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Dual nomenclature in organic-walled dinoflagellate cysts I: concepts, methods and applications

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Abstract :

Dual nomenclature in dinoflagellates is supported under the current nomenclatural code for algae, fungi and plants and allows a fossil-defined (usually cyst) species to bear a name other than that of its equivalent non-fossil species, as established for example by incubation experiments. Two names can then apply to the same cyst morphotype, reflecting the separate concepts and criteria used for fossil- and non-fossil taxa. Fossil-species are normally and logically assigned to fossil-genera and non-fossil species to non-fossil genera, a practice that facilitates dual nomenclature. Inconsistencies and ambiguities arise when binomials combine the names of fossil- with non-fossil taxa. Examples of this hybridized nomenclature and its consequences are examined, with problems identified and potential solutions discussed. Accordingly, a new non-fossil genus Lingulaulax is proposed with Lingulaulax polyedra (von Stein 1883) comb. nov. as its type and equivalent to the fossil-species Lingulodinium machaerophorum (Deflandre and Cookson 1955) Wall 1967, along with the new combination Lingulaulax milneri (Murray and Whitting 1899); the genus Lingulodinium Wall 1967 is retained in its exclusively fossil status. The non-fossil name Gonyaulax ellegaardiae Mertens et al. 2015 is validly published herein

Keywords : Dinocyst, taxonomy, dual nomenclature, hybridized names, Lingulodinium, Lingulaulax

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1. Introduction

Separate taxonomic and nomenclatural traditions have arisen independently among paleontologists studying fossils and biologists examining the entire life cycle. A fossil-species has a holotype that is a fossil, and a non-fossil species has a holotype that is not a fossil (Gravendyck et al. 2021). When a named fossil-species is linked, usually by

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germination studies, to a named species defined using non-fossil (living) material, then two names are available for the same cyst morphotype; no formal rules determine which of these name is used. This is dual nomenclature. The International Code of Nomenclature for algae, fungi and plants (ICN, Turland et al. 2018), which governs the naming of dinoflagellate taxa, allows fossil- and non-fossil taxa to have separate names even when they are subsequently demonstrated to be linked (see Section 3 below). The ICN therefore sanctions the use of dual nomenclature.

The confirmed fossil record of dinoflagellates (division Dinophyta) extends back to the Middle or Late Triassic (e.g. Mangerud et al. 2019) and has been studied extensively (e.g. Stover et al. 1996). This record is based almost exclusively on the cyst stage of the life cycle, as the motile stage rarely preserves (Head 1996). For most species with a fossil record, the cysts are organic-walled and appear in palynological preparations. This article primarily addresses formally named dinoflagellate taxa that produce organic-walled cysts, although many aspects will be relevant also to dinoflagellate cysts with calcareous walls.

Downie et al. (1961) proposed that all dinoflagellates should be treated under the botanical code (now the ICN) rather than the International Code of Zoological Nomenclature (ICZN, Ride et al. 2020) to promote stability and consistency, but also because the botanical code, unlike the ICZN, provides for the use distinct fossil taxa (the successor to “form-genera” as referenced by Downie et al. 1961; see Subsection 3.1 below) which allows the use of dual nomenclature. Presently, all fossil dinoflagellate cyst researchers and nearly all biologists treat dinoflagellates under this code. Nonetheless, because dinoflagellates as a group include heterotrophs, mixotrophs, symbionts and

parasites as well as phototrophs (e.g. Schnepf and Elbrächter, 1992), some biologists (e.g. Balech 1944 et seq., see Head 1996, p. 1227; Coats et al. 2012, p. 4; Choi et al. 2021) have treated dinoflagellates as protozoans and hence named them under the ICZN. Names "available" (validly published) under the ICZN are automatically accepted as validly published when treated under the ICN (Art. 45), where dual nomenclature then applies. The ICZN recognizes only those names treated as "as animals for the purpose of nomenclature" (ICZN Art. 1.1.1). Notably, the ICN requires that the code used by the author be "determined through internal evidence, irrespective of any claim by the author as to the group of organisms to which the taxon is assigned" (Art. 45.1). Evidence of using the ICZN would include the suffixes chosen for suprageneric names (e.g. "-ida" or "-idae" for familial names in the ICZN, rather than "-aceae" under the ICN) and the application of stem augmentation for specific and subspecific epithets (e.g. the specific epithet *tregouboffi*, rather than *tregouboffii* under the ICN). We propose in the interests of nomenclatural stability (see Head, 1996, p. 1227 for further discussion) that such internal evidence extend to the *absence* of a Latin diagnosis as this has never been required under the ICZN. For example, on this basis we accept that Halim (1960) described the important non-fossil genus *Alexandrium* and its holotype species *Alexandrium minutum* under the ICZN, contrary to the views of Woelkerling and Moestrup (2022, but see also McNeill 2023), and is therefore validly published under the ICN. The nomenclatural status of *Alexandrium* is discussed in Table 1.

Fossil-defined names are typically used by those who work primarily with the cyst stage, for example in biostratigraphic age determinations, in documenting the geographic distributions of modern cysts, or in helping to interpret past environmental

conditions, including climate. Non-fossil-defined names are used mainly by biologists, who may have access to all stages of the life cycle and who have in the past mostly focused on the motile stage(s). There is an understandable desire to integrate these two taxonomic and nomenclatural systems, allowing information to flow more freely between biological and geological realms (Ellegaard et al. 2018). However, the inevitable problems with unifying this nomenclature (at least at generic and lower rank; Fensome et al. 1993) have been long anticipated (e.g. Downie et al. 1961; Evitt and Davidson 1964, p. 10–11; Evitt 1970, p. 38; Reid 1974; Dale 1983), and attempts to effect unification (e.g. Harland 1982) have not been widely adopted.

In this article we evaluate the provisions of the ICN that support dual nomenclature and investigate the origins of this duality. We then assess the practical difficulties of unification and explore inconsistencies in nomenclature when binomials are created that combine the names of fossil- with non-fossil taxa (Table 2). Recommendations using dual nomenclature are offered to resolve ambiguities introduced by these hybridized names, and a solution is provided regarding the fossil-genus *Lingulodinium* Wall 1967 emend. Wall and Dale in Wall et al. 1973, which presently contains both non-fossil and fossil-species. Full authorial attributions of taxonomic names cited in the text are listed in Table 1. The ICN (Turland et al. 2018) includes a glossary of nomenclatural terms, and Turland (2019) also contains helpful definitions. For definitions of morphological terms, the reader is directed to Williams et al. (2000). The abbreviation "Art." refers to an article of the current ICN (Turland et al. 2018) unless otherwise stated.

2. The origins of dual nomenclature in dinoflagellates

Living dinoflagellate resting cysts were first documented in the 19th century (noted in von Stein 1878; illustrated e.g. in von Stein 1883; Penard 1891; Schilling 1891; Delage and Herouard 1896). Biologists subsequently studied them from culture (Braarud 1945) and in the plankton (e.g. Nordli 1951), and they were identified from sediment by the paleo- and actuopalynologist Erdtman (1954). These early contributions by Nordli, Erdtman and especially Braarud led the paleontologist Evitt (1961) to his breakthrough realization that dinoflagellate cysts have a long and comprehensive geological record (Dale 2021). Evitt (1961) recognized that many post-Paleozoic chorate organic-walled microfossils with spines or processes, including the important genera *Hystrichosphaera* (now considered a heterotypic synonym of *Spiniferites*), *Hystrichosphaeridium* and *Cannosphaeropsis*, were in fact the chorate cysts of dinoflagellates (although he also considered many proximate cysts to be fossilized motile stages – an error corrected in Evitt 1963, and Evitt and Davidson 1964). Evitt and Davidson (1964) extended this knowledge with observations of modern dinoflagellate cysts, and they discussed the potential complications arising from the separate nomenclatures developing independently for both fossil cysts and motile stages, as first recognized by Downie et al. (1961) and subsequently addressed by Deflandre (1962).

By incubating a living cyst and identifying the emergent motile cell, Wall (1965) directly linked the fossil cyst species *Spiniferites bentorii* (as *Hystrichosphaera bentorii*), described from the Quaternary of the coastal plain of Israel (Rossignol 1964), to its

motile-defined equivalent, *Gonyaulax digitale*. Subsequent incubation studies by Wall and Dale (1966) linked the fossil cyst species *Spiniferites bulloideus* (as *Hystrichosphaera bulloidea*) from the Middle Miocene of Balcombe Bay, Australia (Deflandre and Cookson 1955), to the motile-defined *Gonyaulax scrippsae*. They also identified the prospective equivalencies of *Operculodinium centrocarpum* (as *Baltisphaeridium centrocarpum*) and *Lingulodinium machaerophorum* (as *Baltisphaeridium machaerophorum*), both from the Middle Miocene of Balcombe Bay, Australia (Deflandre and Cookson 1955), with the motile-defined *Protoceratium reticulatum* and *Lingulodinium polyedra* (as *Gonyaulax polyedra*), respectively. Although some of the proposed equivalencies can now be challenged or revised (e.g. Gu et al. 2021; Table 2), these and others studied later revealed that numerous dinoflagellates described as fossils are represented by already-named living organisms (the "living fossils" of Wall and Dale 1966): thus fossil and non-fossil taxonomies and their corresponding nomenclatures were overlapping.

3. ICN and fossil-taxa versus non-fossil taxa

Dual nomenclature essentially requires only that separate names for fossil and non-fossil taxa be allowed, as has long been the case, provided that *equivalence* (Head et al. 2016) and not *synonymy* (a taxonomic decision influenced by conceptual considerations as discussed in Subsection 3.2 below) is invoked. Dual nomenclature for algae, excepting diatoms, is admissible under the current ICN, being supported by Arts. 1.2, 11.1, 11.7,

11.8, with Arts. 13.3 and 52.1 also relevant (Head et al. 2016; Head et al. 2024). The ICN fundamentally distinguishes between non-fossil taxa and fossil-taxa (Art. 1.2), each of which will have its own particular circumscription. Art. 11.1 states that "The use of separate names is allowed for fossil-taxa that represent different parts, life-history stages, or preservational states of what may have been a single organismal taxon or even a single individual." Key developments applicable to fossil and non-fossil dinoflagellate nomenclature are discussed below and summarized in Table 3.

As an aside, the inadmissibility of dual nomenclature for diatoms under the ICN may seem at odds with its availability for dinoflagellates when both algal groups have a resting stage and a vegetative stage. The difference, however, is that the vegetative stage in diatoms is geologically preservable, and this stage is most commonly studied in the fossil record. Because the taxonomy of living diatoms is also based on the vegetative stage, so extinct fossil-species based on the vegetative stage can be assigned to non-fossil genera using morphological criteria alone. Fossil spores have long been neglected in diatom studies (Suto 2004; Suto and Tanaki 2017) but, in parallel with dinoflagellates, fossil-species based on spores cannot easily be integrated into the generic scheme for non-fossil diatoms.

3.1. Historical development of plant fossil and algal nomenclature

The naming of plant fossils long predates what was effectively the first botanical code as adopted by the International Biological Congress in Paris in 1867 (the Paris "Lois" or laws or rules; de Candolle 1867). The nomenclature of organs and fossils was subsequently discussed, and a revised edition of the "Lois" (de Candolle 1883) explicitly

accepted that the rules also applied to plant fossils, although the Vienna Rules of 1906 (Briquet et al. 1906) were the first to acknowledge the special needs of fossils; these were addressed in the Brussels Rules of 1912 (Briquet 1912). With the establishment of the International Association of Plant Taxonomy (IAPT) at the 7th International Botanical Congress in Stockholm in 1950 (Cowan and Stafleu 1982), each successive iteration of the "Rules" was thereafter known as the "International Code of Botanical Nomenclature" (ICBN). This was to change only in 2012, with the Melbourne Code (McNeill et al. 2012) adopting the new title "International Code of Nomenclature for algae, fungi, and plants" (ICN) in acknowledgement that the fungi in particular are not considered plants.

Of crucial significance was a growing awareness that the fragmentary nature of plant fossils required taxonomic approaches that were different from living plants, and separate nomenclatural rules have therefore evolved to meet these particular needs (Table 3). The Stockholm Code of 1952 (Lanjouw et al. 1952) introduced an Appendix on fossils, which included the concepts of "organ-genera" to reflect the different preserved parts of the plant and their modes of preservation, and "form-genera" as a small subset of organ-genera containing species grouped superficially and not generically related in the ordinary taxonomic sense (Cleal and Thomas 2010). The Montreal Code of 1961 (Lanjouw et al. 1961) defined the organ-genus as a genus assignable to a family, and a form-genus as unassignable to a family and hence "artificial in varying degree". The concept of organ-genus was discontinued in the Leningrad Code of 1978 (Stafleu et al. 1978), and the "morphotaxon" was introduced in the St Louis Code of 2000 (Greuter et al. 2000) as "a fossil taxon which, for nomenclatural purposes, comprises only the parts, life-history stages, or preservational states represented by the corresponding

nomenclatural type" (Art. 1.2). This definition was restricted in the Vienna Code of 2006 (McNeill et al. 2006) to apply to a single part, life-history stage, or preservational state (Art. 1.2, and its note 1). The morphotaxon concept was, however, considered too restrictive and was discontinued in the Melbourne Code of 2012 in favour of the simpler and more flexible concept of "fossil-taxon". The term "fossil taxon" had first appeared in the St Louis Code of 2000 for a name based on a fossil type (Art. 13.3), and more prominently featured in the Vienna Code of 2006, in both cases without hyphenation. The Melbourne Code introduced the hyphen, as "fossil-taxon". Fossil-taxa can therefore be regarded conceptually, with qualification, as the successor of organ-genera and form-genera (Cleal and Thomas 2010), although it might be noted that all these concepts effectively allowed fossils representing different life-history stages to bear separate names, with clear relevance to fossil dinoflagellate nomenclature.

The Edinburgh Code of 1966 introduced the requirement of "stratigraphic relations" at the site of original occurrence for fossil taxa, thus distinguishing them from "Recent material" (Art. 13 note 3 in Lanjouw et al. 1966). "Recent" for the first time was capitalized throughout, implying reference to the Holocene Epoch, as these terms were being used interchangeably at that time. The Sydney Code of 1983 clarified the relationship between "fossil" and "recent" (now lowercased) plants by referring to the latter as "non-fossil" plants (Voss et al. 1983), and the Melbourne Code of 2012 saw the elimination of "subfossil" which was introduced in the Stockholm Code of 1952 and had never been defined. This unambiguously allowed cysts recovered from modern naturally deposited sediments to be treated as fossils (Head 2003; Head et al. 2024; and Subsection 3.2 below).

Several starting dates of relevance for the valid publication of fossil-taxa and non-fossil algal taxa introduced over successive editions of the Code are incorporated into the present (Shenzhen) Code of 2018 (Turland et al. 2018): the article numbers that follow are from this Code. The name of a new taxon of non-fossil algae published between 1 January 1958 and 31 December 2011, inclusive, must be accompanied by a Latin description or diagnosis or by reference to such (Art. 44.1, introduced in the Paris Code of 1956 [Lanjouw et al. 1956] and Melbourne Code of 2012). The name of a new fossil-taxon published on or after 1 January 1996 must be accompanied by a Latin or English description or diagnosis or by reference to such (Art. 43.1, introduced in the Tokyo Code of 1994; Greuter et al. 1994); and the same is true for a new non-fossil taxon published from 1 January 2012 (Art. 39.2, introduced in the Melbourne Code of 2012). Latin therefore ceased to become a requirement for the diagnoses or descriptions of non-fossil taxa from 1 January 2012 (this had been the case for fossil-taxa from 1 January 1996), a decision met with spontaneous applause at the Nomenclature Section of the 18th International Botanical Congress in Melbourne in 2011.

A name of a new species or infraspecific taxon of non-fossil algae, from 1 January 1958, must be accompanied by an illustration or figure showing the distinctive morphological features of this taxon, or by a reference to such an illustration or figure (Art. 44.2; introduced in the Paris Code of 1956). The valid publication of a name of a new fossil-species or infraspecific fossil-taxon from 1 January 2001 requires the type specimen to be identified among the validating illustrations (Art. 43.3; introduced in the St Louis Code of 2000). The type of a name of a new non-fossil taxon at the rank of species or below published before 2007 may be an illustration; but from 1 January 2007,

the type must be a specimen except where, in the case of a non-fossil microscopic organism, preservation is technically difficult (Art. 40.4 and 40.5; introduced in the Vienna Code of 2006). A type specimen of an algal taxon may be a culture preserved in a metabolically inactive state (Art. 8.4; introduced in the St Louis Code of 2000); but from 1 January 2019, if a new name has such a type, this must be specified within the protologue (Art. 40.8; introduced in the Shenzhen Code of 2018).

The first example of dual nomenclature in dinoflagellates appeared in the St. Louis Code of 2000 (under Art. 11.7; the fossil-genus *Tuberculodinium* vs. the non-fossil *Pyrophacus*), and the current Shenzhen Code contains a total of three such examples (in Arts. 11.7 and 11.8; but see Head et al. 2024). Texts of the Laws, Rules and Codes noted above are available online, showing successive changes to each version (van Rijckevorsel 2014–2020).

