Desmocysta hadra, a new Late Cretaceous dinoflagellate cyst species: stratigraphic range, palaeogeographic distribution and palaeoecology

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Abstract. A new species of dinoflagellate cyst, Desmocysta hadra sp. nov., is described from the early Campanian (Late Cretaceous) in the Norwegian Sea. This new taxon differs from the other three known species by its particularly robust but highly folded wall and the short, fine filaments arising from the antapex. The short stratigraphic range of early Campanian for this new species was calibrated with other regional well-dated dinoflagellate cysts, making it a good biostratigraphic marker. A review of the taxonomic description of the genus has also been undertaken using the available published data. The available data shows a consistent presence of Desmocysta in the fossil record from the Early Cretaceous to the late Paleocene, although some Late Jurassic occurrences have been reported in the North Sea Basin. The current records also indicate that this genus is restricted to higher latitudes in the Northern Hemisphere. Based on Paleocene and Late Cretaceous occurrences of the genus, and its association with dinoflagellate cysts, prasinophytes and acritarchs, a proximal, highly stressed marine environment for Desmocysta is suggested.

1 Introduction

The genus Desmocysta was defined by Duxbury (1983, p. 43) in his palynological study of Aptian to lower Albian sediments from the Lower Greensand Group on the Isle of Wight (southern England). The genus name is derived from the Greek desmos, a cable, and kystis, a cell or sac, in reference to the characteristic antapical filaments linked to relatively featureless cysts. This genus comprises spheroidal to ovoidal cysts exhibiting virtually absent tabulation except where indicated by a two-plate precingular archaeopyle, although the precise plate equivalence cannot be determined. As described by Duxbury (1983), every cyst possesses fine and long filaments extending from the antapex.

The diagnosis of the first published species, Desmocysta plekta, is similar to that of the genus, although it is mentioned that the long fine filaments (10 or more individual filaments) extend from a small area at the antapex and exhibit a length twice as long as the length of the main body or capsule (Duxbury, 1983, text figs. 20–21). The filaments often terminate in a granular amorphous mass.

In the genus remarks, Duxbury referred to the apparent resemblance to Ophiobolus lapidiaris Wetzel (1933), which possesses an ovoidal main structure with a smooth to microgranulate surface with some strands or filaments connected to the main body. Often, observation of these filaments may be difficult. Evitt (1968) suggested that Ophiobolus could represent the egg case of a planktonic organism and the strands or filaments represent either attachments or buoyancy aids to support the eggs in the planktonic stage. Duxbury (1983) discussed Evitt’s (1968) theory and mentioned that some features in the central body figured in Evitt’s paper could be considered sutural splits between precingular plates. Although Duxbury (1983) only defined a single species of Desmocysta, he mentioned that other species should exist, referring specifically to Ophiobolus sp. A of Davey (1979) and the unpublished Klementia barbata of Warren (1967). Klementia barbata was subsequently formalised as Warrenia californica Monteil (1992), a single species of the genus Warrenia.
comprising smooth to verrucate or spinose ovoidal cysts with no clear tabulation except for a two-plate precingular archaeopyle with or without antapical filaments. The type material from southern France supports a stratigraphic range from the late Tithonian to early Valanginian. Duxbury (1983) also stated that the genus *Desmocysta* differs from the genus *Scuticabolus* Loeblich (1967) in that the latter genus has some type of apical (or at least pre-precingular) archaeopyle as opposed to the 2P type diagnosed in *Desmocysta*.

Duxbury (2001) described *Desmocysta simplex* from late Hauterivian sediments from the central North Sea (UK) as the first formal description of *Ophiobolus* sp. A Davey (1979). *Desmocysta simplex* exhibits similarities to *Desmocysta plekta*, although the cyst is generally larger and possesses fewer antapical filaments.

Duxbury (2018) included smooth to granulate and/or verrucate forms with or without antapical filaments in the genus *Desmocysta*, and *Warrenia californica* Monteil (1992) was emended and transferred to *Desmocysta californica*. This species exhibits a thin wall comparable with *Desmocysta plekta*, and there is clear evidence for the presence of surface granules and/or verrucae on the cyst (see Plate 2, figs. 5 and 6).

