp: posterior sulcal plate. Ss: left sulcal plate. x: canal (preapical) plate. Arrowheads in C–D indicate plate overlap pattern.

In conclusion, there is overwhelming evidence that the organisms described by Ehrenberg (1836) and Stein (1883) are not conspecific (irrespective of which of the heterogeneous illustrations in Stein 1883 are considered), although both they refer nomenclaturally to the same type material (ICN Art. 7.3.; Fig. 1).

Taxonomically, our experimental observations are not in conflict with the protologue and original descriptions of *P. acuminatum* (Ehrenberg 1836, 1838), and the epitypification now allows for reliable determination of this species, also by means of molecular sequence data. This has crucial importance, as *Scrippsiella acuminata*, *comb. nov.* (Thoracosphaeraeaceae, Peridinales) is a member of a species complex comprising many morphologically so far indistinguishable, but genetically differentiated (*i.e.*, 'cryptic') species (Montresor *et al.* 2003, Gottschling *et al.* 2005, Zinssmeister *et al.* 2011, Kretschmann *et al.* 2014). Moreover, minute morphological characters of the species can now be investigated in more detail. The apical pore complex, for example, shows an arrangement that is (with the exception of *Heterocapsa* F.Stein 1883: 9, 13 and relatives) typical for the Peridinales (Dodge & Hermes 1981, Toriumi & Dodge 1993, Calado *et al.* 2009, Tillmann *et al.* 2010). The plate overlap pattern corresponds to the typical

conformation in the Peridinales (Netzel 1982, Nézan *et al.* 2012, Tillmann & Elbrächter 2013) as does the vegetative cell division by eleutheroschisis. The attached cells shown in Fig. 3 D–E can be interpreted as life history stages during sexual reproduction (the same applies to Fig. 6 in Zinssmeister *et al.* 2011).

Ehrenberg (1836, 1838) considered *P. acuminatum* being luminescent, that is not reported from any species of *Scrippsiella*. As C.G. Ehrenberg was unsure himself about his observation (‘micans?’ in Ehrenberg 1838), this is not seriously conflicting with our taxonomic decision (likewise, neither Jørgensen 1899 nor Lemmermann 1910b nor Dodge 1981 did comment on this problem). Bioluminescence was a major issue at that time (Kusber *et al.* 2005), but observation feasibility was very limited. Ehrenberg fished illuminating water drops with a fine brush (German ‘Federpinsel’) in a dark chamber for subsequent microscopy (Ehrenberg 1836: 537). Subsequently, a number of C.G. Ehrenberg’s ‘Leuchttierchen’ turned out later not being bioluminescent (not even *Prorocentrum micans* Ehrenb. 1835: 307–308 is luminescent at the Kiel Fjord, R. Hardeland, Göttingen, *pers. comm.*).

To the best of our knowledge, a single scrippsielloid species predominates in the Kiel Fjord. Its occurrence has been continuously documented over the past century (*e.g.*, Stein 1883, Lemmermann 1910a, 1910b, Peters 1930, Wasmund *et al.* 2008). *Scrippsiella lachrymosa* Lewis ex Head (1996: 1229) has also been reported sporadically from this locality (Nehring 1994, 1997), but this species can be distinguished from the *S. trochoidea*-like species based on the size of the thecate cell as well as from the morphology of the coccoid stage (Lewis 1991). Aligning *P. acuminatum* with *S. trochoidea* has dramatic nomenclatural consequences. All species names today accepted under *Scrippsiella* (approximately 20 of a monophyletic lineage) would have to be transferred to *Heteraulacus* (less than 10 heterogeneously classified), because *H. acuminatus* has priority over *S. trochoidea*. However, taxa assigned to *Heteraulacus* (and *Goniodoma*) are regarded as gonyaulacalean dinophytes (Stein 1883, Drugg & Loeblich Jr 1968, Loeblich Jr & Drugg 1968). It creates fatal instability if this name is associated with peridiniacean dinophytes belonging to the Thoracosphaeraceae (but excluding the gonyaulacalean taxa from *Goniodoma* and *Heteraulacus*). Given the ecological importance and wide distribution of *Scrippsiella* (D’Onofrio *et al.* 1999, Gómez 2003, Vink 2004, Gu *et al.* 2008), such new combinations would most likely not be accepted by the scientific community. Following the guidelines specified by McNeill *et al.* (2007), proposals to conserve *Scrippsiella* against *Heteraulacus* (and *Goniodoma*; ICN Art. 14.; Gottschling & Elbrächter in press) and to reject the name Goniodomataceae (Elbrächter & Gottschling in press) are thus submitted in parallel to this study.