3.2. Theoretical considerations

The name of a fossil-taxon does not compete for priority with that of an equivalent non-fossil taxon where it is not considered a synonym of that non-fossil taxon (Art. 11.8) (Head et al. 2024). For example, Reid (1977) proposed the name *Votadinium spinosum* for a fossil cyst he considered equivalent to the cyst of *Peridinium claudicans* (now *Protoperidinium claudicans*) as illustrated by Wall and Dale (1968), who had incubated this cyst type and identified the emergent theca (see Matsuoka and Head 2013, for further discussion). Reid (1977) did not treat *Protoperidinium claudicans* as a synonym and did not cite its holotype in the synonymy, which would have made the name *Votadinium spinosum* superfluous and hence illegitimate (Art. 52.1). Nor did he

include motile-stage characteristics in his circumscription. Equivalence refers to "a noted morphological similarity or identicality between a fossil-taxon and a part or life-history stage of a non-fossil taxon at the same rank where the names of these two taxa are not considered synonyms" (Head et al. 2024). A synonym is "one of two or more names that apply to the same taxon" (ICN glossary). The difference between equivalence and synonymy rests upon that between paleontological and biological species concepts. A fossil-species may closely resemble, or appear identical with, the morphology of a resting cyst belonging to a named non-fossil species, thus allowing it to be considered "equivalent" although not taxonomically identical (as required of synonyms). The latter would require assumptions that all parts of the life cycle are the same and have remained so perhaps over tens of millions of years. This issue is common to all plankton groups but is exacerbated in dinoflagellates by the fact that non-fossil nomenclature is traditionally based on the motile cell, which rarely fossilizes (see Section 3, above). According to Principle 4 of the ICN, "Each taxonomic group with a particular circumscription, position, and rank can bear only one correct name, the earliest that is in accordance with the rules, except in specified cases." But this does not apply to a non-fossil species and its equivalent fossil-species as the circumscriptions are different even when the non-fossil species is circumscribed to include a description of the cyst. Accordingly, *Votadinium spinosum* as a fossil-defined species can be used as the correct name for the cyst. However, should *Votadinium spinosum* and *Protoperidinium claudicans* be considered conspecific and therefore synonymous, then *Protoperidinium claudicans* would be the correct name because it is defined by a non-fossil type and so has priority over that of a fossil-species (Art. 11.8). It should be emphasized that *equivalence* expresses a

relationship between fossil-defined and non-fossil defined taxa, with the fossil (usually cyst) morphology operating as the intermediary.

Dual and unified nomenclature are equally available under the ICN allowing the practitioner to exercise choice, which reflects separate taxonomic approaches. The purpose of the ICN is not to restrict such approaches but rather to facilitate their nomenclatural expression (Head et al. 2024). The suggestion by Ellegaard et al. (2018 p. 229) that dual nomenclature can be removed from formal nomenclature is not an option while practitioners wish to use it; the decision to use a dual or unified approach is thus a taxonomic rather than a nomenclatural one. Nonetheless, Elbrächter et al. (2023) proposed changes to the ICN that would diminish its support for dual nomenclature. Their proposals have been critiqued by Head et al. (2024).

This raises the question of how a fossil- and a non-fossil taxon are distinguished. A fossil-taxon (diatoms excepted) is defined by a fossil nomenclatural type (Art. 1.2), which must be an actual specimen (Art. 8.5). For a fossil dinoflagellate taxon, this is assumed to be a resting cyst in all but a few cases. The ICN distinguishes fossil- from non-fossil material "by stratigraphic relations at the site of original occurrence". Importantly, "in cases of doubtful stratigraphic relations ... provisions for non-fossil taxa apply" (Art. 13.3). Effectively, the principle of superposition should apply, which is indeed the case for most naturally occurring marine sediments. Bioturbation, which is common in most marine sediments, may blur stratigraphic relations but on a broad scale does not completely destroy them. There is a long tradition of treating cysts from surface sediments as fossils, whether these sediments are from nearshore grab samples or from the tops of deep-sea cores. For example, taxa described from surface sediments around

the coast of the British Isles by Reid (1974, 1977) are widely accepted as fossil-taxa. They include the genera *Ataxiodinium*, *Dubridinium*, *Trinovantedinium*, *Votadinium* and *Xandarodinium*, and the species *Ataxiodinium choane*, *Brigantedinium auranteum*, *Brigantedinium majusculum* (but see below for the genus *Brigantedinium*), *Dubridinium caperatum*, *Dubridinium cassiculum*, *Dubridinium cavatum*, *Dubridinium ulsterum*, *Spiniferites delicatus*, *Spiniferites elongatus*, *Spiniferites lazus*, *Votadinium calvum*, *Votadinium spinosum*, and *Xandarodinium xanthum* (Mertens et al. 2020; Van Nieuwenhove et al. 2020).

In reality, such surface sediment samples may contain living as well as dead/fossil cysts, and viable cysts have been found in sediments as old as 100 years (Ellegaard and Ribeiro 2018). The definition of a fossil under Art. 13.3 is also discussed by Head et al. (2024). The type specimen of a non-fossil taxon may have been alive when collected, even though it cannot be living when serving as type material (except under specific circumstances; Art. 8.4). In contrast, it is reasonable to require of a specimen treated nomenclaturally as a fossil that it was not demonstrably living at the time of collection. This question does not arise if the specimen is an empty germinated cyst but becomes theoretically pertinent if it has cell contents. In practice, the usual chemical processing of surface marine sediment using HCl and HF will kill any living cysts, so it will not be known whether the cyst was dead when collected. It is therefore simply assumed for nomenclatural purposes that cysts having undergone palynological processing were dead at the time of collection. For example, *Spiniferites elongatus* and *Echinidinium karaense* have holotypes containing degraded cell contents yet are treated as fossil-taxa. It would serve no good purpose to treat them otherwise. In the case of a thin-walled cyst, it may

indeed be desirable for the holotype to have cell contents because these (especially the cellulosic endospore) keep the cyst wall inflated, allowing its morphological details to be studied more easily. The holotypes of *Echinidinium karaense* and *Islandinium brevispinosum* provide examples of this, and a specimen of *Islandinium minutum* with cell contents (pl. 1, figs. d–i of Head et al. 2001) was used to elucidate the unusual archeopyle style in this common arctic species. Dinoflagellate cysts with preserved endospores are known from Middle Pleistocene deposits as old as 767 ka (fig. 7b, g in Balota et al. 2021).

A non-fossil species is defined by a non-fossil nomenclatural type. The type can be either a specimen or an illustration (Art. 8.1), although for algae from 1 January 2007 an illustration cannot be used (Art. 40.4) unless "there are technical difficulties of specimen preservation or if it is impossible to preserve a specimen that would show the features attributed to the taxon by the author of the name" (Art. 40.5). In the case of a specimen, the organism is not usually living (Art. 8.4), as noted above. Traditionally, non-fossil dinoflagellate species have been typified using an illustration of the motile stage. However, Ellegaard et al. (2002) typified the name *Gonyaulax baltica* using a cyst from culture rather than a motile stage. It is not clear whether the holotype is the cyst itself (a curated dead specimen on a scanning electron microscope [SEM] stub) or the SEM illustration of it (fig. 3A in Ellegaard et al. 2002), but either is acceptable under the ICN because publication predates 1 January 2007. The observations were from a living unialgal culture (one grown from a single wild resting cyst), and this appropriately allowed the protologue (everything associated with a name at its valid publication) to include information on both the cyst and motile stage. In typifying *Gymnodinium nolleri*,

Ellegaard and Moestrup (1999) used a fixed (dead) and embedded sample of unialgal culture which presumably included cysts as well as motile cells, an acceptable holotype under the ICN (Art. 8.2). Their figure 1 illustrates both cyst and motile stages of *Gymnodinium nolleri* from this unialgal culture which, now preserved, serves as the holotype.

3.3. Problematic cases

In defining the non-fossil *Gonyaulax ellegaardiae* from Izmir Bay, Turkey, Mertens et al. (2015) attempted to establish a dual nomenclatural relationship between it and the fossil-species *Spiniferites pachydermus*, the latter having been described from the subsurface Pleistocene or Holocene of the coastal plain of Israel (as *Hystrichosphaera furcata* var. *pachyderma* in Rossignol et al. 1964). Mertens et al. (2015) selected two illustrations (their figs. 2 and 5a–i) as the holotype. Their fig. 5a–i illustrates an incubated cyst from which a thecate cell (their fig. 2) emerged. While it is sound biological practice to illustrate both stages of the life cycle, only one illustration can be used as a holotype; moreover, from 1 January 2007 only a specimen can be designated unless there are technical difficulties with specimen preservation (Art. 40.5). The specimens illustrated as types were not preserved (Mertens et al. 2015, p. 564) owing to such difficulties. Here we designate fig. 2 of Mertens et al. (2015) as the holotype of *Gonyaulax ellegaardiae* Mertens, Aydin, Takano, Yamaguchi and Matsuoka in Mertens et al. (2015), completing requirements for valid publication. This illustration is of a specimen of the motile stage. Although Mertens et al. (2015) considered *Gonyaulax ellegaardiae* to be equivalent to *Spiniferites pachydermus*, this relationship appears to be incorrect and a new fossil-

species will be formally proposed (MJH and KNM in prep.). A dual nomenclatural approach allows both species, each typified by its own holotype, to remain as useful individual concepts despite their problematic relationship.

Reid (1974, 1977) established numerous fossil-species that were typified using cyst specimens recovered mostly from intertidal surface sediments around the British Isles, as noted in Subsection 3.2 above. The status of these holotypes as fossils is widely accepted on the basis that they were obtained from naturally deposited sediment where the principle of superposition broadly applies. In contrast, the genus *Echinidinium* and its holotype species *Echinidinium granulatum* were typified by a cyst recovered from a sediment trap (Zonneveld 1997) where stratigraphic relations could not be reasonably inferred (Head 2003). The genus and its holotype species were therefore to be treated as non-fossil taxa (Head 2003). The genus and selected species were validated only when Head et al. (2001) provided Latin diagnoses, as then required for non-fossil taxa. Other species were validated by Mertens et al. (2020).

A similar example involves the genus *Brigantedinium* and its holotype species *Brigantedinium simplex*. The type specimen, known then as *Chytroeisphaeridia simplicia*, was recovered from a settling tray at the bottom of the aquarium at Woods Hole Oceanographic Institution (Wall 1965). This specimen cannot be treated as a fossil because sediments accumulated in such settling trays are prone to disturbance and the trays themselves are periodically emptied. Stratigraphic relations are therefore doubtful at best, and where doubt exists provisions for non-fossil taxa apply (Art. 13.3). However, because these taxa had been proposed as fossil-taxa, no Latin diagnoses were provided.

The names were only validly published when Lentin and Williams (1993, p. 67) supplied Latin diagnoses, as discussed in Subsection 6.2 below.

4. Obstacles to a unified nomenclature

Wall and Dale (1968) showed that cysts corresponding to three fossil-genera, now known as *Nematosphaeropsis*, *Spiniferites*, and *Tectatodinium*, all give rise to motile stages assignable to a single theca-defined non-fossil species complex that includes *Gonyaulax spinifera*. It is now accepted that at least six such genera, *Ataxiodinium*, *Bitectatodinium*, *Impagidinium*, *Nematosphaeropsis*, *Spiniferites* and *Tectatodinium*, are produced by the non-fossil species *Gonyaulax spinifera* and its allies (Head 1996) including a species closely related to *Gonyaulax polygramma* in the case of *Ataxiodinium choane* (Mertens et al. 2017a). Subsuming these six fossil-genera and their contained species into a single non-fossil genus would result in an unacceptable loss of detail within the fossil-defined classification. Considerable progress in expanding and refining cyst-theca relationships within the genus *Gonyaulax* has been made since the pioneering work of Wall and Dale (Gu et al. 2021, 2022, 2023, and references therein). Recent molecular phylogenetic studies confirm the attribution of these fossil-genera to the non-fossil genus *Gonyaulax*, but the studies demonstrate that the fossils are polyphyletic, with species of *Tectatodinium*, *Bitectatodinium*, *Ataxiodinium* and *Impagidinium* intermingling with those of *Spiniferites* in phylogenetic trees (Gu et al. 2021; Fig. 1). These results make any efforts to integrate the fossil-genera with the genus *Gonyaulax* or indeed with its four

subgenera proposed by Kofoid (1911; *Gonyaulax*, *Fusigonyaulax*, *Steiniella*, *Acanthogonyaulax*) very complicated. In general, the motile stage of *Gonyaulax* has a more conserved morphology than that of its cyst counterparts, although small differences in motile stage morphology that might allow placement in other genera have been noted in some species, including *Gonyaulax polygramma* and *Gonyaulax geomunensis* (Kim et al. 2023) and *Gonyaulax hyalina* (Escalera et al. 2018; but see Carbonell-Moore and Mertens 2019).

A similar number of fossil-defined genera has been assigned to the large non-fossil genus *Protoperidinium*. Harland (1982) attempted to integrate these fossil-genera by reassigning them as sections of the genus *Protoperidinium*. However, the resulting four-element name (genus, subgenus, section, species) while informative was an unwieldy solution not adopted by the community (see Ellegaard et al. 2018 for further discussion). This community includes a large and active group of palynologists/actuopalynologists working on fossil dinoflagellate cysts as well as many working on relationships with motile forms and utilising genetic techniques on cysts and motile forms. The various sections of *Protoperidinium* conform to a certain extent with the molecular phylogenies for this genus, although some are polyphyletic (Mertens et al. 2017b). More data are certainly needed before a thorough revision of the genus *Protoperidinium* is possible.

Another difficulty emerges when a fossil-genus contains both extant and extinct species. For example, the fossil-genus *Bitectatodinium* is typified by the holotype, a fossil, of the extant *Bitectatodinium tepikiense*. This species had been linked by incubation studies (Lewis et al. 2001) to the non-fossil *Gonyaulax digitale*. This

relationship is now known to be in error, although cysts assignable to *Bitectatodinium tepikiense* are possibly produced by a thecal morphotype from the Faeroe Islands that was misidentified by Kofoid (1911) as *Gonyaulax digitale* (Gu et al. 2021). The link to *Gonyaulax* is nonetheless not questioned, but *Bitectatodinium* cannot be subsumed or synonymized with *Gonyaulax* because *Bitectatodinium* also contains several extinct species for which the motile stage will likely never be known. Also, a molecular phylogeny shows *Bitectatodinium tepikiense* embedded in the genus *Gonyaulax*/*Spiniferites* (Gu et al. 2021; Fig. 1). The genus *Bitectatodinium* is therefore retained primarily for practical reasons and, as presently circumscribed, it does not represent an evolutionary entity distinct from the large fossil-genus *Spiniferites*.

The demonstration that dinoflagellate cyst distributions in modern marine sediments are strongly influenced by climate (Williams 1965, 1971) has led to the systematic mapping of cysts throughout the world's oceans (e.g. Wall et al. 1977; Rochon et al. 1999; Zonneveld et al. 2013; de Vernal et al. 2001, 2020) and an increasing use of dinoflagellate cysts for quantitative as well as qualitative paleoclimatic reconstructions, especially in mid- and high latitudes. This has led to a large and expanding literature on Quaternary dinoflagellate cysts (Van Nieuwenhove et al. 2020a, and references therein). The fossil-defined names used in the paleoenvironmental literature are now deeply entrenched, imparting a natural resistance to nomenclatural unification even when the motile stage eventually becomes known. A similar argument may be made regarding the use of fossil-defined names in the literature dealing with the older fossil record. The taxonomy and nomenclature of organic-walled dinoflagellate cysts throughout their Triassic to Quaternary fossil record (Riding et al. 2023) is deeply integrated, and has a

long history extending into the 19th century (e.g. Ehrenberg 1837; Mantell 1850, p.191). Although most fossil dinoflagellate cyst genera are now extinct, a few extend back tens, or even hundreds of millions of years. An example is *Spiniferites*, which, through its perhaps 120-million-year history, has accommodated more than 100 species (Fensome et al. 2019): it is unknowable whether the motile equivalent of most of these species would be assignable to *Gonyaulax*.

There may also be uncertainty in cyst-motile equivalencies, as with *Gonyaulax digitale*, which has been linked both to *Spiniferites bentorii* by Wall (1965), Wall and Dale (1967, p. 352) and Dodge (1989, p. 283) and to *Bitectatodinium tepikiense* by Lewis et al. (2001); it is now known to be linked to neither (Gu et al. 2021; Table 2). While such ambiguities are usually the result of uncertainty in the identification of the non-fossil species, they are avoided by continuing to use fossil-defined names for the cysts. However, the obstacle of uncertain cyst-motile equivalence is diminishing. Molecular genetics now provides an excellent and increasingly affordable tool for identifying species with greater certainty than by relying exclusively on morphological characters. Molecular approaches can be used to link the motile stage definitively with the cyst. Establishing correct equivalencies in combination with ribotyping is important as these approaches are intrinsic to DNA databases used in metabarcoding such as PR^2 (Guillou et al. 2013) and SILVA (Quast et al. 2013). Cultures of *Gonyaulax*, for instance, display enormous variations and aberrations that make unambiguous identification of species often difficult without such genetic characterization. Fossil-defined taxonomies therefore should adapt where practicable to incorporate these new advances. In some cases, however, neither cyst nor thecal morphology adequately reflect the diversity revealed in

molecular genetics. For example, *Protoceratium reticulatum* produces cysts that are commonly reported in Quaternary sediments globally as *Operculodinium centrocarpum* sensu Wall and Dale (1966). Small differences in the internal transcribed spacer ribosomal DNA (ITS rDNA) sequences in *Protoceratium reticulatum* have revealed what appears to be cryptic speciation, with ribotypes not being distinguishable by either cyst or thecal morphology (Wang et al. 2019). Genetic drift over geological time, which may not be expressed in the cyst morphology, adds further complexity in understanding the relationships between fossil and modern taxa. A final caveat is that any molecular approach assumes that the motile stage was correctly identified at the outset, but if it is not then the genetic sequence will be linked to the wrong species. The same is true of a cyst, but such errors in identification are more contained when using dual nomenclature.