Since the definition of this genus, occurrences of *Desmocysta plekta* have been reported in several publications ranging from the Barremian of northwest Greenland and the North Atlantic (Nøhr-Hansen, 1993; Ogg, 1994) to the Thanetian of southeast England (Jolley, 1992, 1998) (Fig. 1). The other two species (*D. simplex* and *D. californica*) have not yet been reported further in published literature after their formal definition. Representatives of this genus have also been observed in Late Jurassic, middle–early Kimmeridgian, late Kimmeridgian and middle Volgian material, including common occurrences in the late Kimmeridgian of UKCS Block 14/19 (Stan Duxbury, personal observation, 2020).

In this paper, we describe a new species of *Desmocysta* and discuss the stratigraphic relevance of this genus, its geographic distribution and previously unpublished records from the Shell northwest Europe offshore microfossil database.

### 2 Material and methods

The *Desmocysta* specimens identified and illustrated here are from cutting samples collected from the 6304/3-1 well drilled in the Norwegian Sea.

The available cuttings were treated to standard palynological preparation techniques, including acid digestion using hydrochloric acid (HCl) to eliminate carbonates and hydrofluoric acid (HF) to eliminate silicates. The resulting residue was subject to oxidation using concentrated nitric acid (HNO₃). The remaining organic fraction was sieved through a 20µm mesh nylon sieve to concentrate the kerogen, which was then air-dried on coverslips and mounted on slides using Petroxoy 154 resin as permanent mounts. Slides were scanned under a Leica DM 1000 microscope, and the specimens were identified, counted and described. All photographs were taken using a Leica MC170HD camera.

The illustrated specimens are identified by their sample depth, followed by the respective position using England Finder (EF) co-ordinates. The slide with the new species holotype is deposited at the Natural History Museum in the London palynology slide repository. The suprageneric classification follows Fensome et al. (1993). The morphological terminology follows Stover and Evitt (1978) and Williams et al. (2000).

### 3 Systematic palaeontology

**Division** Dinoflagellata (Bütschli 1885) Fensome et al. 1993

**Subdivision** Dinokaryota Fensome et al. 1993

**Class** Dinophyceae Pascher 1914

**Subclass** Peridiniphycidae Fensome et al. 1993

**Order** Gonyaulacales Taylor 1980

**Family** uncertain

**Genus** *Desmocysta* Duxbury 1983

**Type species**

*Desmocysta plekta* Duxbury, 1983

*Desmocysta hadra* sp. nov.

Plate 1, figs. 1–12

**Derivation of name**

From the Greek *hadros*, well-developed, bulky and stout, referring to the robust nature of this species.

**Diagnosis**

A subspherical to ovoidal dinoflagellate cyst with a two-plate precingular archaeopyle. The wall is thick, up to 2µm, and highly folded with a scabrate–punctate surface. Fine, usually short filaments arise from a small area at the antapex (Fig. 2).
Figure 1. Summary of the published chronostratigraphic occurrences of *Desmocysta* species by author and geographic distribution.

Figure 2. Interpretative drawing of *Desmocysta hadra* sp. nov. (a) Dorsal view; (b) left-lateral view.

Holotype

Plate 1, fig. 1; from a cutting sample at 3495 m; EF co-ordinates 157/3; central body length 58 µm, width 48 µm, length of filaments 15 µm.

Stratigraphic horizon

Early Campanian of well 6304/3-1.

Description

The dinoflagellate cyst is of intermediate size, subspherical to ovoidal in shape and highly folded. These folds usually seem to run approximately parallel to the margin of the cyst. The wall is thick, up to 2 µm, and scabrate–punctate. The fine grana are well-developed, up to 3 µm, tending to concentrate in the lower third of the body where the filaments originate. The filaments are usually short, fine and thread-like (occasionally some specimens show longer filaments), arising from the antapex and usually less than 1/3 the length of the cyst. The archaeopyle is two-plate precingular, and the operculum is usually free, although the opercular pieces can occasionally be seen inside the cyst (see Plate 1 – figs. 4 and 7). In some cysts it is possible to observe a small incision between the two archaeopyle plates. The presence of opercular pieces inside the cyst, together with a highly folded wall and well-developed granulation particularly concentrated in a small area where the filaments are attached to the antapex, is not reported in other *Desmocysta* species.