Taxonomic conclusions

Morphology and molecular sequences of *P. acuminatum* are distinct from *P. cinctum*, the type species of *Peridinium*. Instead, the results of our study confirm conspecificity between *P. acuminatum* and *S. trochoidea*. As *P. acuminatum* is the older scientific name (Ehrenberg 1836, 1838) it has priority over the basionym of *S. trochoidea* (Stein 1883). Therefore, we recombine here *P. acuminatum* with the established taxon *Scrippsiella*. The cells depicted on pls VII 1–16, VIII 1–2 in Stein (1883) under ‘*Go. acuminatum*’ are explicitly excluded from *S. acuminata*, *comb. nov.*

Scrippsiella acuminata (Ehrenb.) Kretschmann, Elbr., Zinssmeister, S. Soehner, Kirsch, Kusber & Gottschling, *comb. nov.*

Basionym: *Peridinium acuminatum* Ehrenb., *Abhandlungen der Königlichen Akademie der Wissenschaften in Berlin* 1834: 541, 575, pl. II 5, 1836.

≡ *Heteraulacus acuminatus* (Ehrenb.) Diesing, *Systema helminthum* 1: 100–101, 1850.

≡ *Goniodoma acuminatum* (Ehrenb.) F. Stein, *Der Organismus der arthrodelen Flagellaten nach eigenen Forschungen in systematischer Reihenfolge bearbeitet* 2: 12–13, 1883.

≡ *Glenodinium acuminatum* (Ehrenb.) E. Jørgensen, *Bergens Museums Aarbog* 1899.6: 32, 1899.

≡ *Yesevius acuminatus* (Ehrenb.) Özdikmen, *Munis Entomology & Zoology* 4: 23, 2009, *nom. illeg.*

Type:—FEDERAL REPUBLIC OF GERMANY. Baltic Sea: Schleswig-Holstein, Kiel Fjord, August 1834 [extant], *G.A. Michaelis*, *s.n.* (holotype: fig. II 5! in *Abhandlungen der Königlichen Akademie der Wissenschaften in Berlin* 1834, 1836, original drawing sub No. 938 at BHUPM!, no physical material found; Baltic Sea, off Federal Republic of Germany, Schleswig-Holstein, Kiel Fjord, 18th March 2009 [extant]: *M. Gottschling, K.J.S. Meier, S. Söhner & C. Zinßmeister*, *s.n.* [GeoB 427], Epitype designated here: CEDiT2014E40!, Centre of Excellence for Dinophyte Taxonomy, isoepitypes: B400041372! M2297511!; illustrated here in Fig. 2).

= *Scrippsiella trochoidea* (F.Stein) A.R.LoebL., *Journal of Protozoology* 23: 25, 1976.

Basionym: *Glenodinium trochoideum* F.Stein, *Der Organismus der arthrodelen Flagellaten nach eigenen Forschungen in systematischer Reihenfolge bearbeitet* 2: pl. III 27–29, 1883.

≡ *Peridinium trochoideum* (F.Stein) Lemmerm., *Archiv für Hydrobiologie und Planktonkunde* 5: 336–338, figs 33–36, 1910b.

Type:—FEDERAL REPUBLIC OF GERMANY. Baltic Sea: Schleswig-Holstein, Kiel Fjord, *s.d.* [extant]: *S.F.N.R. von Stein, s.n.* (holotype: pl. III 27–29! in *Der Organismus der arthrodelen Flagellaten nach eigenen Forschungen in systematischer Reihenfolge bearbeitet* 2, 1883; Baltic Sea, off Federal Republic of Germany, Schleswig-Holstein, Kiel Fjord, *Apr 2000* [extant]: *K.J.S. Meier, s.n.* [GeoB*185], Epitype designated in Zinssmeister *et al.* (2011: 155): CEDiT2011E13!, isoepitypes B400040745! BREM! M156524!).