5. Conceptual underpinning of dual nomenclature

Conceptual as well as practical issues underlie the difficulties in uniting fossil with non-fossil cyst nomenclatures. Non-fossil names are traditionally based on classifications centred on the morphology of the motile cell, but increasingly incorporate all elements of the life cycle including the cyst and may include molecular (genetic) information, striving for integrative taxonomy (Dayrat 2005). Indeed, such approaches can reveal weaknesses in exclusively morphology-based taxonomies. For example, five non-fossil species of the important *Alexandrium tamarense* species complex – *A. australiense*, *A. catenella*, *A. mediterraneum*, *A. pacificum*, and *A. tamarense* – could not be reliably distinguished using morphological criteria alone, although collectively they

partitioned into five cryptic species based on phylogenies using multiple regions in the rDNA operon (John et al. 2014). In order to stabilize the nomenclature, John et al. (2014) provided emended and new species circumscriptions that combine morphological and molecular information with details of toxicity (see also Litaker et al. 2018).

Extinct species on the other hand are based exclusively on morphological attributes of the cyst, except for rare cases (e.g. the motile and other stages of *Succiniperidinium inopinatum* preserved in mid-Cretaceous amber; Masure et al. 2013). The relative importance of each attribute should nonetheless be influenced by any known biological affinity to produce as "natural" a classification as possible. One potential example is the fossil-genus *Selenopemphix*, its holotype species *Selenopemphix nephroides* having been described from the Oligocene of Germany (Benedek 1972). This cyst-defined species occurs in modern sediments and seems to be produced by the non-fossil *Protoperidinium subinerme* (Rochon et al. 1999). The fossil-genus *Multispinula* was considered synonymous with and junior to *Selenopemphix* by Matsuoka (1985c) and Head (1993). Its holotype species *Multispinula quanta* (now *Selenopemphix quanta*) was described from modern sediments of the Persian Gulf (Bradford 1975), and it seems to be equivalent to the non-fossil species *Protoperidinium conicum* (although more research on this relationship is needed; Matsuoka and Head 2013). Molecular phylogenetic analysis of *Selenopemphix nephroide*s and its equivalent *Protoperidinium subinerme* has not yet been undertaken, but that of the morphologically similar *Selenopemphix undulata* described from late Quaternary sediments of the Pacific Ocean (Verleye et al. 2011) places it in a different clade from that of *Protoperidinium conicum* (putatively equivalent to *Selenopemphix quanta*) (fig. 3 of Mertens et al. 2017b; Fig. 2). *Selenopemphix* as

presently circumscribed might therefore be polyphyletic, raising the question of whether *Multispinula* and *Selenopemphix* should be treated as separate fossil-genera (Mertens et al. 2017b). If such separation were justified, attention could focus on the offset of the archeopyle (epicystal asymmetry) and details of ornamentation. Molecular phylogeny therefore allows new questions to be asked with respect to morphology-based cyst taxonomy. The cyst-defined non-fossil genus *Brigantedinium* is certainly polyphyletic, and potential solutions are discussed below.

Nonetheless, an extinct fossil-species, with rare exception, can only be defined by the morphological features of a single stage in the life cycle. There is no certainty that an extant fossil-species in the geological past produced a motile stage identical to its modern counterpart. This is especially true of extant fossil-species with long stratigraphic ranges, such as *Tectatodinium pellitum* and *Lingulodinium machaerophorum*, both of which evolved in the Paleocene (Head and Nøhr-Hansen 1999, and Heilmann-Clausen 1985, respectively).

Dapsilidinium pastielsii was described from the Lower Eocene of southeastern England (Davey and Williams 1966) and had its inception in the Early Paleocene or before. Living cysts equated with this fossil-species have been incubated to yield a motile stage belonging to an as-yet-unnamed non-fossil species and genus (Mertens et al. 2014). Following the practice of dual nomenclature, and pending further study, this non-fossil species will be formally described as new, based on all aspects of its life cycle and molecular characterization, and typified by a motile cell or its illustration. It will bear a new name and be assigned to a non-fossil genus. *Dapsilidinium pastielsii* will then be considered equivalent to, but not conspecific with, this new non-fossil species.

Applying a non-fossil name to a Paleocene specimen would assume that because the cyst morphology has not changed significantly over ~60 million years, its motile stage has not changed either, when instead it might be a different biological species retaining conservative cyst morphological features. This of course is true of any living group with a fossil record, but in dinoflagellates the geologically preservable cyst (usually assumed to be a hypnozygotic resting stage) is only one part of the life cycle, and the part used historically in non-fossil taxonomy and nomenclature is the motile stage. The cyst itself provides the overlap and point of connection between these different but complementary biological (entire life cycle) and paleontological concepts (Fig. 3).

Because dual nomenclature reflects actual differences in taxonomic criteria between fossils and non-fossils (cyst alone vs. motile stage and potentially cyst) it is possible to determine equivalencies at the species level but not between genera. Nonetheless, at the suprageneric level, which relies primarily on tabulation, as reflected both in fossils (to varying degrees) and non-fossils, the two taxonomic systems can be successfully aligned (e.g., Fensome et al. 1993).

In summary, dual nomenclature (and its underlying dual classification) is considered a practical and conceptually sound approach in handling organic-walled cyst-producing dinoflagellates. However, as with any other approach, consistency in application is desirable, and dual nomenclature is a work in progress. Many modern cyst morphotypes are not yet integrated into a fossil cyst classification scheme at generic or lower rank and have only a non-fossil name. Some have fossil names but are not yet linked to a non-fossil species. Others have hybridized names, such as when a fossil name is attributed or transferred to a non-fossil genus. These variants all introduce practical and

conceptual difficulties that require clarifying and resolving. Examples, with potential solutions where available, are discussed below.

6. Nomenclatural hybrids in dual nomenclature

6.1. A non-fossil cyst-typified species assigned to a fossil-genus

Nematosphaeropsis labyrinthus was initially described from the plankton off the Faeroe Islands by Ostenfeld (1903). Ostenfeld assigned his new species to the green algal prasinophyte genus *Pterosperma*, although his line drawings and certainly later observations by, for example, Reid (1974), support the contention that the species is a trabeculate dinoflagellate cyst. Reid (1974) transferred this species to the fossil-genus *Nematosphaeropsis*. Although a common cyst in modern North Atlantic sediment, its thecal equivalence has not yet been determined with certainty. If the motile stage, when known, can be attributed to a species named before that of Ostenfeld's species (1903), the epithet *labyrinthus* will become a junior heterotypic synonym and therefore unavailable. If the motile stage has not been named or was named after Ostenfeld's species, it will take the epithet *labyrinthus* although the species would then be transferred to the appropriate non-fossil genus, presumably *Gonyaulax*. Either way, the name *Nematosphaeropsis labyrinthus* will be rendered unavailable for this important cyst species.

An additional question is whether *Nematosphaeropsis labyrinthu*s is equivalent to *Nematosphaeropsis lemniscata*, described from the Upper Miocene of the Bering Sea (Bujak 1984), as discussed in Head and Wrenn (1992) and by Rochon et al. (1999). Modern cysts attributed to *Nematosphaeropsis labyrinthu*s have been reported with exclusively gonal processes (Reid et al. 1974; Van Nieuwenhove et al. 2020b) whereas intergonal processes, identified by bifurcate process terminations, may also be present in *Nematosphaeropsis lemniscata* (Bujak 1984). Bujak (1984) used relatively harsh chemical processing treatments, and his microscope slides were prepared using a synthetic mountant in a procedure that flattens delicate specimens. The original type material may not therefore be helpful, and new material from the type stratum should be examined. If *Nematosphaeropsis labyrinthus* and *Nematosphaeropsis lemniscata* indeed prove morphologically equivalent, then *Nematosphaeropsis lemniscata* would become the fossil-defined equivalent name for the non-fossil species we now call *Nematosphaeropsis labyrinthus*. This would potentially allow dual nomenclature to operate but again ultimately with the loss of the name *Nematosphaeropsis labyrinthu*s.

Names normally unavailable due to strict application of the rules can be conserved (retained) if such an action would best serve nomenclatural stability (Arts. 14.1 and 14.2). If the name *Nematosphaeropsis labyrinthus* is to continue being used into the future following a tradition initiated by Reid in 1974, it will require conservation to that of a fossil-species by the selection of a new (fossil) type (Art. 14.9). The equivalent non-fossil stage when subsequently identified, if unassignable to an existing species, would be described as a new species and placed in a non-fossil genus. *Nematosphaeropsis*

lemniscata, upon reexamination of topotype material, would be a junior heterotypic synonym or a distinct species depending on the outcome.

Conservation of the name *Nematosphaeropsis labyrinthus* with a new (fossil) type would initially require submission of a formal proposal to the journal *Taxo*n whereupon the International Association for Plant Taxonomy (IAPT) Permanent Nomenclature Committee for Fossils would be called upon to provide a recommendation. The proposal would ultimately require approval by the IAPT General Committee and final ratification by the Nomenclature Section of an International Botanical Congress (e.g. McNeill et al. 2018; Carbonell-Moore 2018; Wilson 2023; and see Turland 2019, p. 86, 87).

6.2. A non-fossil genus treated as if a fossil-genus

The genus *Brigantedinium* was established by Reid (1977) with its nomenclatural type the holotype of *Brigantedinium simplex*. This species was initially proposed under the name *Chytroeisphaeridia simplicia* by Wall (1965), and its holotype was recovered from a settling tray at the bottom of the aquarium at Woods Hole Oceanographic Institution (Wall 1965). This specimen therefore cannot be treated as a fossil as it lacks stratigraphic relations (Art. 13.3), even though it is an empty cyst and was not demonstrably living at the time of collection (see Subsection 3.1, above). (The genus name *Chytroeisphaeridia* is based on a [Jurassic] gonyaulacacean cyst and hence is not appropriate for a protoperidiniacean species.)

As a non-fossil, this species at the time of publication was required to have a Latin diagnosis, and because it was not provided by Wall (1965) the name was not validly published. In addition, Reid (1977) did not provide a Latin diagnosis for his *Brigantedinium* although this was required for a non-fossil genus. In fact, *Brigantedinium* and *Brigantedinium simplex* were not validly published until Lentin and Williams (1993, p. 67) provided Latin diagnoses and complete citations for them (Fensome et al. 2019). It remains that both the name of the genus *Brigantedinium* and that of its holotype species, *Brigantedinium simplex*, are defined by a non-fossil type specimen. Seven fossil-species have since been assigned to *Brigantedinium* (Fensome et al. 2019), representing another category of hybridized names (see Subsection 6.4).

Brigantedinium simplex has been identified by excystment studies as the cyst of the non-fossil species *Protoperidinium conicoides* (Wall and Dale 1968; Head 1996). Because both names are defined by non-fossil types, they compete for priority and *Protoperidinium conicoides* becomes the senior heterotypic synonym. The genus *Brigantedinium* then becomes a junior heterotypic synonym of *Protoperidinium*. The complication is that *Brigantedinium* is an ecologically important Quaternary cyst genus (de Vernal et al. 2020) represented by eight species including *Brigantedinium simplex* (Mertens et al. 2020). Of these, seven are typified by specimens from ocean-floor sediment and are treated as fossils. Hence a situation emerges where fossil-defined species are assigned to a non-fossil defined genus that is now a junior heterotypic synonym and therefore unavailable.

The least disruptive solution *prima facie* would be for the generic name *Brigantedinium* and that of its holotype species, *Brigantedinium simplex*, to be conserved

with a new (fossil) type (Art. 14.9) and instated as fossil-taxa along with the remaining seven fossil-species, given that all eight species have always been treated as such. However, molecular phylogenetic studies show that *Protoperidinium conicoides*, which includes the holotype species *Brigantedinium simplex*, is basal to the Pyriforma clade of *Protoperidinium* (Fig. 2) and is separated from other non-fossil species related to *Brigantedinium* (*Protoperidinium abei*, *P. avellana*, *P. denticulatum*, *P. pentagonum*, and *P. punctulatum*) (fig. 75 in Gu et al. 2015; fig. 1 in Gurdebeke et al. 2020; Fig. 4). Accordingly, the genus *Brigantedinium* is polyphyletic. Moreover, *Brigantedinium simplex* has two ventral depressions representing flagellar scars and may have slightly raised cingular margins (Rochon et al. 1999) whereas all other species of the genus lack expressions of tabulation other than the archeopyle. *Brigantedinium simplex* is accordingly a morphological as well as phylogenetic outlier.

Conserving *Brigantedinium* in a manner allowing it to accommodate the eight species presently assigned to it would compare with the fossil-genus *Spiniferites* which, probably along with *Selenopemphix* (see above), is also known to be polyphyletic. Alternatively, *Brigantedinium* could be conserved against *Protoperidinium* with a new (fossil) type, and restricted to the holotype species *Brigantedinium simplex*, with other species transferred to one or more newly created fossil-defined genera. Instead, we recommend that *Brigantedinium simplex* be redefined with a fossil type and transferred to a new fossil-genus, with the name *Brigantedinium* conserved using, as a new (fossil) type, a holotype of one of the other species of *Brigantedinium*, such as *Brigantedinium cariacoense*. This would allow *Brigantedinium* and all its fossil-species to continue being used as they are presently, except for *Brigantedinium simplex* which, as a morphological

and phylogenetic outlier, would appropriately be transferred to a new fossil-genus. In practical terms, most *Brigantedinium* species are distinguished from one another primarily by the archeopyle shape, which is often obscured in palynological preparations; except for *Brigantedinium simplex* which can be identified also by additional traces of tabulation. The useful term *Brigantedinium* spp. would therefore be sustained. Meanwhile, as a practical solution for routine counting, where critical details of the archeopyle are often not discernible, we recommend use of the informal collective term "round brown cysts" as this will include all species presently assignable to the genus *Brigantedinium*.

The cyst-defined genus *Echinidinium* and its holotype species *Echinidinium granulatum* were not validly published by Zonneveld (1997) because Latin diagnoses had not been provided. This was necessary at the time because the holotype of *Echinidinium granulatum* had been recovered from a sediment trap suspended in the water column and, with doubtful stratigraphic relations (Art. 13.3), could not therefore be considered a fossil (Head 2003). Head et al. (2001) validated both the genus *Echinidinium* and its holotype species, *E. granulatum*, by providing Latin diagnoses. Eight validly published cyst-defined species have been assigned to the genus *Echinidinium*, of which seven are typified by specimens from ocean floor sediment and are therefore treated as fossils. Hence, as with *Brigantedinium*, the genus *Echinidinium* is a widely reported non-fossil cyst genus, proposed with the intention of being a fossil-genus, and to which fossil-species have been assigned. Cysts of *Echinidinium granulatum* have been incubated and genetic sequencing performed, allowing attribution to a species not previously described and close to *Protoperidinium monovelum* (KNM unpublished data). If *Echinidinium*

granulatum were transferred to *Protoperidinium*, the genus *Echinidinium* would become unavailable. The preferred solution would be for the names *Echinidinium* and *Echinidinium granulatum* to be conserved with a new (fossil) type, protecting them from competition for priority against *Protoperidinium* and any of its species. This approach would cause minimal disruption because *Echinidinium* and *Echinidinium granulatum* have always been treated as fossil-taxa and all other species assigned to *Echinidinium* are already fossil-species.

6.3. A fossil-genus emended to incorporate non-fossil species

The fossil-genus *Islandinium* is typified by the holotype of *Islandinium minutum* (basionym: *Multispinula*? *minuta* Harland and Reid in Harland et al. 1980), a cyst obtained from modern sediments of the Beaufort Sea (Harland et al. 1980) and which can therefore be treated as a fossil. A significant characteristic of this protoperidinioidean genus is the presence of a saphopylic Type A3 apical archeopyle (i.e. the full release of three opercular plates).

Living cysts were subsequently germinated by Potvin et al. (2013), who then characterized the motile stage both with respect to its morphology and SSU and LSU rDNA-based molecular phylogeny. They accordingly emended the genus *Islandinium* and its holotype species *Islandinium minutum* to include details of the tabulation and morphology of the motile stage as well as some aspects of the cytology, and they incorporated new details of the cyst morphology. They also transferred the motile-defined

non-fossil species *Protoperidinium tricingulatum*, which had been diagnosed using both thecal and cyst characteristics (Kawami et al. 2009), to the genus *Islandinium*. This decision was supported at the time by molecular phylogeny showing *Protoperidinium tricingulatum* closely related to *Islandinium minutum* (Potvin et al. 2013). In doing so, Potvin et al. (2013) emended the genus *Islandinium* to include cysts with apical archeopyles that can be theropylic, as in *Protoperidinium tricingulatum*, as well as saphopylic.