Dimensions

Central body length 46(58)67 µm, width 43(49)61 µm, length of filaments 10(24)35 µm. Number of specimens measured 20.

Remarks

This new species differs from *D. plekta* (Plate 2, figs. 1–4) by its larger size, thicker wall and shorter filaments, as well as from *D. simplex* (Plate 2, fig. 7) by its numerous, relatively short antapical filaments. *Desmocysta californica* (Plate 2, figs. 5–6) differs by the presence of granules and/or verrucae on its surface. *Desmocysta hadra* sp. nov. also differs from those species by its highly folded wall and the concentration...
Desmocysta hadra sp. nov. All specimens were recovered from cutting samples at 3495 m in the 6304/3-1 well. (1) Holotype. Specimen in dorsal orientation exhibiting the finely granular ornament, mainly concentrated towards the antapex where the short filaments arise. Central body length 58 µm, width 48 µm, filaments length 15 µm; slide co-ordinate EF. J57/3. (2–12) Paratypes. (2) Specimen in dorsal orientation. Central body length 58 µm, width 48 µm, filaments length 24 µm; slide co-ordinate EF. N54/3. (3) Specimen in left-lateral orientation. Central body length 61 µm, width 57 µm, filaments length 20 µm; slide co-ordinate EF. U44/4. (4) Specimen in right-lateral orientation with the opercular plates inside the cyst. Central body length 56 µm, width 55 µm, filaments length 33 µm; slide co-ordinate EF. J56. (5) Specimen in right-lateral orientation. Central body length 54 µm, width 56 µm, filaments length 32 µm; slide co-ordinate EF. R51/2. (6) Specimen in right-lateral orientation. Central body length 56 µm, width 57 µm, filaments length 26 µm; slide co-ordinate EF. N44/4. (7) Specimen in dorsal orientation with the opercular plates detached but in situ inside the cyst. Central body length 62 µm, width 61 µm, filaments length 27 µm; slide co-ordinate EF. U43/4. (8) Specimen in dorsal orientation with the opercular plates detached but in situ, showing the finely granular ornament concentrated at the antapex. Central body length 62 µm, width 57 µm, filaments length 23 µm; slide co-ordinate EF. P46/2. (9) Specimen in right-lateral orientation with the opercular plates detached but in situ, clearly showing the finely granular ornament, which is mainly concentrated towards the antapex. Central body length 61 µm, width 52 µm, filaments length 28 µm; slide co-ordinate EF. U42. (10) Specimen in dorsal orientation. Central body length 56 µm, width 56 µm, filaments length 14 µm; slide co-ordinate EF. L50/2. (11) Specimen in dorsal orientation. Central body length 56 µm, width 53 µm, filaments length 10 µm; slide co-ordinate EF. F42/2. (12) Specimen in dorsal orientation showing the two-plate precingular archaeopyle. Central body length 57 µm, width 53 µm, filaments length 1 µm; slide co-ordinate EF. J59.
of fine grana in the lower part of the body, particularly where the filaments originate.

**Associated taxa**

The sample from which the holotype is recorded is dominated by the new species (nearly 40% of the overall dinoflagellate cyst assemblage), together with the common *Heterosphaeridium bellii–heteracanthum*, *Palaeoperidinium pyrophorum* and *Spiniferites ramosus* group and frequent occurrences of *Cerodinium diebelii*, *Chatangiella* spp. and *Trithyrodinium evitti*. Other taxa recorded include rare *Alterbidinium acutulum*, *Amphidiadema denticulata*, *Hystrichochodinium pulchrum*, *Odontochitina diducta*, *Palaeohystrichochora infusorioidea*, *Raphidodinium fucatum*, *Spongodinium delitiense* and *Trichodinium castanea*. Frequent occurrences of the pollen type *Aquilapollenites* spp. are also recorded.