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Electronic Supplement

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Determined as *Goniodoma acuminatum* F.Stein (1883: 12–13), S.F.N.R. von Stein investigated material from the Kiel Fjord (pl. VII 1–2, 9–12) and the Atlantic Ocean as well (pls VII 3–8, 13–16, VIII 1–2; Fig. S1). He provides a detailed description of heavily armoured gonyaulacoid cells with a distinctly punctulate surface (p. 12–13) and refers explicitly to pl. VII 1–8 in the text. These descriptions and illustrations are the taxonomic basis for determining such organisms currently as species of *Goniodoma* F.Stein (1883: 9, 12, 13, 16, 19, 21) [and *Heteraulacus* Diesing (1850: 9, 100)]. Additionally, Stein (1883) noted stages of life history comprising unarmoured motile, coccoid and juvenile cells in the figure captions to pl. VII 9–16 (but not in the main text) and illustrated them as well. None of these figures, however, can be unequivocally assigned to *Peridinium acuminatum* Ehrenb. (1836: 541, 575, pl. II 5; Ehrenberg 1838), whose taxonomic identity has been clarified based on material collected at the type locality in the Kiel Fjord in the main text as species of *Scrippsiella* Balech (1959: 199–200) (Thoracosphaeraceae, Peridinales). Thus, the identity of S.F.N.R. von Stein's species (*i.e.*, “*Goniodoma acuminatum*”) remains to be discussed.

It finally remains unresolved whether Stein (1883) truly regarded *Go. acuminatum* as a dinophyte species exhibiting different morphologies. Today—after more than a century of dinophyte research—species currently assigned to *Goniodoma* (and *Heteraulacus*) are exclusively known as thecate cells with a prominent gonyaulacoid tabulation and ornamentation (*i.e.*, without any unarmoured or coccoid life history stages: Fensome *et al.* 1993). This concept corresponds to S.F.N.R. von Stein's pl. VII 3, 6–7, which were all drawn from material collected in the Atlantic Ocean and were variously reproduced as *Go. acuminatum* or *Goniodoma polyedricum* (C.H.G.Pouchet) Jørg. (1899: 33) in identification and textbooks such as Paulsen (1908), Lindemann (1928), Schiller (1937) and Fensome *et al.* (1993). Moreover, organisms currently assigned to *Goniodoma* are—to the best of our knowledge—not documented (as unequivocal images) from the Baltic Sea in general and from the Kiel Fjord in particular over a long period of time. Doubts are thus allowed that S.F.N.R. von Stein's illustrations represent a single species, which he collectively regarded as conspecific with *P. acuminatum* (as objective synonym).

Since Bütschli (1885: 1004), *Go. acuminatum* (pl. VII 3, 6–7 in Stein 1883) and *Go. polyedricum* are considered heterotypic synonyms of the same species (that is not conspecific with C.G. Ehrenberg's *P. acuminatum*). A number of authors followed that conclusion (Jørgensen 1899, Paulsen 1908, Lemmermann 1910, Lindemann 1928, Schiller 1937, Balech 1979, Dodge 1981, Sournia 1984), implying various, partly contradicting nomenclatural consequences (see main text and Gottschling & Elbrächter in press). Opposing the authors of previous publications, we postulate that i) the drawings in Stein (1883) represent heterogeneous material from distant localities corresponding to at least three morphotypes (and presumably species) differing in general shape, size, tabulation and shape of nucleus; and ii) the drawings of pl. VII 3–7 in Stein (1883) are not conspecific with *Peridinium polyedricum* C.H.G. Pouchet (1883: 440, pl. XX 34).