There are presently no extinct species assigned to *Islandinium*, but were this to happen, such species would not fully satisfy the circumscription of this genus as emended by Potvin et al. (2013) because information on the motile stage would not be known, or indeed, be knowable. It is a matter of taxonomic choice whether to accept the emendation of Potvin et al. (2013), although in maintaining dual nomenclature we advocate the retention of *Islandinium* in its status as a fossil-genus. A proposal to erect an equivalent non-fossil genus is in preparation.

A further issue exists. *Islandinium minutum* subsp. *barbatum* was established by Potvin et al. (2018) to accommodate cysts that have pronounced barbs on the processes; *Islandinium minutum* subsp. *minutum* (autonym) by default represents morphotypes with smooth to minutely ornamented process surfaces. *Islandinium pacificum* was similarly erected by Gurdebeke et al. (2019) for cysts with pronounced barbs on their processes, differing only from *Islandinium minutum* subsp. *barbatum* in having a smooth rather than faintly granulate central body surface. Both *Islandinium minutum* subsp. *barbatum* and *Islandinium pacificum* are typified by holotypes that are empty cysts from ocean

sediments and so can be treated as fossils. Both are diagnosed exclusively on cyst morphology.

Islandinium minutum subsp. *barbatum* was not successfully germinated, but molecular phylogeny performed on the cysts gave results that were largely indistinguishable from *Islandinium minutum* subsp. *minutum*. This supported the decision to erect *barbatum* as a subspecies rather than a separate species. The theca of *Islandinium minutum* subsp. *barbatum* would presumably therefore conform with that of *Islandinium minutum* subsp. *minutum* as documented by Potvin et al. (2013), although this has yet to be confirmed.

Islandinium pacificum was, in contrast, successfully incubated and the emergent theca identified as *Protoperidinium mutsuense*. The thecal morphology of *Protoperidinium mutsuense* differs from that of *Islandinium minutum* subsp. *minutum* in specific details but according to Gurdebeke et al. (2019) broadly conforms to the thecal morphology attributed to the genus *Islandinium* by Potvin et al. (2013). Both *Protoperidinium mutsuense* and *Islandinium minutum* are assignable to the *Americanum* subclade of the *Monovela* clade of the genus *Protoperidinium* (Gurdebeke et al. 2019).

Detailed comparative research is needed to establish whether *Islandinium minutum* subsp. *barbatum* and *Islandinium pacificum* can be distinguished from one another in routine palynological analysis. If they can, then both names stand. If they cannot, but can be routinely separated from *Islandinium minutum* subsp. *minutum*, then the name *Islandinium pacificum* should be used – even though *Islandinium minutum* subsp. *barbatum* (Potvin et al. 2018) was published before *Islandinium pacificum* (Gurdebeke et al. 2019), “a name has no priority outside the rank at which it is published”

(Art. 11.2). Either way, this need not affect the application of dual nomenclature, although it is possible that *Islandinium pacificum* if synonymized with *Islandinium minutum* subsp. *barbatum* will then represent two non-fossil species.

The fossil-genus *Lingulodinium* is typified by the holotype of *Lingulodinium machaerophorum* from the Miocene of Balcombe Bay, Australia (Deflandre and Cookson 1955). The genus name refers to the "small tongue" (lingula) formed on the epicyst after the release of precingular plates during archeopyle formation. The equivalent theca-defined non-fossil species is *Gonyaulax polyedra* (Wall and Dale 1966, 1967, 1968), described from the Baltic Sea off Kiel, Germany by von Stein (1883) and since restudied from the type locality (Tillman et al. 2021). Dodge (1989) emended *Lingulodinium* to include thecal characteristics and transferred *Gonyaulax polyedra* to it, as *Lingulodinium polyedra*, along with another non-fossil species *Gonyaulax milneri*, as *Lingulodinium milneri*. *Lingulodinium milneri* is not known to produce a cyst. No other non-fossil species have been assigned to the genus *Lingulodinium*. Thirteen fossil-species are attributed to this genus including the holotype species (Fensome et al. 2019), collectively extending the genus back to the Late Cretaceous. Since most of the fossil-defined species are extinct, determining whether their motile stages would have conformed to the emended diagnosis given by Dodge (1989) is practically impossible. Nonetheless, *Lingulodinium* is distinct from *Gonyaulax*, the holotype species of which is *Gonyaulax spinifera*, using both morphological (Dodge 1989) and molecular phylogenetic (e.g. Orr et al. 2012; Mertens et al. 2015, 2017a; Tillmann et al. 2021) criteria. The genus *Lingulodinium* is accordingly now placed in the family Lingulodiniaceae whereas *Gonyaulax* (as presently understood and including *Gonyaulax spinifera*) is placed in the

family Gonyaulacaceae (Zhang et al. 2020; Tillmann et al. 2021). This separation had been recognized previously, although at subfamilial level, with *Lingulodinium* assigned to the Cribroperidinioideae and *Gonyaulax* to the Gonyaulacoideae (Fensome et al. 1993). The solution advanced here, following a dual nomenclatural approach, is to accept the emended diagnosis of Wall and Dale in Wall et al. (1973), which is restricted to cyst morphology, and to establish a new non-fossil genus, *Lingulaulax* gen. nov., for *Gonyaulax polyedra* and *Gonyaulax milneri*, which then become *Lingulaulax polyedra* (von Stein 1883) comb. nov. and *Lingulaulax milneri* (Murray and Whitting 1899) comb. nov., respectively (see Systematics section, below).

6.4. A fossil-species assigned or transferred to a non-fossil genus

There is a long history of fossil-species being placed in non-fossil genera, an early example being the Cretaceous *Peridinium pyrophorum*, a name not validly published by Ehrenberg (1837) but which was subsequently validated and transferred to a fossil-genus as *Palaeoperidinium pyrophorum* (Table 1). Many additional examples are listed in Fensome et al. (2019, appendix B). Two examples are discussed below.

Tuberculodinium vancampoae is a fossil-species described from the subsurface Pleistocene of Israel (Rossignol 1962). Rossignol (1962) treated this species as a form of incertae sedis and assigned it questionably to the fossil-genus *Pterospermopsis*. Wall (1967) erected the fossil-genus *Tuberculodinium*, with the holotype of *Tuberculodinium vancampoae* serving as its type. Cyst incubation experiments subsequently demonstrated a link with the non-fossil genus *Pyrophacus* (Wall and Dale 1971). Wall and Dale (1971)

accordingly emended the genus *Pyrophacus* to include cyst morphology, and transferred *Tuberculodinium vancampoae* to *Pyrophacus*, as *Pyrophacus vancampoae*, while at the same time emending this species to incorporate the motile stage morphology. Wall and Dale (1971) had considered *Pyrophacus vancampoae* to be different from the non-fossil species *Pyrophacus steinii.* However, Balech (1979) treated *Pyrophacus vancampoae* as a subspecies of *Pyrophacus steinii*. It is not in fact clear whether differences exist between the morphologies of the cysts of *Pyrophacus steinii* subsp. *steinii* and *Pyrophacus steinii* subsp. *vancampoae*. Matsuoka et al. (1985a) later showed that *Tuberculodinium vancampoae* is equivalent to the cyst of *Pyrophacus steinii*, a judgement now generally accepted (Head 1996). Dual nomenclature offers the choice of using either the name *Pyrophacus steinii* or *Tuberculodinium vancampoae* depending on context and preference (Head et al. 2016). In addition, maintaining *Tuberculodinium vancampoae* allows use of the fossil-defined genus *Tuberculodinium* which presently contains four fossil-species. Furthermore, the genera *Pyrophacus* and *Tuberculodinium* overlap but are not identical. *Pyrophacus horologium*, the holotype species of *Pyrophacus*, produces a non-tuberculate cyst that cannot be assigned to *Tuberculodinium* and may indeed be the motile stage of the fossil-species *Desotodinium wrennii* from the Pliocene of Belgium (De Schepper et al. 2004). Dual nomenclature keeps these distinctive fossil-genera available.

Peridinium ponticum is typified by an empty cyst recovered at a depth of 6–7 cm in sediment core 1451G from the Black Sea (Wall and Dale in Wall et al. 1973). The protologue is restricted to the cyst morphology, no motile stage then being known for this species. No Latin diagnosis was provided by Wall and Dale but this was not needed for a

fossil algal species (Art. 44.1). The holotype is therefore treated as a fossil. The assignment of this species to the non-fossil genus *Peridinium* was not directly explained by Wall and Dale but presumably relates to a general similarity with the cysts of *Protoperidinium claudicans* as discussed by Wall and Dale (in Wall et al. 1973). The combination "*Protoperidinium ponticum*" by Matsuoka (1985b) was not validly published because the basionym was not fully referenced (Fensome et al. 2019); the name in any case is now occupied by the different species *Protoperidinium ponticum*. The motile equivalent of *Peridinium ponticum* has been identified as *Protoperidinium* cf. *divergens* by Dale (1983) although no genetic sequences are available to offer further insights. The appropriate dual-nomenclatural solution would be to erect a new fossil-defined genus for this species, although its variable ornamentation and especially an outline that varies between pentagonal and subspherical (Wall et al. 1973; Mudie et al. 2017) would need to be considered.

6.5. A non-fossil theca-defined species assigned to a fossil-defined genus

Protoperidinium stellatum was described, as *Peridinium stellatum*, from the plankton at Woods Hole, Massachusetts, U.S.A. (Wall in Wall and Dale 1968). A preserved motile stage was chosen as the holotype (Wall in Wall and Dale 1968, pl. 3, fig. 16), this specimen having been incubated from a cyst collected from this plankton. The diagnosis is based on the morphology of both the cyst and the incubated motile stage. Bradford (1975) subsequently described the fossil-genus *Stelladinium* for species conforming to the general morphology of the cysts of *Protoperidinium stellatum*. He established

Stelladinium reidii as the holotype species, considering it to represent the cyst of *Protoperidinium stellatum*. Reid (1977) did not accept this equivalence, a judgement since followed by others (Head et al. 2020). He accordingly attempted to transfer *Protoperidinium stellatum* (as *Peridinium stellatum*) to the genus *Stelladinium*, as *"Stelladinium stellatum*" (Reid 1977), but failed to cite the basionym fully because he excluded the holotype (a motile stage). Had the transfer been validly published, the non-fossil theca-typified species *Protoperidinium stellatum* would have resided uncomfortably within the fossil-defined genus *Stelladinium*. Until now, *Protoperidinium stellatum* has remained without an equivalent fossil-species name. The erection of such a name based on an equivalent cyst is in progress (MJH and KNM in prep.).

7. Systematics

We use modified Kofoidian plate labelling which includes the identification of plate homologues as indicated by an asterisk (Bujak 1980; Fensome et al. 1993, text fig. 62) and sulcal plate labelling following Evitt (1985).

Division DINOFLAGELLATA (Bütschli 1885) Fensome et al. 1993 emend. Adl et al. 2005

Subdivision DINOKARYOTA Fensome et al. 1993

Class DINOPHYCEAE Pascher 1914

Subclass PERIDINIPHYCIDAE Fensome et al. 1993

Order GONYAULACALES Taylor 1980

Suborder GONYAULACINEAE (Autonym)

Family LINGULODINIACEAE Sarjeant and Downie 1974 emend. Gu, Mertens, Li and Shin in Zhang et al. 2020

Type genus. *Lingulodinium* Wall 1967 emend. Wall and Dale in Wall et al. 1973

Remarks. The family Lingulodiniaceae was established by Sarjeant and Downie (1974) based on both cyst and thecal morphology, with a plate formula 3–6′, 0–4a, 6″, 6C, 6‴, 1p, 1′′′′ where it could be determined, and resting cysts if produced having an archeopyle formed by loss of one to five precingular plates. Sarjeant and Downie (1974) included two fossil-genera, *Lingulodinium* Wall 1967 and *Operculodinium* Wall 1967, and one non-fossil genus, *Protoceratium* Bergh 1881. Fensome et al. (1993) considered the family Lingulodiniaceae to be synonymous with and junior to the family Gonyaulacaceae Lindemann 1928. Fensome et al. (1993) placed the genus *Lingulodinium* (and questionably *Protoceratium* and by extension *Operculodinium*) within the Gonyaulacaceae and in their new subfamily Cribroperidinioideae Fensome et al. 1993 which is characterized by an L-type ventral organization and dextral torsion. Zhang et al. (2020) restricted the family Gonyaulacaceae to genera with an S-type ventral organization, and retained and emended the family Lingulodiniaceae for genera with an L-type ventral organization; a more or less symmetrical antapical outline; six or seven precingular plates; when present, two or more anterior intercalary plates; and when

present a small ventral pore located between 1′, 4′ (or 5′) and 2a (Gu et al. in Zhang et al. 2020, p. 258). They assigned four genera to the family Lingulodiniaceae: the non-fossil genera *Amylax* Meunier 1910 and *Sourniaea* Gu et al. in Zhang et al. 2020, and the fossil-genera *Lingulodinium* and *Pyxidinopsis* Habib 1976, these assignations being supported by molecular phylogeny (Zhang et al. 2020; Tillmann et al. 2021; Fig. 1).

Genus *Lingulaulax* gen. nov.

Type. Pl. IV, fig. 8 of von Stein 1883, designated by Tillmann et al. (2021) as the lectotype of the non-fossil species *Lingulaulax polyedra* (von Stein 1883) comb. nov.

Status. A non-fossil genus.

Accepted species.

Lingulaulax polyedra (von Stein 1883) comb. nov.

Lingulaulax milneri (Murray and Whitting 1899) comb. nov.

Etymology. A contraction of the generic names *Lingulodinium* and *Gonyaulax*, with reference to the nomenclatural history of this genus.

Diagnosis. A lingulodiniacean genus in which the motile cell has no pronounced spines or horns, and the plate formula APC (po, X, cp), 3′, 3a, 6″, 6c, 7s, 5‴ (*2‴–*6‴), 1p,

1‴′. The 3′ plate is small, and positioned along the right side of the apical pore. The cingulum is offset by up to about two cingular widths, sulcus straight (L-type ventral organization). Thecal plates are thick with circular depressions over the surface of the plates. Cingular and sulcal lists are present. Plate 6″ is 5-sided, and plate 3′ is small. Torsion is dextral. Resting cysts when present have a precingular archeopyle, and if processes occur, they are non-sutural in distribution. (Adapted in part from Dodge 1989, p. 291).

Remarks. The genus *Gonyaulax* Diesing 1866 emend. Dodge 1989 differs from *Lingulaulax* gen. nov. in its epicystal tabulation which is characterized by two anterior intercalary plates rather than three (Dodge 1989), and an S-type ventral organization. *Gonyaulax* also often has a conspicuous ventral pore between 3′ and 2a (Mertens & Carbonell-Moore 2018). *Amylax* Meunier 1910 differs in having a large 3′ plate (Dodge 1989), and *Sourniaea* Gu et al. in Zhang et al. 2020 differs in having four apical and two anterior intercalary plates, and smooth resting cysts with an apical archeopyle. *Sourniaea* may also have pronounced antapical horns, as in the holotype species *Sourniaea diacantha* (Gu et al. in Zhang et al. 2020).

Establishment of the new non-fossil genus *Lingulaulax* allows the fossil-genus *Lingulodinium* to be used exclusively for fossil-species.

Lingulaulax polyedra (von Stein 1883) comb. nov.

Figure 5

Basionym. *Gonyaulax polyedra* von Stein 1883, p. 13, pl. IV, figs. 7–9.

Synonymy. *Lingulodinium polyedra* (von Stein 1883) Dodge 1989, p. 291.

Equivalent fossil-species. *Lingulodinium machaerophorum* (Deflandre and Cookson 1955) Wall 1967.

Lectotype. Holotype not designated by von Stein (1883). Lectotype, von Stein 1883, pl. IV, fig. 8 designated by Tillmann et al. (2021).

Isotype. SEM stub [U. Tillmann K3-G8] s.n. (CEDiT2020E108!), Tillmann et al. (2021).

Description. Motile cell heptagonal in dorsovental outline, with margins nearly straight, and nearly circular in polar outline. An obtuse angle marks the precingular and apical plate series contact. A small, raised apical pore complex (APC) is present on the epitheca. The hypotheca is trapezoidal in outline and has a flat antapex lacking projections. There is no dorso-ventral compression. Plate formula, APC (Po, X, cp), 3′, 3a, 6″, 6c, 6s, 6‴*, 1p, 1⁗. The cingulum is narrow, almost median, fairly deeply incised and with narrow lists, descending without overlap, and offset by about two cingulum widths. The sulcus is vertical, straight, broad at the posterior and narrow towards the anterior where it just enters the epitheca, and bordered by sulcal lists. The thecal plates are thick and have prominent ridges along the sutures on the overlap margins. The surface of mature plates

is coarsely areolate and includes ring-shaped ridges around the numerous trichocyst pores. Ridges connect adjacent areolae on mature plates. The first apical plate is long and narrow and has a ventral pore on its right margin. Plate 2′ is heptagonal and large. Plate 3′ (on the right side) is small and narrow, curving around the right-hand margin of the apical pore complex. The APC contains an elongated oval pore plate bordered by a raised rim. The centre of the pore plate contains a cover plate bearing small, elongate structures. There are three pentagonal anterior intercalary plates all of similar size situated on the right side of the epitheca. The six cingular plates are all approximately similar in size. Apart from the ms plate, sulcal plates are at least partly ornamented and porate. Plate 1‴* is small, occurs within the sulcus, and may not contact cingulum. Keystone plates are 3″, c3 and 4‴* in the precingular, cingular and postcingular series, respectively. Cell length, 39–53 μm; cell width, 34–48 μm (Adapted from Dodge 1989; Tillmann et al. 2021; Fig. 5.)