**4 Discussion**

**4.1 Taxonomic remarks**

The presence of a two-plate precingular archaeopyle is one of the defining features of the genus *Desmocysta*. Although there are some references to cysts attributed to *Desmocysta* exhibiting atypical morphologic features (Nøhr-Hansen, 1993; Torricelli, 2000), those forms require further research in order to establish specific differences with the generic definition of Duxbury (1983). Nøhr-Hansen (1993) studied several sections of late–early Barremian to late Albian ages from east Greenland and reported the presence of *Desmocysta plekta* exhibiting the characteristic features of the species. In the same publication, Nøhr-Hansen recognised another form, very similar in size and appearance to *D. plekta* from a section of Albian age, although this cyst appears to have an apical archaeopyle (see Plate 2, fig. 8). That form was still included in the latter species, but according to Nøhr-Hansen (1993) the recognition of a different archaeopyle in this cyst type may support the definition of a new species and possibly a new genus.

Torricelli (2000) reported two dinoflagellate cysts identified as cf. *Desmocysta plekta* from late Albian samples of the Cismon core (southern Alps, northeast Italy). These specimens were referred to cf. *D. plekta* based on their similarity in size and appearance, although they show an apical archaeopyle. Analysing the published illustration (see Plate II, fig. 9), the cyst is subspherical in shape with a rounded apex and also does not seem to exhibit the defined antapical filaments characteristic of *D. plekta*, rather having what appear to be flange-like extensions. Duxbury (1983) suggested that the genus *Scuticabolus* may have an apical or precingular archaeopyle; possibly these forms reported by Nøhr-Hansen (1993) and Torricelli (2000) could be included in the genus *Scuticabolus*. A restudy of the material of Nøhr-Hansen (1993) and Torricelli (2000) might allow for a direct comparison of both forms with *Desmocysta*, allowing for some revision of the generic definition or description of a new genus.

**4.2 Biostratigraphy and palaeogeographic distribution**

*Desmocysta hadra* was identified in the upper part of the early Campanian aged sediments from well 6304/3-1 (offshore Norway). This species was consistently recorded in 30 m of mudstones across nine cutting samples in notable numbers (10%–20% of the assemblage). In one of the analysed samples (at 3495 m), *Desmocysta hadra* constitutes 42% of the overall dinoflagellate cyst assemblage. The FDO (first downhole occurrence) of the new species occurs below the FDO of *Trichodinium castanea* and *Callaiosphaeridium asymmetricum* in an assemblage dominated by *Heterosphaeridium bellii–heteracanthum*. The presence of *C. asymmetricum* and *T. castanea* suggests an age no younger than early Campanian (Costa and Davey, 1992; Fensome et al., 2009; Gradstein et al., 2010). The record of common to abundant *H. bellii* was also reported by Radmacher et al. (2014a, b, 2015) in middle–early Campanian aged sediments from Norwegian Sea and Barents Sea wells.

The LDO (last downhole occurrence) of *Desmocysta hadra* is observed below the FDO of *Chatangiella manumii* and the downhole increase in relative numbers of *Trithyrodinium suspectum*, *Chatangiella niiga* and *Palaeohystrichochora infusorioidea*, events also observed within the early Campanian across the Norwegian Sea region. In the 6304/3-1 well, the LDO of *Spongodinium delitiense* occurs just 3 m above the LDO of *Desmocysta hadra*. According to several publications (Williams et al., 2004; Radmacher et al., 2014a, b) the oldest occurrence of *S. delitiense* is recorded in the early Campanian.

The short stratigraphic range of *Desmocysta hadra* observed in this well allows for the potential use of this species in regional biostratigraphy as an early Campanian marker. More wells need to be studied in order to confirm the stratigraphic range and the geographic distribution of this species.

In the Norwegian Sea, particularly in the Møre and Vøring basins, deep-sea turbidite systems deposited sandstone reservoirs throughout the Late Cretaceous interval. The use of short-range biostratigraphic markers with regional expression can be crucial for well correlations.