ad Postulate 1:—Stein (1883) stated that he was not able to establish the complete tabulation of his organism based on the material from the Kiel Fjord and subsequently succeeded with material collected in the Atlantic Ocean. The thecate cells depicted in pl. VII 1–2, 9 represent material from the Kiel Fjord. They are obviously smaller than those shown in pl. VII 3–8 based on material from the Atlantic Ocean. Moreover, they are all in dorsal view and do not show the characteristic ventral, apical or antapical tabulation of currently accepted *Go. acuminatum*. In pl. VII 1–2, 9–10, we speculate that S.F.N.R. von Stein illustrated cells of *Gonyaulax polyedra* F.Stein (1883: 13, pl. IV 7–9) [= *Lingulodinium polyedrum* (F.Stein) J.D.Dodge (1989: 291)], which he also described from the Kiel Fjord (compare to pl. IV 7–9 in Stein 1883). The same may apply to the taxon Schütt (1887) collected at the Kiel Fjord, which he identified as ‘*Peridinium acuminatum* Ehrenb. = *Goniodoma acuminatum*, Stein’. Thecate (and corresponding coccoid) cells of *L. polyedrum* are reported from the Kiel Fjord (*obs.* Elbrächter; Nehring 1994, 1997; Hällfors 2004), while *Go. acuminatum* in the sense of Stein (1883: pl. VII 3, 6–7) is not unequivocally documented at this locality. We will not speculate here about the identity of such putatively coccoid cells as depicted in pl. VII 11–12, particularly those with intracellular daughter cells, as well as the ‘juvenile stages’ shown in pl. VII 15–16.

ad Postulate 2:—*Peridinium polyedricum* was described from the Mediterranean Sea (at Bouches-du-Rhône, Marseille), and pl. XX 34 in Pouchet (1883) is the type of the species, as no original material could be relocated in the course of this survey. According to Kofoid (1911: 208–209), Pouchet (1883) dates back to a few months earlier (July or August) than Stein (1883) (mid or end of November), giving the epithet ‘*polyedricum*’ priority if both are regarded as conspecific. Moreover, the illegitimate approach of Dodge (1981) to replace *Goniodoma* (and *Heteraulacus*) with *Triadinium* J.D.Dodge (1981: 278) was superfluous (ICN Arts 52.1, 52.2), as he included the type

of a name (*i.e.*, *Goniodoma* with the type *P. acuminatum* in synonymy) which ought to have been adopted under the rules (Sournia 1984, Fensome *et al.* 1993). *Triadinium* is not available under the ICZN (Art. 52.2) as well, because it is a later homonym of a ciliate. In consequence, Nakada (2010) introduced *Pyrrhotriadinium* Nakada (2010: 205), with the type species *Pyrrhotriadinium polyedricum* (C.H.G. Pouchet) Nakada (2010: 205). This generic name is well suited to harbour all gonyaulacoid taxa listed by Nakada (2010) and so far assigned to *Goniodoma* (and *Heteraulacus* and *Triadinium*) by various authors and depicted in identification or textbooks (Paulsen 1908, Lindemann 1928, Schiller 1937, Fensome *et al.* 1993).

C.H.G. Pouchet's species and that of Stein (1883) with pl. VII 3–8 are doubtlessly similar and likely elements of *Pyrrhotriadinium*. Particularly, pl. VII 13–14 of Stein (1883) is in agreement with the plate designation for *P. polyedricum* of Fensome *et al.* (1993), with the first apical homologue ('1u') narrower and more extended to the apex than the right sulcal homologue ('1i'). This is likewise recognisable in figures 9–10 of Dodge (1981) and in accordance with the illustrations of Pouchet (1883). However, morphological differences can be stated for the other illustrations: the plates '1u' and '1i' are more or less symmetric in pl. VII 3–8, which distinguishes such cells from the true *P. polyedricum*. Moreover, the presence of characteristically elevated lists aligning the sutures of the major thecal plates is a distinctive trait of *P. polyedricum* described and illustrated in pl. XX 34 of Pouchet (1883) and clearly confirmed by the SEM figures 9–11 in Dodge (1981) a century later. In all figures of Stein (1883) showing thecate cells or their parts (*i.e.*, pls VII 1–9, VIII 1–2), such lists are not shown, with the only exception of pl. VII 13–14 that can be reliably determined as *P. polyedricum*.

In conclusion, we disagree with Jørgensen (1899) and subsequent authors that S.F.N.R. von Stein's species is based on homogeneous material and would be conspecific with *P. polyedricum*. The species determined as *G. acuminatum* (Stein 1883) and depicted in pl. VII 3, 6–7 remains a weakly known and so far unnamed taxon under *Pyrrhotriadinium* from the Atlantic Ocean that requires morphological and molecular re-investigation.