The resting cyst has a spherical to ovoid central body and a granulate to microrugulate surface. The archeopyle is usually precingular representing the individual release of one or more precingular plates (up to 1″–5″) but with the apical plates remaining attached to the sulcus (Wall 1967); although an epitractal archeopyle may be occasionally developed. The archeopyle margin has rounded angles. Processes are nontabular, hollow, with circular bases, and tend to flatten distally; distal ends are closed and taper to fine points or may occasionally be capitate. Processes may be slightly constricted at their base, and have smooth surfaces but may bear fine spinules along their distal third. Process length can vary considerably (0–35 μm). There are no other

indications of tabulation. Central body diameter, 35–60 μm (Adapted from Wall and Dale in Wall et al. 1973; Van Nieuwenhove et al. 2020b.)

Remarks. Detailed SEM observations of motile cells from the type locality in the Baltic Sea off Kiel, Germany are provided by Tillmann et al. (2021). Nehring (1994) illustrated cysts from modern sediments of the Kiel Bight.

Lingulaulax milneri (von Stein 1883) comb. nov.

Basionym. *Goniodoma milneri* Murray and Whitting 1899, p. 325, pl. 27, fig. 2a–d.

Synonyms.

Heterodinium milneri (Murray and Whitting 1899) Kofoid 1906, p. 353.

Gonyaulax milneri (Murray and Whitting 1899) Kofoid 1911, p. 203.

Remarks. Kofoid (1911) placed *Gonyaulax milneri* with *Gonyaulax polyedra* in his *Polyedra* group. SEM illustrations by Taylor (1976, pl. 44, figs. 517a–c) show a polyhedral outline and epithecal tabulation very similar to that of *Lingulaulax polyedra*, although the epitheca is considerably shorter than the hypotheca. In proposing this species, the authors illustrated different cells (Murray and Whitting 1899, fig. 2a–d) and did not designate a holotype (this became a requirement only on 1 January 1958; Art. 40.1). Therefore, no holotype exists for this species.

8. Summary and conclusions

Biological nomenclature must be flexible to reflect new phylogenetic information but also conservative to promote stability and continuity. The ICN explicitly distinguishes between fossil- and non-fossil algal taxa (diatoms excepted), recognising the fundamental differences in their underlying taxonomic concepts. Living organisms can be circumscribed potentially on the basis of their entire life history and genome, whereas fossils cannot. These concepts and this distinction form the basis for dual nomenclature. Therefore, inconsistencies and ambiguities arise when binomials are created that combine fossil with non-fossil names. In some cases, these hybridized names result from misunderstandings over the fossil or non-fossil status of these names. In examining this hybridized nomenclature and the problems it may create, solutions and courses of action have been proposed and are summarized below.

Nematosphaeropsis labyrinthus is a commonly reported non-fossil species assigned to a fossil-genus. When its motile stage has been identified, *Nematosphaeropsis labyrinthus* will either require transfer to a non-fossil genus or will become a junior heterotypic synonym unless it is conserved with a new (fossil) type, as we recommend, allowing it to be used in the manner always intended for this species.

The ecologically important Quaternary genus *Brigantedinium* is typified by the holotype of *Brigantedinium simplex* which is a non-fossil cyst. Incubation studies have linked *Brigantedinium simplex* to the theca-defined non-fossil species *Protoperidinium conicoides* which is the senior heterotypic synonym. In turn, *Brigantedinium* is a junior

heterotypic synonym of the large non-fossil genus *Protoperidinium.* Moreover, the genus *Brigantedinium* is polyphyletic and *Brigantedinium simplex* a morphological outlier. Our preferred solution would be to conserve the name *Brigantedinium simplex* with a new (fossil) type and transfer to a new fossil-genus, and the name *Brigantedinium* conserved using as a new type the holotype of one of the fossil-species of *Brigantedinium*. With the exception of *Brigantedinium simplex*, this would allow *Brigantedinium* and all its fossil-species to continue being used as they are presently. The informal term "round brown cysts" would remain a useful collective label for all these cyst morphotypes.

The cyst-defined *Echinidinium* is similarly a non-fossil genus because its type, the holotype of *Echinidinium granulatum*, is a non-fossil specimen. Incubation and genetic sequencing studies have linked *Echinidinium granulatum* to an undescribed species of *Protoperidinium.* Upon the publication of that new *Protoperidinium* species, the genus *Echinidinium* and its holotype species *Echinidinium granulatum* will become junior heterotypic synonyms unless these names are conserved with a new (fossil) type, which we recommend as it will then allow *Echinidinium* and all its species to be used as originally intended.

Based on incubation studies, the fossil-genus *Islandinium* and its holotype species *Islandinium minutum* were emended by Potvin et al. (2013) to include characters of the motile cell. If an extinct species should be assigned to *Islandinium* an ambiguity will exist because its motile stage would be unknowable. Following the application of dual nomenclature, *Islandinium* is here treated as a fossil-genus as had been initially intended, and a proposal is being prepared to create an equivalent non-fossil genus.

The fossil-genus *Lingulodinium* is typified by the holotype of *Lingulodinium*

machaerophorum, an extant fossil-species from the Miocene of Australia (Deflandre and Cookson 1955). The theca-defined non-fossil species equivalent to *Lingulodinium machaerophorum* is *Gonyaulax polyedra*. Dodge (1989) emended *Lingulodinium* to include thecal characteristics and transferred *Gonyaulax polyedra* to it, as *Lingulodinium polyedra*. However, most fossil-defined species of *Lingulodinium* are extinct, their motile stage morphologies hence unknowable. The genus *Lingulodinium* is therefore returned to its fossil status and the new non-fossil genus, *Lingulaulax* gen. nov., is proposed along with the new combinations *Lingulaulax polyedra* (von Stein 1883) comb. nov. and *Lingulaulax milneri* (Murray and Whitting 1899) comb. nov., for the non-fossil *Gonyaulax polyedra* von Stein 1883 and *Gonyaulax milneri* (Murray and Whitting 1899) Kofoid 1911, respectively.

Peridinium ponticum, a distinctive fossil-species assigned to a non-fossil genus, is reported frequently from Paratethyan Quaternary deposits from where it was first described, but also occurs along the Atlantic margin of Portugal (García-Moreiras et al. 2018, 2023) and France (KNM pers. obs.). Creating a new fossil-defined genus for this species might be desirable, although the species shows considerable morphological variability that would require consideration.

Protoperidinium stellatum is a theca-defined non-fossil species with a distinctive stellate cyst clearly conforming to the fossil-genus *Stelladinium*. Following dual nomenclature, a new fossil-species will be proposed to serve as the equivalent fossil name for *Protoperidinium stellatum* (MJH and KNM in prep.).

Gonyaulax ellegaardiae was not validly published at the time of publication because it was typified by two illustrations. Requirements for valid publication are

completed herein by designating one of these illustrations (fig. 2 in Mertens et al., 2015) as the holotype.

In order to improve taxonomic integration between extant fossilizable cyst morphotypes and those of deeper geological time, we advocate the establishment of equivalent fossil-defined names for *all* such extant morphotypes where practicable. The application of such names will benefit from the typification of a cyst as a holotype. This exercise, illustrated by the case of *Protoperidinium stellatum* cysts (above), should take advantage of molecular as well as other phylogenetic evidence when constructing such a taxonomy. Dual nomenclature in dinoflagellates should be consistently available for those who wish to use it.

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Table captions

Table 1. All taxonomic names cited in the text, with full authorial attributions. A (◉) indicates that the type is treated as a fossil for nomenclatural purposes.

Table 2. Nomenclatural status and, where known, motile–cyst equivalence of those fossil-taxa and cyst-producing non-fossil taxa discussed in the text. A fossil-species is one in which the type is a fossil. A name-element in bold face indicates that it is based on a type that is a fossil.

Table 3. Summary of changes to the nomenclatural Codes that affect those fossil- and non-fossil algal taxa, as explained in the text, with reference to each International Botanical Congress (IBC) from 1950 and the published Code resulting from it.

Figure captions

Figure 1. Phylogeny of the fossil-genera *Ataxiodinium*, *Bitectatodinium*, *Impagidinium*, *Spiniferites* and *Tectatodinium* inferred from partial large subunit (LSU) rRNA gene sequences using Bayesian inference. These genera have all been linked by incubation studies to the non-fossil *Gonyaulax spinifera* and *Gonyaulax polygramma* complexes, and all are paraphlyetic. These genera nonetheless all include extinct species, and as presently circumscribed are needed in fossil cyst nomenclature. Branch lengths drawn to scale; scale bar indicates number of nucleotide substitutions per site. Numbers on branches are statistical support values to clusters on their right (left: Bayesian posterior probabilities; right: maximum likelihood (ML) bootstrap support values). Only Bayesian posterior probabilities above 0.9 and ML bootstrap support values above 50 are shown. An asterisk (*) indicates maximal support (BI posterior probability = 1.0, ML bootstrap support = 100). The scale bar represents inferred evolutionary distance in changes/site. From fig. 77 of Gu et al. (2021).

Figure 2. Phylogeny of the *Protoperidinium* sensu stricto clade inferred from LSU rRNA gene sequences using Bayesian inference, and its taxonomic implications for the fossil-genera *Selenopemphix* and *Multispinula*. *Selenopemphix undulata* plots within the Tabulata clade whereas *Protoperidinium conicum*, to which *Selenopemphix* (formerly *Multispinula*) *quanta* has been attributed, groups within the Conica 2 clade, suggesting that *Selenopemphix* and *Multispinula* might be treated as separate fossil-genera.

Protoperidinium subinerme (its fossil-defined equivalent being *Selenopemphix nephroides*) has not yet been sequenced. The maximum likelihood (ML) bootstrap support values (ML) over 50 and Bayesian posterior probabilities (PP) over 0.7 are shown at the nodes (ML/PP), where an asterisk (*) indicates maximal support. Clades within the *Protoperidinium* sensu stricto clade are shown. The scale bar represents inferred evolutionary distance in changes/site. From fig. 3 of Mertens et al. (2017b).

Figure 3. Conceptual foundation for dual nomenclature. Biological species concepts potentially incorporate all aspects of the life cycle as well as genetic and other molecular information on the living organism. The species is typified by a non-fossil specimen or illustration, and a single non-fossil species name applies to all parts of the life history and may include information from genome sequencing. The paleontological species concept is, with rare exception, confined to the morphology of the fossilized resting cyst wall, although the significance of morphological attributes may be informed by independent evidence of phylogeny (e.g. molecular) where species are extant. The species is typified by a fossil specimen, and a fossil-species name is applied. Living cysts provide the overlap between these two nomenclatural systems: dual nomenclature allows both names *Selenopemphix nephroides* and (the cyst of) *Protoperidinium subinerme* to be used for the illustrated cyst according to context and preference. The SEM illustration of *Protoperidinium subinerme* is from Hansen and Larson (1992) and the illustration of *Selenopemphix nephroides* is from modern sediments of the Gulf of Mexico (KNM, unpublished).

Figure 4. Phylogeny of the family Protoperidiniaceae based on large subunit (LSU) rDNA. Names in red boldface type are linked to cysts assignable to the cyst-defined non-fossil genus *Brigantedinium*, including the holotype species *Brigantedinium simplex* which is linked to *Protoperidinium conicoides*. Node numbers indicate bootstrap support values (1000 replicates). An asterisk (*) indicates nodes found in all replicates. From fig. 1 of Gurdebeke et al. (2020).

Figure 5. *Lingulaulax polyedra* (von Stein 1883) comb. nov. A, B, D, E, tracings of different motile stage cells from an SEM stub (strain K3-G8 isolated from the type locality off Kiel in the Baltic Sea) which serves as the epitype (from figs. 4B, 4G, 4D, and 4H respectively in Tillmann et al. 2021); ventral, apical, dorsal, and antapical views respectively. C and F, schematic representation of C, apical pore complex and surrounding plates (from fig. 6C in Tillmann et al. 2021), and F, mid-ventral area showing details of sulcus and surrounding plates (from fig. 6D in Tillmann et al. 2021). Solid green arrows indicate plate overlap, open green arrows indicate uncertain direction of plate overlap, and the red dashed line indicates line along which plates separate during cell division (from fig. 6 in Tillmann et al. 2021). Scale bars = 10 μm. Modified kofoidian plate labeling includes: APC = apical pore complex, vp = ventral pore, cp = cover plate, po = pore plate, X = X-plate; and the sulcal plates, as = anterior, ras = right accessory, ms = median, rs = right, ls = left, as = anterior. The first postcingular homologue (*1‴) is designated as such because it lies within the sulcus and may not contact the cingular plate series.

Table ~~2~~1. ~~Taxonomic~~ All taxonomic names cited in the text, with full authorial attributions. A (◉) indicates that the type is treated as a fossil for nomenclatural purposes.

Genus *Alexandrium* Halim 1960*
Alexandrium australiense Murray in John et al.~~,~~ 20~~09~~14
Alexandrium catenella (Whedon and Kofoid 1936) Balech 1985
Alexandrium mediterraneum John in John et al. 2014
Alexandrium pacificum Litaker in John et al. 2014
Alexandrium tamarense (Lebour 1925) Balech 1995

Genus *Ataxiodinium* Reid 1974 (◉)
Ataxiodinium choane Reid 1974 (◉)

Genus *Amylax* Meunier 1910

Genus *Bitectatodinium* Wilson 1973 (◉)
Bitectatodinium tepikiense Wilson 1973 (◉)

Genus *Brigantedinium* Reid 1977 ex Lentin and Williams 1993
Brigantedinium auranteum Reid 1977 ex Lentin and Williams 1993 (◉)
Brigantedinium majusculum Reid 1977 ex Lentin and Williams 1993 (◉)
Brigantedinium simplex Wall 1965 ex Lentin and Williams 1993

Genus *Chytroeisphaeridia* (Sarjeant 1962) Downie and Sarjeant 1965 (◉)
Chytroeisphaeridia simplicia Wall 1965 (now *Brigantedinium simplex*)

Genus *Dapsilidinium* Bujak et al. 1980
Dapsilidinium pastielsii (Davey and Williams 1966) Bujak et al. 1980 (◉)

Genus *Desotodinium* De Schepper, Head and Louwye 2004 (◉)
Desotodinium wrennii De Schepper, Head and Louwye 2004 (◉)

Genus *Diplopsalopsis* Meunier 1910
Diplopsalopsis orbicularis (Paulsen 1907) Meunier 1910

Genus *Dubridinium* Reid 1977 (◉)
Dubridinium caperatum Reid 1977 (◉)
Dubridinium cassiculum Reid 1977 (◉)
Dubridinium cavatum Reid 1977 (◉)
Dubridinium ulsterum Reid 1977 (◉)

Genus *Echinidinium* Zonneveld 1997 ex Head, Harland and Matthiessen 2001
Echinidinium granulatum Zonneveld 1997 ex Head, Harland and Matthiessen 2001
Echinidinium karaense Head, Harland and Matthiessen 2001 (◉)

Genus *Goniodoma* Stein 1883

Goniodoma milneri Murray and Whitting 1899 (now *Lingulaulax milneri*)

Genus *Gonyaulax* Diesing 1866
Gonyaulax digitale (Pouchet 1883) Kofoid 1911
Gonyaulax ellegaardiae Mertens, Aydin, Takano, Yamaguchi and Matsuoka in Mertens et al. 2015 ex Head, Mertens and Fensome (herein)
Gonyaulax geomunensis Kim, Li, Gu, Mertens and Shin in Kim et al. 2023~~Gonyaulax digitale (Pouchet 1883) Kofoid 1911~~

Gonyaulax hyalina Ostenfeld and Schmidt 1901
Gonyaulax milneri (Murray and Whitting 1899) Kofoid 1911 (now *Lingulaulax milneri*)
Gonyaulax nezaniae Gu and Mertens in Gu et al. 2021
Gonyaulax ovum (Gaarder 1954) Head et al. (in revision)
Gonyaulax polygramma Stein 1883
Gonyaulax polyedra Stein 1883 (now *Lingulaulax polyedra*)
Gonyaulax scrippsae Kofoid 1911

Genus *Gymnodinium* Stein 1878
Gymnodinium nolleri Ellegaard and Moestrup 1999

Genus *Heterodinium* Kofoid 1906
Heterodinium milneri (Murray and Whitting 1899) Kofoid 1906 (now *Lingulaulax milneri*)

Genus "*Hystrichosphaera*" Wetzel 1933, ex Deflandre 1937
Hystrichosphaera furcata var. *pachyderma* Rossignol et al. 1964 (now *Spiniferites pachydermus*)

Genus *Islandinium* Head, Harland and Matthiessen 2001 (◉)
Islandinium brevispinosum Pospelova and Head 2002 (◉)
Islandinium minutum (Harland and Reid in Harland et al. 1980) Head, Harland and Matthiessen 2001 (◉)
Islandinium minutum subsp. *minutum* (autonym) (◉)
Islandinium minutum subsp. *barbatum* Potvin et al. 2018 (◉)
Islandinium pacificum Gurdebeke, Mertens, Pospelova, Van Nieuwenhove and Louwye 2019 (◉)

Genus *Lingulaulax* n. gen.
Lingulaulax milneri (Murray and Whitting 1899) ~~n.~~ comb. nov.
Lingulaulax polyedra (von Stein 1883) ~~n.~~ comb. nov.