*Desmocysta simplex*, described in late Hauterivian sediments from the central North Sea, is also a good stratigraphic marker. The occurrence of this species has been recorded in many wells from the North Sea to the Barents Sea (Fig. 3). *Desmocysta californica* also exhibits a short stratigraphic range (Berriasian–early Valanginian), although the biostratigraphic calibration potential is more difficult to discuss due to the lack of published data. There are several reported occurrences of *Desmocysta* spp. in the Shell northwest Europe basin.
Plate 2. (1–4) *Desmocysta plekta* photographs from the Danian in the Ormen Lange field (Norwegian Sea basin). The scale bar represents 30 µm for all specimens of *D. plekta*. (5–6) *Desmocysta californica* (Duxbury, 2018 plate 13, figs. 9 and 10). Specimens are from the Speeton Clay, early Valanginian. Duxbury illustrated the variations in the size of the granules and verrucae on the cyst surface and the long antapical filaments. (7) *Desmocysta simplex* (Duxbury, 2001 fig. 7.3). Paratype specimen in lateral orientation. Scale bar represents 10 µm. (8) Cyst attributed to *Desmocysta plekta* in Nørh-Hansen (1993) Plate 7, fig. 12 exhibiting an apical archaeopyle. (9) Cyst attributed to cf. *Desmocysta plekta* in Torricelli (2000) Plate III, fig. 5 exhibiting an apical archaeopyle.
microfossil database (Fig. 3), but without a definition to the species level we cannot be sure if they refer to *Desmocysta californica*, *Desmocysta hadra* or possibly other unpublished species.

*Desmocysta plekta* is the species with the most published occurrences. The fossil record extends from Barremian (Nøhr-Hansen, 1993) and North Atlantic (Ogg, 1994) to Thanetian (Jolley, 1992, 1998). Vieira and Jolley (2020) discussed the distribution of territorially sourced and marine palynomorphs in the Forties Sandstone Member, a deep marine turbidite fan system deposited from the late Thanetian (ca. 56.8 Ma) through the Ypresian (ca. 55.3 Ma). Rare occurrences of *D. plekta* have been recorded across a small number of wells, although they were considered to be reworked from older Thanetian sediments. If these occurrences were in situ, then the record of *D. plekta* will extend into the Ypresian.

Setoyama et al. (2013), in a study of a submarine fan system in the Voring Basin (offshore Norway), used the first downhole occurrence (FD0) of *D. plekta* as a late Campanian marker, although due to its long stratigraphic range, it is difficult to use this species for age determination. *Desmocysta plekta* seems to be frequently recorded across the Campanian. Radmacher et al. (2015) recorded abundant specimens at that level in well 6707/10-1 in the Norwegian Sea.

Across the study area, *Desmocysta hadra* and *D. plekta* are noted to co-occur within the same stratigraphic interval. There is a possibility that previous palynological studies may have informally assigned *D. hadra* to *Desmocysta* spp., purely because it did not correspond to features already described for *D. plekta* or *D. simplex*.

All the known occurrences of *Desmocysta californica*, *D. plekta* and *D. simplex* discussed here are from the Northern Hemisphere. The Early Cretaceous occurrences extend across Arctic Canada (Nøhr-Hansen and McIntyre, 1998), northeast Greenland (Nøhr-Hansen, 1993), the north Barents Sea (Kairanov et al., 2018), the North Sea (Duxbury, 1983, 2001, 2018) and the North Atlantic (Ogg, 1994). There are also some unpublished records of *D. simplex* and *D. plekta* in Early Cretaceous sediments from the Jeanne d’Arc Basin, offshore Canada, and the north Caspian Sea, offshore Kazakhstan, that have been recorded in oil and gas wells (source: Shell Microfossil Database).

Other than *D. hadra* n. sp., only *D. plekta* occurs in the Late Cretaceous, extending from west Greenland (Nøhr-Hansen, 1994a, b, c, 1996; Dam et al., 1998, 2000), southeast Greenland (Nøhr-Hansen, 2012) and offshore Norway (Setoyama et al., 2013; Radmacher et al., 2015). Paleocene records are limited to the Norwegian Sea (Vieira et al., 2018a, b), central North Sea (Vieira et al., 2020), northern Greenland (Lyck and Stemmerik, 2000) and southeast England (Jolley, 1992, 1998) (Fig. 1). The records from well data in the Shell northwest Europe offshore microfossil database, illustrated in Fig. 3, comprise mainly Cretaceous to Paleocene occurrences from the southern North Sea Basin across to the Barents Sea Basin.