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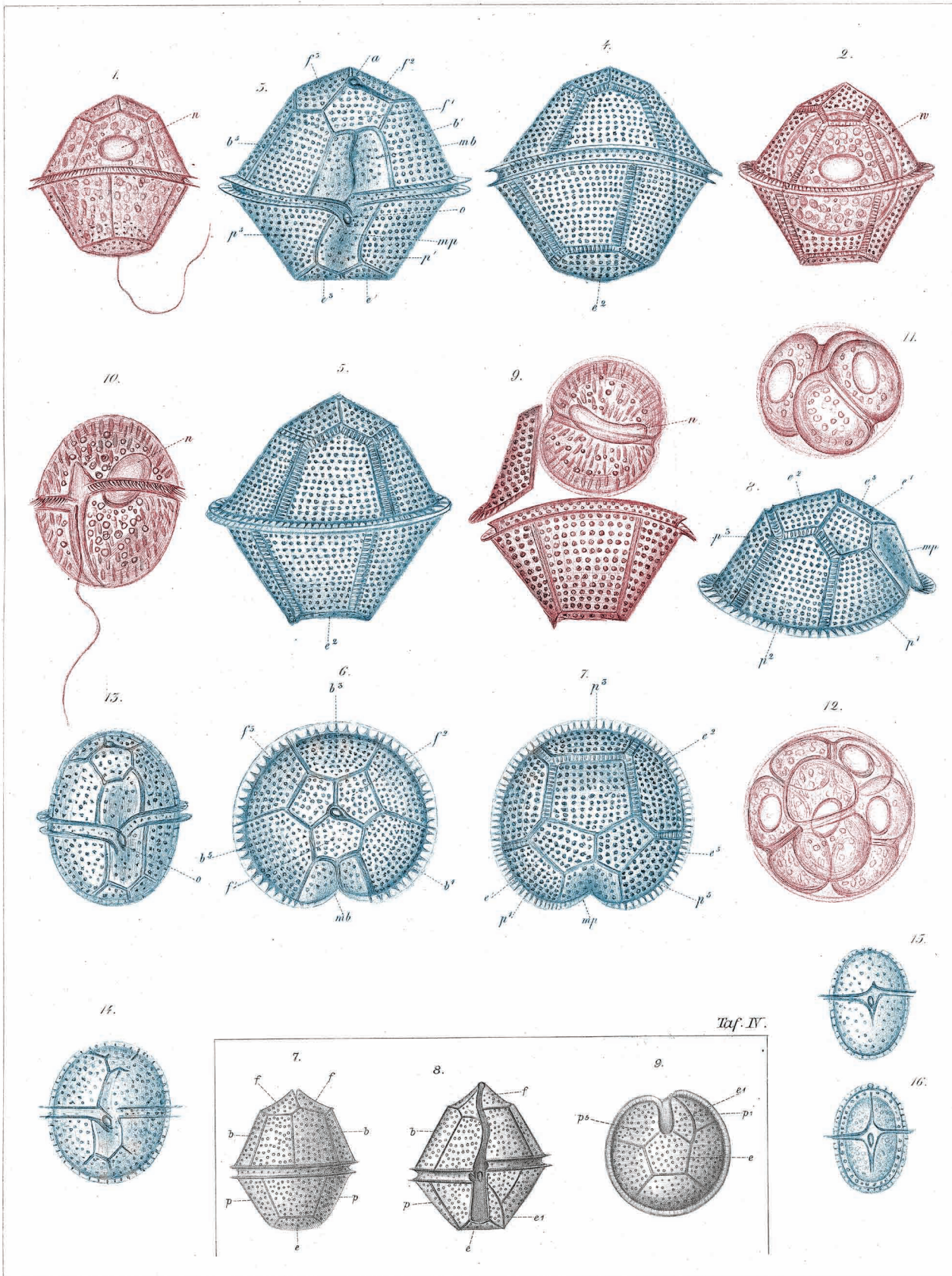


FIGURE S1: Selected reproduction of plates (Stein 1883) illustrating *Goniodoma acuminatum* (pl. VII; material from the Baltic Sea is stained in red, while Atlantic material is blue) and *Gonyaulax polyedra* (pl. IV: type).