Genus *Lingulodinium* Wall 1967 (◉)
Lingulodinium machaerophorum (Deflandre and Cookson 1955) Wall 1967 (◉)
Lingulodinium milneri (Murray and Whitting 1899) Dodge 1989 (now *Lingulaulax milneri*)
Lingulodinium polyedra (von Stein 1883) Dodge 1989 (now *Lingulaulax polyedra*)

Genus *Multispinula* Bradford 1975 (◉)
Multispinula minuta Bradford 1975 (◉) (now *Selenopemphix quanta*)

Genus *Nematosphaeropsis* Deflandre and Cookson 1955 (◉)
Nematosphaeropsis labyrinthus (Ostenfeld 1903) Reid 1974 (◉)
Nematosphaeropsis lemniscata Bujak 1984 (◉)

Operculodinium Wall 1967 (◉)
Operculodinium centrocarpum (Deflandre and Cookson 1955) Wall 1967 (◉)

Genus *Palaeoperidinium* Deflandre 1934 ex Sarjeant 1967 (◉)
Palaeoperidinium pyrophorum (Ehrenberg 1837 ex Wetzel 1933) Sarjeant 1967 (◉)

Genus *Peridinium* Ehrenberg 1832
Peridinium claudicans Paulsen 1907 (now *Protoperidinium claudicans*)
Peridinium ponticum Wall and Dale in Wall et al. 1973 (◉)

Genus *Preperidinium* Mangin 1913
Preperidinium meunieri (Pavillard 1913) Elbrächter 1993

Genus *Protoceratium* Bergh 1881
Protoceratium reticulatum (Claparède and Lachmann 1859) Bütschli 1885

Genus *Protoperidinium* Bergh 1881
Protoperidinium claudicans (Paulsen 1907) Balech 1974
Protoperidinium conicoides (Paulsen 1905) Balech 1974
Protoperidinium conicum (Gran 1900) Balech 1974
Protoperidinium denticulatum (Gran and Braarud 1935) Balech 1974
Protoperidinium divergens (Ehrenberg 1841) Balech 1974
Protoperidinium latidorsale (Dangeard 1927) Balech 1974
Protoperidinium mutsuense (Abé 1936) Balech 1974
Protoperidinium ponticum Vershinin and Morton 2005
Protoperidinium sinuosum Lemmermann 1905
Protoperidinium stellatum (Wall in Wall and Dale 1968) Balech 1994
Protoperidinium subinerme (Paulsen 1904) Loeblich III 1969
Protoperidinium tricingulatum Kawami, van Wezel, Koeman and Matsuoka 2009

Genus *Pterosperma* Pouchet 1893
Pterosperma labyrinthus Ostenfeld 1903 (now *Nematosphaeropsis labyrinthus*)

Genus *Pyrophacus* von Stein 1883
Pyrophacus horologium Stein 1883
Pyrophacus steinii (Schiller 1935) Wall and Dale 1971
Pyrophacus steinii (Schiller 1935) Wall and Dale 1971 subsp. *steinii* autonym
Pyrophacus steinii (Schiller 1935) Wall and Dale 1971 subsp. *vancampoae* (Rossignol 1962) Balech 1979 (◉)

Pyrophacus vancampoae (Rossignol 1962) Wall and Dale 1971 (◉)

Genus *Pyxidinopsis* Habib 1976 (◉)

Genus *Selenopemphix* Benedek 1972 ~~emend. Head 1993~~ (◉)
Selenopemphix nephroides Benedek 1972 (◉)
Selenopemphix quanta Bradford 1975 (◉)
Selenopemphix undulata Verleye, Pospelova, Mertens and Louwye 2011

Genus *Sourniaea* Gu, Mertens, Li and Shin in Zhang et al. 2020
Sourniaea diacantha (Meunier 1919) Gu, Mertens, Li and Shin in Zhang et al. 2020

Genus *Spiniferites* Mantell 1850 ~~emend. Sarjeant 1970~~ (◉)
Spiniferites bentorii (Rossignol 1964) Wall and Dale 1970 (◉)
Spiniferites bulloideus (Deflandre and Cookson 1955) Sarjeant 1970 (◉)
Spiniferites delicatus Reid 1974 (◉)
Spiniferites elongatus Reid 1974 (◉)
Spiniferites lazus Reid 1974 (◉)
Spiniferites pachydermus (Rossignol 1964) Reid 1974 (◉)

Genus *Succiniperidinium* Masure et al. 2013
Succiniperidinium inopinatum Masure et al. 2013

Genus *Tectatodinium* Wall 1967 ~~emend. Head 1994~~ (◉)
Tectatodinium pellitum Wall 1967 ~~emend. Head 1994~~ (◉)

Genus *Tuberculodinium* Wall 1967 (◉)
Tuberculodinium vancampoae (Rossignol 1962) Wall 1967 (◉)

Genus *Votadinium* Reid 1977 (◉)
Votadinium calvum Reid 1977 (◉)
Votadinium spinosum Reid 1977 (◉)

Genus *Xandarodinium* Reid 1977 (◉)
Xandarodinium xanthum Reid 1977 (◉)

* The genus *Alexandrium* was considered a junior heterotypic synonym of *Blepharocysta* Ehrenberg 1873 (Elbrächter et al. 2018, 2019). However, the conservation of an epitype for *Blepharocysta splendor-maris* and its genus *Blepharocysta* allows *Blepharocysta* to be understood in a way that includes no currently accepted species of *Alexandrium* (Carbonell-Moore 2018; Wilson 2023). We provisionally accept that *Alexandrium* was validly published

under the ICZN (see text for discussion), athough according to Wilson et al. (2023) the ICZN commissioners will be asked to provide a ruling on this matter.

Table ~~1~~2. Nomenclatural status and, where known, motile–cyst equivalence of those fossil-taxa and cyst-producing non-fossil taxa discussed in the text. A fossil-~~-~~species is one in which the type is a fossil. A name-element in bold face indicates that it is based on a type that is a fossil.

Fossil-species	**Non-fossil species** (c=cyst, m-~~=~~motile stage)
Ataxiodinium choane Reid 1974	? *Gonyaulax polygramma* Stein 1883
Bitectatodinium tepikiense Wilson 1973	*Gonyaulax* sp. indet. (n~~N~~ot *Gonyaulax digitale* (Pouchet 1883) Kofoid 1911 -(m)~~—~~
Brigantedinium ***auranteum*** Reid 1977	Unknown
Brigantedinium ***majusculum*** Reid 1977	*Protoperidinium sinuosum* Lemmermann 1905 (m)
Dapsilidinium pastielsii (Davey and Williams 1966) Bujak et al. 1980	No equivalent non-fossil name.
? ***Desotodinium wrennii*** De Schepper et al. 2004	*Pyrophacus horologium* Stein 1883 (m)
Dubridinium caperatum Reid 1977	*Preperidinium meunieri* (Pavillard 1913) Elbrächter 1993 (m)
Dubridinium cassiculum Reid 1977	Unknown
Dubridinium cavatum Reid 1977	*Diplopsalopsis orbicularis* (Paulsen 1907) Meunier 1910 (m)
Dubridinium ulsterum Reid 1977	Unknown
Islandinium minutum (Harland and Reid in Harland et al. 1980) Head et al. 2001	Emended by Potvin et al. (2013) to include thecal characteristics. Otherwise no equivalent non-fossil name.
Islandinium pacificum Gurdebeke et al. 2019	*Protoperidinium mutsuense* (Abé 1936) Balech 1974 (m)
Lingulodinium machaerophorum (Deflandre and Cookson 1955) Wall 1967	*Lingulaulax polyedra* (von Stein 1883) ~~n. gen et~~ comb. nov. (m)
? ***Nematosphaeropsis lemniscata*** Bujak 1984	***Nematosphaeropsis*** *labyrinthus* (Ostenfeld 1903) Reid 1974 (c)
Operculodinium centrocarpum (Deflandre and Cookson 1955) Wall 1967 Bütschli~~,~~ 1885 (m)	Unknown (n~~N~~ot *Protoceratium reticulatum* (Claparède and Lachmann 1859)) ~~1885 (m)~~

Peridinium ***ponticum*** Wall and Dale in Wall et al. 1973 ~~equivalent non-fossil name.~~	*Protoperidinium* sp. cf. *P. divergens* (Ehrenberg 1841) Balech 1974 (m)~~No~~
Selenopemphix quanta Bradford 1975	? *Protoperidinium conicum* (Gran 1900) Balech 1974
Selenopemphix nephroides Benedek 1972	*Protoperidinium subinerme* (Paulsen 1904) Loeblich III 1969 (m)
Spiniferites bentorii (Rossignol 1964~~Wall 1965~~) Wall and Dale ~~1967~~1970	*Gonyaulax nezaniae* Gu and Mertens in Gu et al. 2021 (m)
Spiniferites bulloideus (Deflandre and Cookson 1955) Sarjeant 1970	? *Gonyaulax scrippsae* Kofoid 1911 (m)
Spiniferites delicatus Reid 1974	Unknown
Spiniferites elongatus Reid 1974	*Gonyaulax ovum* (Gaarder 1954) Head et al. (in revision) (m)
Spiniferites lazus Reid 1974	Unknown
Stelladinium reidii Bradford 1975	No equivalent non-fossil name.
Tuberculodinium vancampoae (Rossignol 1962) Wall 1967	*Pyrophacus steinii* (Schiller 1935a) Wall and Dale 1971 (m)
Votadinium calvum Reid 1977	*Protoperidinium latidorsale* (Dangeard 1927) Balech 1974 (m)
Votadinium spinosum Reid 1977	*Protoperidinium claudicans* (Paulsen 1907) Balech 1974 (m)
Xandarodinium xanthum Reid 1977	Unknown
No equivalent fossil name.	*Brigantedinium simplex* Wall 1965, ex Lentin and Williams 1993 (c). A heterotypic junior synonym of *Protoperidinium conicoides* (Paulsen 1905) Balech 1974 (m)
No equivalent fossil name.	*Echinidinium granulatum* Zonneveld 1997 ex Head et al. 2001 (c)
No equivalent fossil name.	*Gonyaulax baltica* Ellegaard et al. 2002 (c)
No equivalent fossil name (not ***Spiniferites pachydermus*** (Rossignol 1964) Reid 1974)	*Gonyaulax ellegaardiae* Mertens, Aydin, Takano, Yamaguchi and Matsuoka in Mertens et al. 2015 ex Head, Mertens and Fensome (herein) 2015 (m).
No equivalent fossil name.	***Islandinium*** *tricingulatum* (Kawami et al. 2009) Potvin et al. (2013) (m)

No geologically preservable cyst known.

No equivalent fossil name.

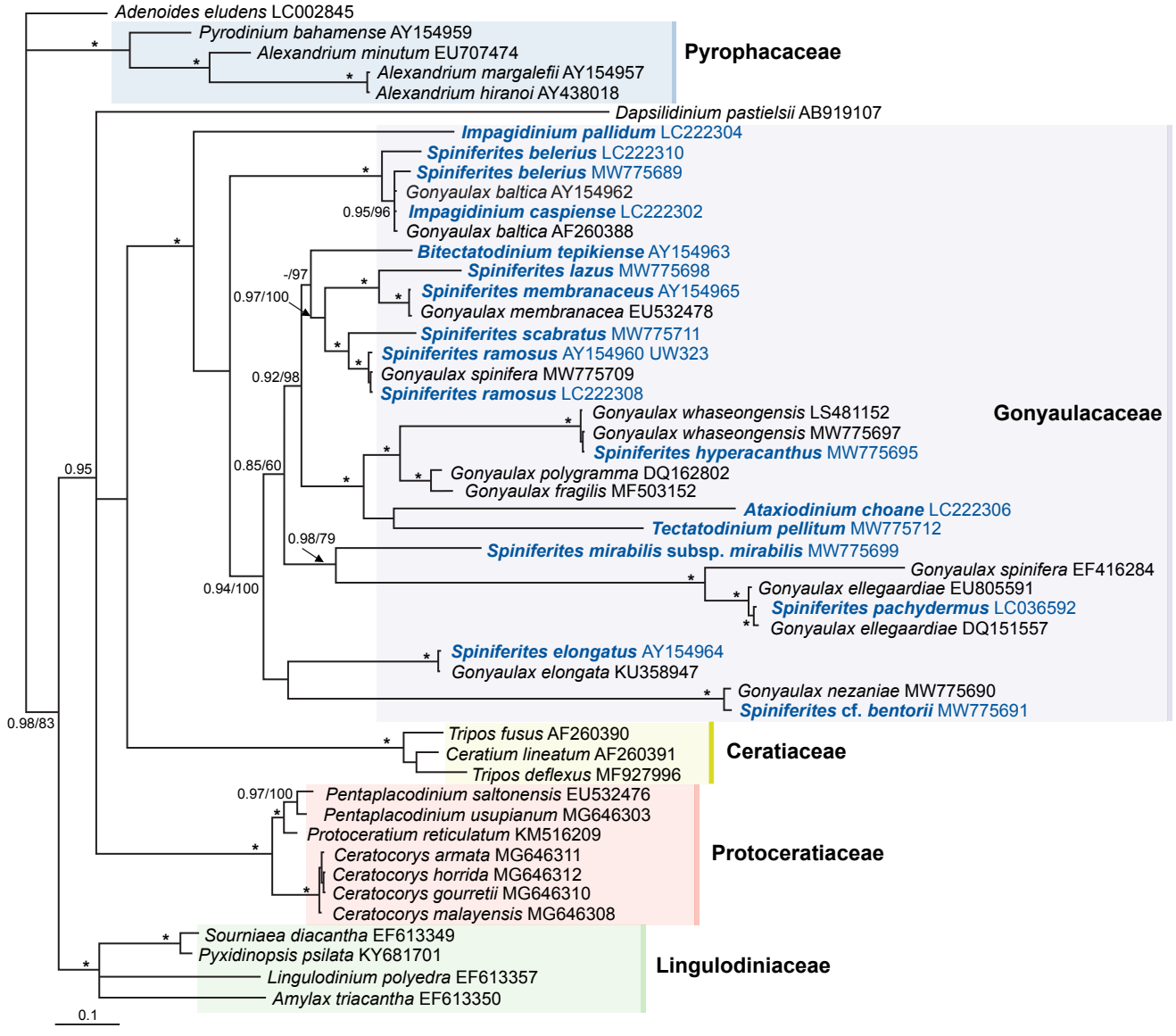
Lingulaulax milneri (Murray and Whitting 1899) n. gen et comb. (m)

Protoperidinium stellatum (Wall in Wall and Dale 1968) Balech 1994 (m)

IBC and year	Code and authors	Relevant introduction or change
7th IBC, Stockholm 1950	Stockholm Code (Lanjouw et al. 1952)	Appendix on fossils introduced that includes "organ-genera" and "form-genera"; the term "subfossil" also introduced for which the same provisions apply as for fossils.
8th IBC, Paris 1954	Paris Code (Lanjouw et al. 1956)	Names of non-fossil algae require illustration showing distinctive features, from 1 January 1958; and Latin description/diagnosis between 1 January 1958 and 31 December 2011.
9th IBC, Montreal 1959	Montreal Code (Lanjouw et al. 1961)	Appendix on fossils integrated into the main body of the Code. "Organ-genera" and "form-genera" redefined as mutually exclusive concepts.
10th IBC, Edinburgh 1964	Edinburgh Code (Lanjouw et al. 1966)	Requirement of "stratigraphic relations" at the site of original occurrence introduced for fossil taxa as a means to distinguish from "Recent material".
12th IBC, Leningrad 1975	Leningrad Code (Stafleu et al. 1978)	"Organ-genera" discontinued.
13th IBC, Sydney 1981	Sydney Code (Voss et al. 1983)	Relationship clarified between "fossil" and "recent" (now lowercased) plants by referring to the latter as "non-fossil" plants.
15th IBC, Tokyo 1993	Tokyo Code (Greuter et al. 1994)	Names of new taxa of "fossil plants" require Latin or English description or diagnosis or full and direct reference to such from 1 January 1996 (hence Latin no longer required).
16th IBC, St Louis 1999	St Louis Code (Greuter et al. 2000)	"Morphotaxa" introduced for fossils that consist of a part, life-history stage, or preservational state. The term "fossil taxon" appears, along with first example of dual nomenclature in dinoflagellates. The type specimen of the name of a new fossil-taxon must be identified among the validating illustrations, from 1 January 2001. A type specimen of the name of an algal taxon may be a culture if metabolically inactive.
17th IBC, Vienna 2005	Vienna Code (McNeill et al. 2006)	The type of a name of a new non-fossil taxon at the rank of species or below from 1 January 2007 must be a specimen (illustrations allowed previously for algae) except where preservation is difficult.
18th IBC, Melbourne 2011	Melbourne Code (McNeill et al. 2012)	New title "International Code of Nomenclature for algae, fungi, and plants" (ICN) introduced. Discontinuation of terms "subfossil" and "morphotaxon", instead distinguishing only between "fossil-taxa" and "non-fossil taxa". Names of new non-fossil taxa require Latin or English description or diagnosis or full and direct reference to such from 1 January 2012 (hence Latin no longer required).
19th IBC,	Shenzhen Code	Simple distinction between "fossil-taxa" and "non-fossil

Table 3. Summary of changes to the nomenclatural Codes that affect those fossil- and non-fossil algal taxa, as explained in the text, with reference to each International Botanical Congress (IBC) from 1950 and the published Code resulting from it.