The palaeolatitude of the Cretaceous records shows that *Desmocysta* is mainly restricted to the boreal warm climate belt of Scotese et al. (2014). Only the Barremian record from the North Atlantic (Ogg, 1994) suggests the presence of this taxon in the latitude of the arid climatic belt (Fig. 4).

### 4.3 Palaeoenvironmental remarks for the genus *Desmocysta*

Although most of the published records of *Desmocysta* species refer to taxonomy or biostratigraphy, the Paleocene record seems to reveal more about the palaeoenvironmental preferences for *Desmocysta plekta*. In his study of the late Paleocene Thanet Beds in eastern England, Jolley (1992) reported in some sections the occurrence of *Desmocysta plekta* in association with *Areoligera gippingensis* in two of the defined association sequences (T6 and T8). Jolley discussed the fact that the taxa that accompany *A. gippingensis* in that interval appear to be related to biofacies associations. Three of the sections yielded associations of *Leiosphaeridia* spp., *Desmocysta plekta* and *Paralecaniella indentata* together with *A. gippingensis*. Jolley (1992) concluded that these taxa are apparently abundant in proximal, high-stress marine environments. Jolley (1998) published a similar association in a sample from the Pegwell Bay section, with the presence of *D. plekta* in an assemblage of abundant *Areoligera cf. coronata*, *A. gippingensis* and *P. indentata*. He also suggested that *A. gippingensis* is most common in turbid-water transgressive environments, which seems to indicate that in the late Paleocene *D. plekta* would prefer the same environmental conditions.

The Paleocene record of *D. plekta* in the Thyra Ø Formation, Wandel Sea Basin (northern Greenland), from Lyck and Stemmerik (2000) shows dinoflagellate cyst assemblages composed mainly of peridinioids associated with *P. indentata* and abundant pollen, fungal spores and phytoleasts. The authors interpreted the deposition in a shallow, protected environment, and deposition most likely took place in shallow-marine lagoons and marshes due to the association of siltstones and coals. It was also noted that lack of bioturbation or the absence of marine macrofossils may indicate a biologically stressed (possible anoxic, suboxic) environment during deposition. This seems to suggest comparable environmental conditions as described by Jolley (1992, 1998), although Lyck and Stemmerik reported high amounts of Late Cretaceous reworking, making it questionable if the occurrence of *D. plekta* is actually in situ.

Vieira et al. (2018b) reported the occurrence of *D. plekta* from the Danian Egga reservoir in the Ormen Lange area (Norwegian Sea). The abundance generally increases downwards towards the lower part of the reservoir interval. In the samples with higher relative abundances, *D. plekta* is associated with abundant *Areoligera coronata* and a diverse as-
semblage of peridinioid genera, including *Palaeoperidinium, Palaeocystodinium, Deflandrea, Senegalinium* and *Trithyrodinium*, as well as less abundant gonyaulacoids, such as *Operculodinium, Spiniferites* and *Hystrichosphaeridium*. Also noticeable is the consistent presence of *Paralecaniella indentata* in the assemblages, similar to those observed in the Thanetian sites described by Jolley (1992, 1998), which could infer that *D. plekta* could be part of an inner neritic plankton community tolerating turbid waters and stressed marine environments.

We do not have sufficient data from Cretaceous material to make consistent palaeoenvironmental assumptions, although *Desmocysta hadra* was recognised in assemblages dominated by *Heterosphaeridium bellii–heteracanthum*, which like most areoligeracean phototroph gonyaulacoids, is usually well-represented in more proximal facies.
Figure 4. Distribution maps of *Desmocysta plekta* (red circles) and *D. simplex* (green circles) from the Early Cretaceous to the Paleocene. The base palaeogeographic maps are adapted from Cao et al. (2017), and the palaeoclimate zones are from Scotese et al. (2014).

Most of the data gathered from offshore wells, used to understand the potential palaeoenvironmental preference of the genus, targeted specific stratigraphic intervals with the occurrence of turbiditic facies; therefore, the discussed environmental preferences of this species can be biased due to focused sampling. We cannot exclude the occurrence of the genus in deeper marine settings as other wells in basinal areas need to be studied for comparison. Also, other environmental factors such as temperature, salinity and water stratification might affect the occurrence and abundance of *Desmocysta* spp. In addition, long-ranging species such as *D. plekta* might have variable preferences at different stratigraphic levels. More data will need to be gathered in order to clarify the potential palaeoenvironmental use of this genus.

5 Conclusions

This contribution formally describes *Desmocysta hadra*, identified in early Campanian sediments from the Norwegian Sea. This species seems to have a short stratigraphic range, making it a good biostratigraphic marker, while *D. plekta* has a much wider range, spanning from the Early Cretaceous to late Paleocene. The available published data show that the different species belonging to this genus are restricted to the higher latitudes in the Northern Hemisphere.

The defining features that characterise the unusual genus *Desmocysta* are also discussed to include a species with short, fine filaments as well as thick, robust and highly folded cysts exhibiting a unique scabrate–granular ornament typically increasing towards the antapex. The further study of cysts resembling *Desmocysta* but differing by possessing an apical archaeopyle remains in need of taxonomic treatment.

Although it is challenging to identify environmental preferences for fossil taxa, the genus *Desmocysta* is suggested here to have preferred turbid waters and stressed marine environments based on the available Paleocene and Late Cretaceous records. Future research might allow for a further discussion of other palaeoenvironmental controls on the occurrence of *Desmocysta* species.
Appendix A

This Appendix alphabetically lists all formally described microfossil taxa below the generic level which are mentioned in this contribution, with full author citations following Fensome et al. (2019).

*Alterbidinium acutulum* (Wilson, 1967) Lentin and Williams, 1985
*Ampidiadema denticulata* Cookson and Eisenack, 1960
*Areoligera coronata* (Wetzel, 1933) Lejeune-Carpentier, 1938
*Areoligera gippingensis* Jolley, 1992
*Cerodinium diebelii* (Alberti, 1959) Lentin and Williams, 1987
*Chatangiella manumii* (Vozzhennikova, 1967) Lentin and Williams, 1976
*Chatangiella niiga* (Vozzhennikova, 1967) Lentin and Vozzhennikova, 1990
*Desmocysta plekta* Duxbury, 1983
*Desmocysta simplex* Duxbury, 2001
*Desmocysta californica* (Monteil, 1992) Duxbury, 2018
*Heterosphaeridium bellii* Radmacher et al., 2014a
*Heterosphaeridium heteracanthum* (Deflandre and Cookson, 1955) Radmacher et al., 2014a
*Hystrichodinium pulchrum* Deflandre, 1935
*Odontochitina diducta* Pearce, 2010
*Palaeohystrichophora infusorioides* Deflandre, 1935
*Palaeoperidinium pyrophorum* (Ehrenberg, 1837) Sarjeant, 1967
*Paralecaniella indentata* (Deflandre and Cookson, 1955) Elsik, 1977
*Raphidodinium fucatum* (Deflandre, 1936) Sarjeant and Downie, 1982
*Spiniferites ramosus* (Ehrenberg, 1837) Mantell 1854
*Spongodinium delitiense* (Ehrenberg, 1837) Lucas-Clark, 1987
*Trichodinium castanea* (Deflandre, 1935) Clarke and Verdier, 1967
*Trithyrodinium evittii* (Drugg, 1967) Nøhr-Hansen and Dam, 1999
*Trithyrodinium suspectum* (Manum and Cookson, 1964) Davey, 1969
Data availability. The slide with the new species holotype is deposited at the Natural History Museum in the London palynology slide repository.

Author contributions. Both authors conceptualised and wrote the paper.

Competing interests. The authors declare that they have no conflict of interest.

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