Shenzhen 2017	(Turland et al. 2018)	taxa" continued. Three examples of dual nomenclature in dinoflagellates provided in total (in Arts. 11.7 and 11.8). If a type specimen of the name of an algal taxon is a metabolically inactive culture, from 1 January 2019 this must be specified within the protologue.


Adenoides eludens LC002845
Pyrodinium bahamense AY154959
Alexandrium minutum EU707474
Alexandrium margalefii AY154957
Alexandrium hiranoi AY438018
Pyrophacaceae
Dapsilidinium pastielsii AB919107
Impagidinium pallidum LC222304
Spiniferites belerius LC222310
Spiniferites belerius MW775689
Gonyaulax baltica AY154962
Impagidinium caspiense LC222302
Gonyaulax baltica AF260388
Bitectatodinium tepikiense AY154963
Spiniferites lazus MW775698
Spiniferites membranaceus AY154965
Gonyaulax membranacea EU532478
Spiniferites scabratus MW775711
Spiniferites ramosus AY154960 UW323
Gonyaulax spinifera MW775709
Spiniferites ramosus LC222308
Gonyaulax whaseongensis LS481152
Gonyaulax whaseongensis MW775697
Spiniferites hyperacanthus MW775695
Gonyaulax polygramma DQ162802
Gonyaulax fragilis MF503152
Gonyaulacaceae
Ataxiodinium choane LC222306
Tectatodinium pellitum MW775712
Spiniferites mirabilis subsp. mirabilis MW775699
Gonyaulax spinifera EF416284
Gonyaulax ellegaardiae EU805591
Spiniferites pachydermus LC036592
Gonyaulax ellegaardiae DQ151557
Spiniferites elongatus AY154964
Gonyaulax elongata KU358947
Gonyaulax nezaniae MW775690
Spiniferites cf. bentorii MW775691
Tripos fusus AF260390
Ceratium lineatum AF260391
Tripos deflexus MF927996
Ceratiaceae
Pentaplacodinium saltonensis EU532476
Pentaplacodinium usupianum MG646303
Protoceratium reticulatum KM516209
Ceratocorys armata MG646311
Ceratocorys horrida MG646312
Ceratocorys gourretii MG646310
Ceratocorys malayensis MG646308
Protoceratiaceae
Sourniaea diacantha EF613349
Pyxidinopsis psilata KY681701
Lingulodinium polyedra EF613357
Amylax triacantha EF613350
Lingulodiniaceae
0.95
0.98/83
0.85/60
0.98/79
0.94/100
0.92/98
-/97
0.97/100
0.95/96
0.97/100
0.1

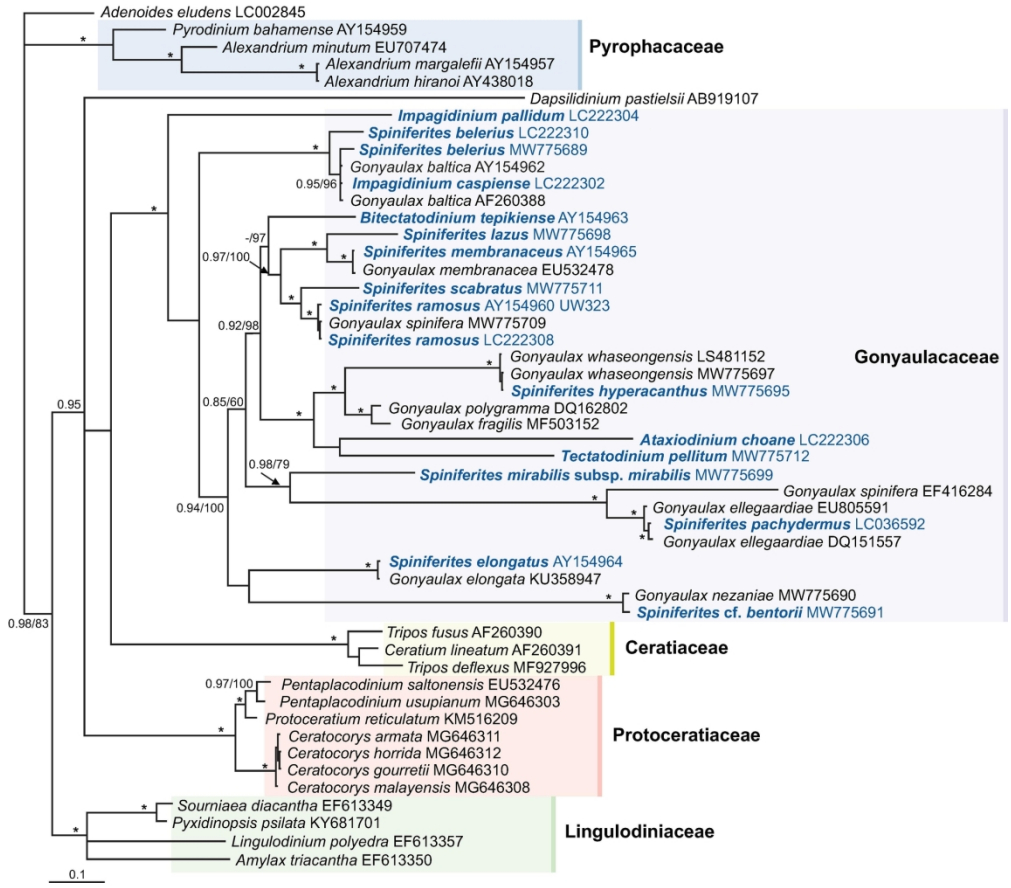
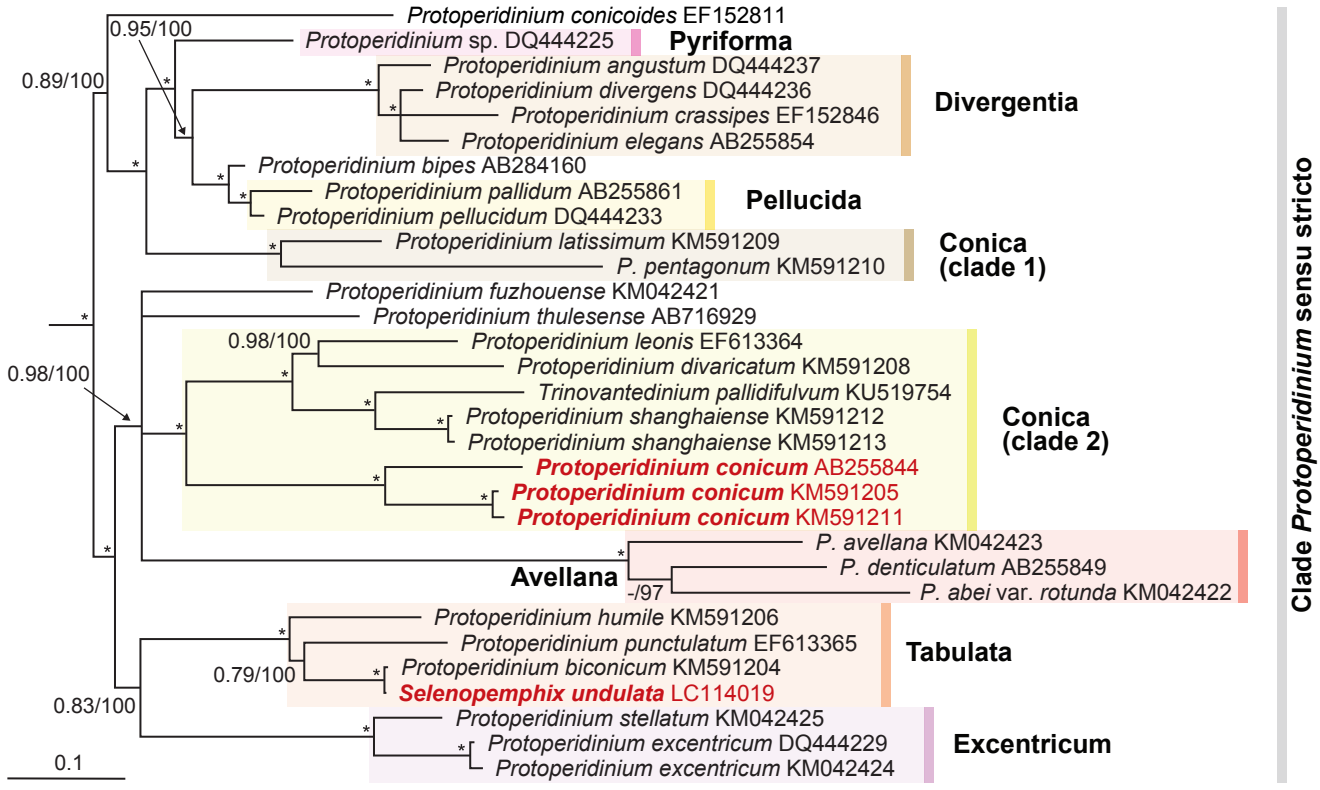


Figure 1. Phylogeny of the fossil-genera Ataxiodinium, Bitectatodinium, Impagidinium, Spiniferites and Tectatodinium inferred from partial large subunit (LSU) rRNA gene sequences using Bayesian inference. These genera have all been linked by incubation studies to the non-fossil Gonyaulax spinifera and Gonyaulax polygramma complexes, and all are paraphlyetic. These genera nonetheless all include extinct species, and as presently circumscribed are needed in fossil cyst nomenclature. Branch lengths drawn to scale; scale bar indicates number of nucleotide substitutions per site. Numbers on branches are statistical support values to clusters on their right (left: Bayesian posterior probabilities; right: maximum likelihood (ML) bootstrap support values). Only Bayesian posterior probabilities above 0.9 and ML bootstrap support values above 50 are shown. An asterisk (*) indicates maximal support (BI posterior probability = 1.0, ML bootstrap support = 100). The scale bar represents inferred evolutionary distance in changes/site. From fig. 77 of Gu et al. (2021).

172x151mm (300 x 300 DPI)


Protoperidinium conicoides EF152811
0.95/100
Protoperidinium sp. DQ444225
Pyriforma
0.89/100
Protoperidinium angustum DQ444237
Protoperidinium divergens DQ444236
Protoperidinium crassipes EF152846
Protoperidinium elegans AB255854
Divergentia
Protoperidinium bipes AB284160
Protoperidinium pallidum AB255861
Protoperidinium pellucidum DQ444233
Pellucida
Protoperidinium latissimum KM591209
P. pentagonum KM591210
Conica (clade 1)
Protoperidinium fuzhouense KM042421
Protoperidinium thulesense AB716929
0.98/100
Protoperidinium leonis EF613364
0.98/100
Protoperidinium divaricatum KM591208
Trinovantedinium pallidifulvum KU519754
Protoperidinium shanghaiense KM591212
Protoperidinium shanghaiense KM591213
Protoperidinium conicum AB255844
Protoperidinium conicum KM591205
Protoperidinium conicum KM591211
Conica (clade 2)
P. avellana KM042423
P. denticulatum AB255849
Avellana
-/97
P. abei var. rotunda KM042422
Protoperidinium humile KM591206
Protoperidinium punctulatum EF613365
0.79/100
Protoperidinium biconicum KM591204
Selenopemphix undulata LC114019
Tabulata
0.83/100
Protoperidinium stellatum KM042425
Protoperidinium excentricum DQ444229
Protoperidinium excentricum KM042424
Excentricum
0.1
Clade Protoperidinium sensu stricto

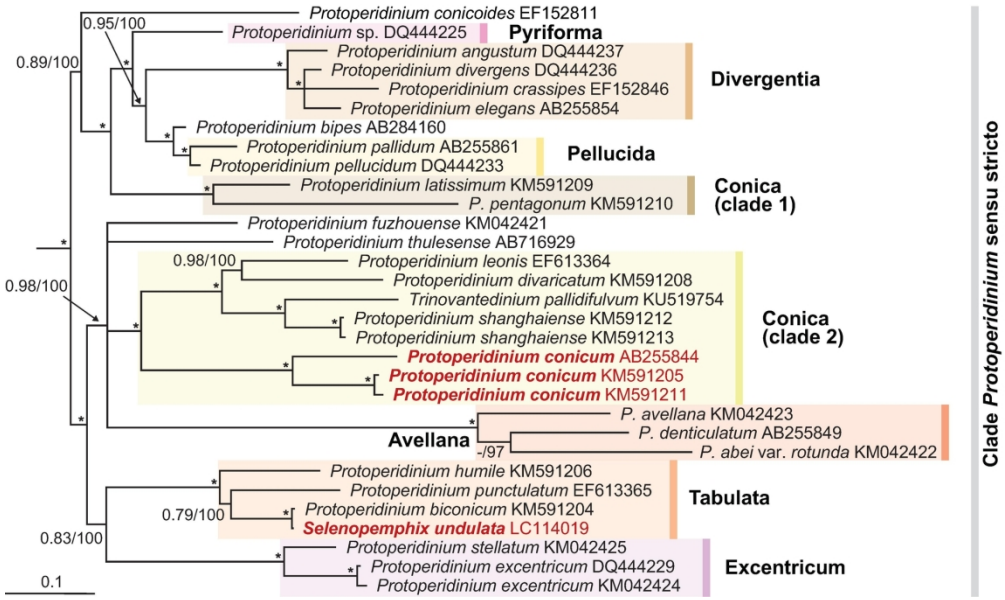
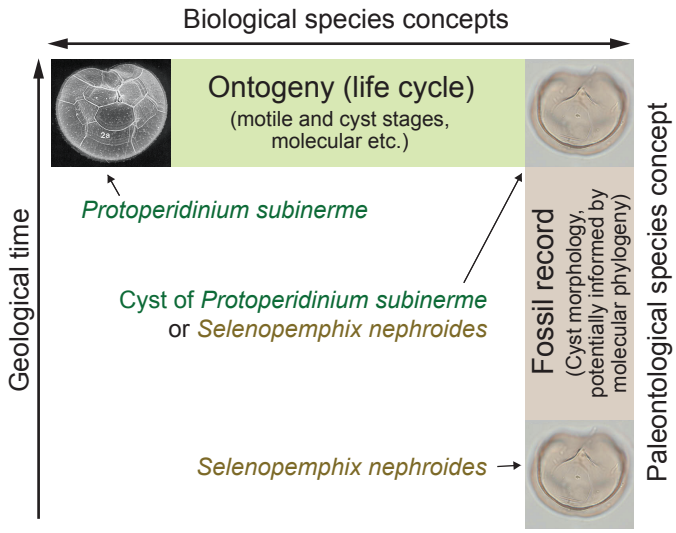


Figure 2. Phylogeny of the Protoperidinium sensu stricto clade inferred from LSU rRNA gene sequences using Bayesian inference, and its taxonomic implications for the fossil-genera Selenopemphix and Multispinula. Selenopemphix undulata plots within the Tabulata clade whereas Protoperidinium conicum, to which Selenopemphix (formerly Multispinula) quanta has been attributed, groups within the Conica 2 clade, suggesting that Selenopemphix and Multispinula might be treated as separate fossil-genera. Protoperidinium subinerme (its fossil-defined equivalent being Selenopemphix nephroides) has not yet been sequenced. The maximum likelihood (ML) bootstrap support values (ML) over 50 and Bayesian posterior probabilities (PP) over 0.7 are shown at the nodes (ML/PP), where an asterisk (*) indicates maximal support. Clades within the Protoperidinium sensu stricto clade are shown. The scale bar represents inferred evolutionary distance in changes/site. From fig. 3 of Mertens et al. (2017b).

173x103mm (300 x 300 DPI)


Biological species concepts
Ontogeny (life cycle)
(motile and cyst stages, molecular etc.)
Protoperidinium subinerme
Cyst of Protoperidinium subinerme
or Selenopemphix nephroides
Selenopemphix nephroides
Fossil record
(Cyst morphology, potentially informed by molecular phylogeny)
Geological time
Paleontological species concept

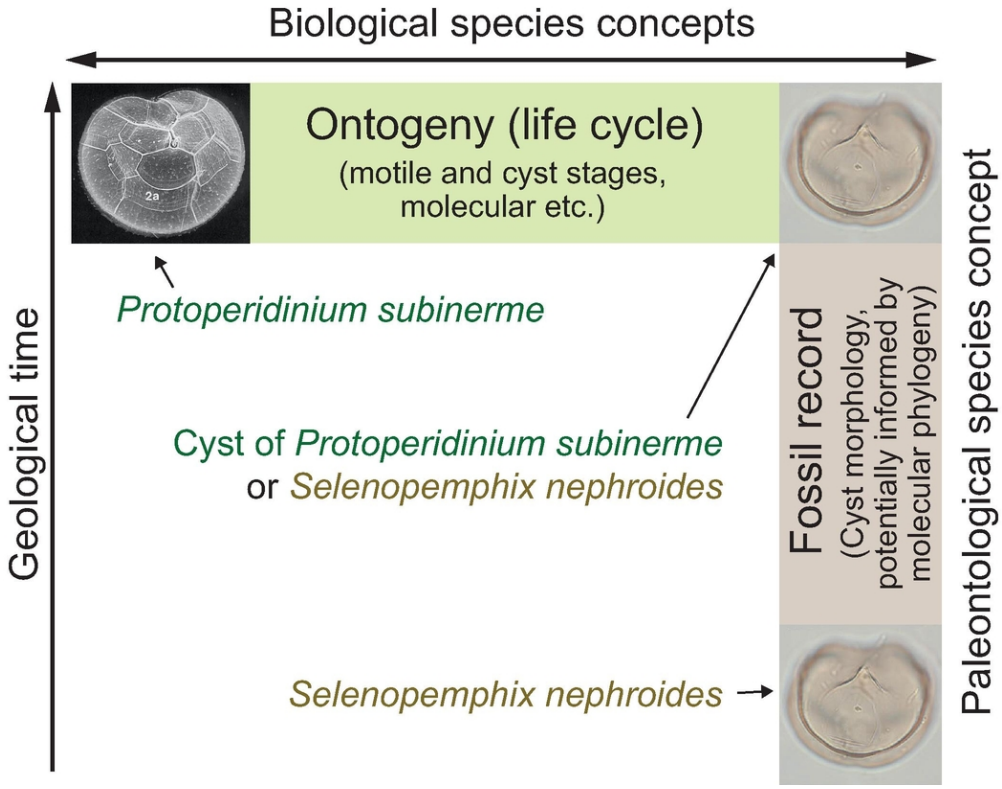
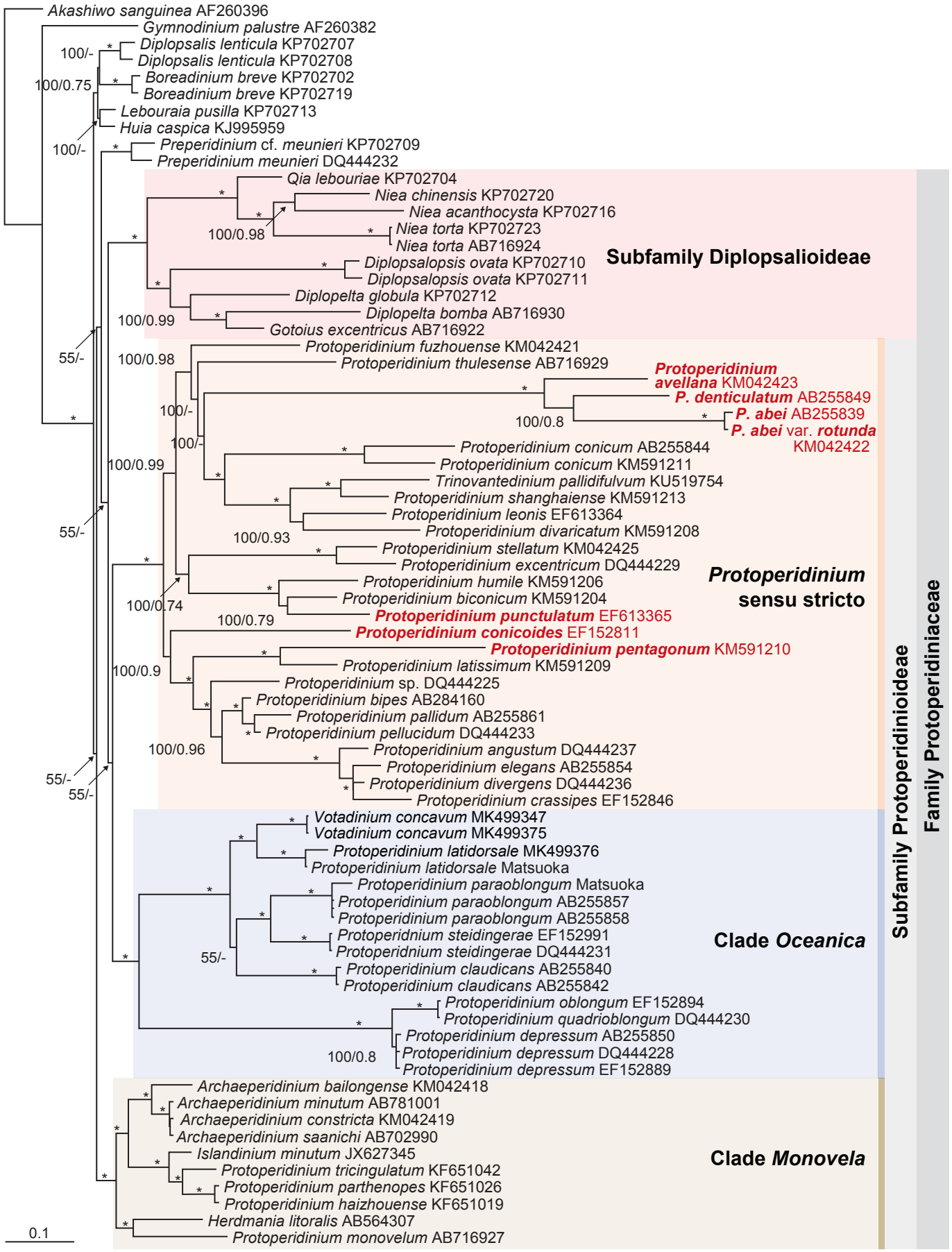
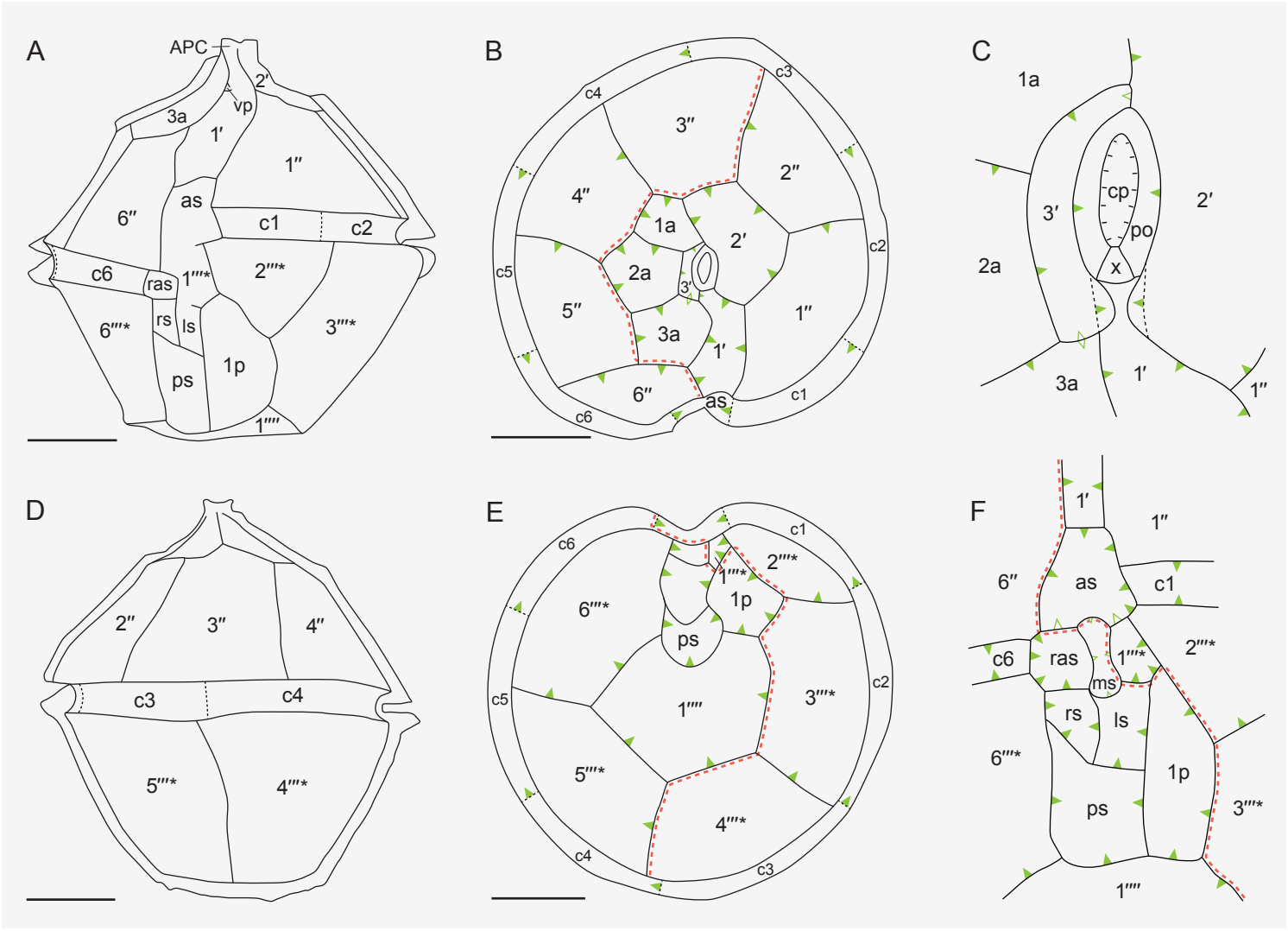


Figure 3. Conceptual foundation for dual nomenclature. Biological species concepts potentially incorporate all aspects of the life cycle as well as genetic and other molecular information on the living organism. The species is typified by a non-fossil specimen or illustration, and a single non-fossil species name applies to all parts of the life history and may include information from genome sequencing. The paleontological species concept is, with rare exception, confined to the morphology of the fossilized resting cyst wall, although the significance of morphological attributes may be informed by independent evidence of phylogeny (e.g. molecular) where species are extant. The species is typified by a fossil specimen, and a fossil-species name is applied. Living cysts provide the overlap between these two nomenclatural systems: dual nomenclature allows both names Selenopemphix nephroides and (the cyst of) Protoperidinium subinerme to be used for the illustrated cyst according to context and preference. The SEM illustration of Protoperidinium subinerme is from Hansen and Larson (1992) and the illustration of Selenopemphix nephroides is from modern sediments of the Gulf of Mexico (KNM, unpublished).

88x74mm (300 x 300 DPI)


Akashiwo sanguinea AF260396
Gymnodinium palustre AF260382
Diplopsalis lenticula KP702707
Diplopsalis lenticula KP702708
Boreadinium breve KP702702
Boreadinium breve KP702719
Lebouraia pusilla KP702713
Huia caspica KJ995959
Preperidinium cf. meunieri KP702709
Preperidinium meunieri DQ444232
Qia lebouriae KP702704
Niea chinensis KP702720
Niea acanthocysta KP702716
Niea torta KP702723
Niea torta AB716924
Diplopsalopsis ovata KP702710
Diplopsalopsis ovata KP702711
Diplopelta globula KP702712
Diplopelta bomba AB716930
Gotoius excentricus AB716922
Subfamily Diplopsalioideae
Protoperidinium fuzhouense KM042421
Protoperidinium thulesense AB716929
Protoperidinium avellana KM042423
P. denticulatum AB255849
P. abei AB255839
P. abei var. rotunda KM042422
Protoperidinium conicum AB255844
Protoperidinium conicum KM591211
Trinovantedinium pallidifulvum KU519754
Protoperidinium shanghaiense KM591213
Protoperidinium leonis EF613364
Protoperidinium divaricatum KM591208
Protoperidinium stellatum KM042425
Protoperidinium excentricum DQ444229
Protoperidinium humile KM591206
Protoperidinium biconicum KM591204
Protoperidinium punctulatum EF613365
Protoperidinium conicoides EF152811
Protoperidinium pentagonum KM591210
Protoperidinium latissimum KM591209
Protoperidinium sp. DQ444225
Protoperidinium bipes AB284160
Protoperidinium pallidum AB255861
Protoperidinium pellucidum DQ444233
Protoperidinium angustum DQ444237
Protoperidinium elegans AB255854
Protoperidinium divergens DQ444236
Protoperidinium crassipes EF152846
Protoperidinium sensu stricto
Votadinium concavum MK499347
Votadinium concavum MK499375
Protoperidinium latidorsale MK499376
Protoperidinium latidorsale Matsuoka
Protoperidinium paraoblongum Matsuoka
Protoperidinium paraoblongum AB255857
Protoperidinium paraoblongum AB255858
Protoperidnium steidingerae EF152991
Protoperidnium steidingerae DQ444231
Protoperidinium claudicans AB255840
Protoperidinium claudicans AB255842
Protoperidinium oblongum EF152894
Protoperidinium quadrioblongum DQ444230
Protoperidinium depressum AB255850
Protoperidinium depressum DQ444228
Protoperidinium depressum EF152889
Clade Oceanica
Archaeperidinium bailongense KM042418
Archaeperidinium minutum AB781001
Archaeperidinium constricta KM042419
Archaeperidinium saanichi AB702990
Islandinium minutum JX627345
Protoperidinium tricingulatum KF651042
Protoperidinium parthenopes KF651026
Protoperidinium haizhouense KF651019
Herdmania litoralis AB564307
Protoperidinium monovelum AB716927
Clade Monovela
Subfamily Protoperidinioideae
Family Protoperidiniaceae
100/-
100/0.75
100/-
100/0.98
100/0.99
55/-
100/0.98
100/-
100/0.8
100/-
100/0.99
55/-
100/0.93
100/0.74
100/0.79
100/0.9
100/0.96
55/-
55/-
55/-
100/0.8
0.1


A
APC
2′
vp
3a
1′
1″
as
6″
c1
c2
c6
ras
1‴*
2‴*
6‴*
rs
ls
3‴*
1p
ps
1‴′
B
c4
c3
3″
2″
4″
1a
2′
c2
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3′
5″
1″
3a
1′
6″
as
c1
c6
C
1a
cp
2′
3′
po
2a
x
3a
1′
1″
D
2″
3″
4″
c3
c4
5‴*
4‴*
E
c6
c1
2‴*
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6‴*
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ps
c2
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4‴*
c4
c3
F
1′
1″
6″
as
c1
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ras
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ms
rs
ls
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1p
ps
3‴*
1‴′

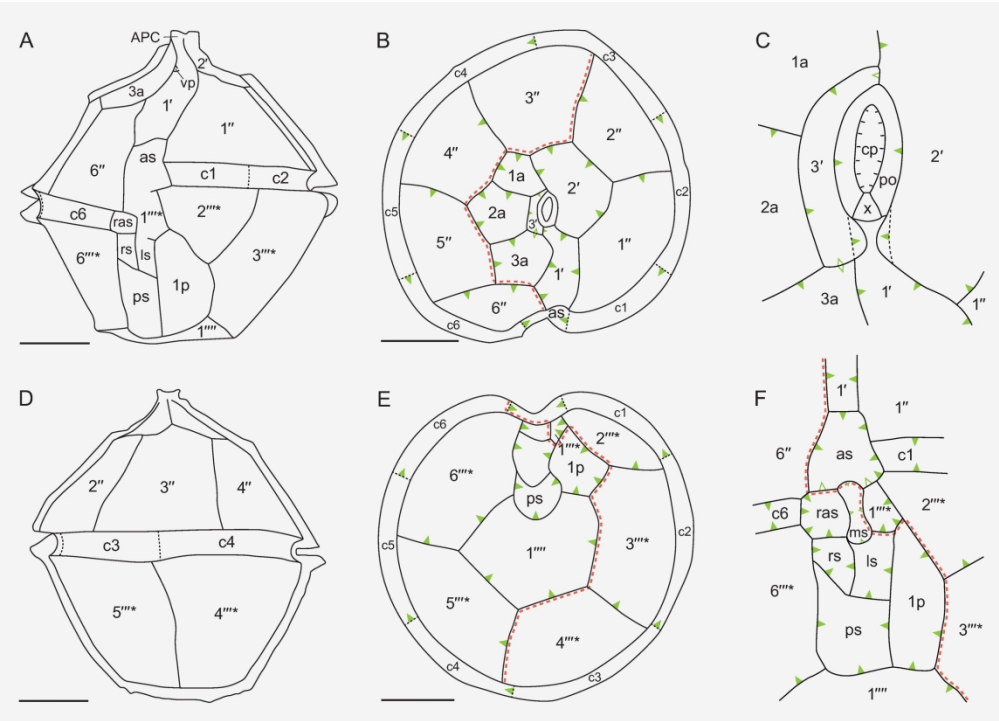

Figure 5. Lingulaulax polyedra (von Stein 1883) comb. nov. A, B, D, E, tracings of different motile stage cells from an SEM stub (strain K3-G8 isolated from the type locality off Kiel in the Baltic Sea) which serves as the epitype (from figs. 4B, 4G, 4D, and 4H respectively in Tillmann et al. 2021); ventral, apical, dorsal, and antapical views respectively. C and F, schematic representation of C, apical pore complex and surrounding plates (from fig. 6C in Tillmann et al. 2021), and F, mid-ventral area showing details of sulcus and surrounding plates (from fig. 6D in Tillmann et al. 2021). Solid green arrows indicate plate overlap, open green arrows indicate uncertain direction of plate overlap, and the red dashed line indicates line along which plates separate during cell division (from fig. 6 in Tillmann et al. 2021). Scale bars = 10 µm. Modified kofoidian plate labeling includes: APC = apical pore complex, vp = ventral pore, cp = cover plate, po = pore plate, X = X-plate; and the sulcal plates, as = anterior, ras = right accessory, ms = median, rs = right, ls = left, as = anterior. The first postcingular homologue (*1′′′) is designated as such because it lies within the sulcus and may not contact the cingular plate series.

196x141mm (300 x 300 DPI)