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To cite this article: Julian D. Hartman, Francesca Sangiorgi, Peter K. Bijl & Gerard J.M. Versteegh (2019) Nucicla umbiliphora gen. et sp. nov.: a Quaternary peridinioid dinoflagellate cyst from the Antarctic margin, Palynology, 43:1, 94-103, DOI: 10.1080/01916122.2018.1430070

To link to this article: https://doi.org/10.1080/01916122.2018.1430070

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Published online: 26 Mar 2018.

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**Nucicla umbiliphora** gen. et sp. nov.: a Quaternary peridinioid dinoflagellate cyst from the Antarctic margin

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**ABSTRACT**

In the southern high latitudes, dinoflagellate cysts are an important microfossil group for both biostratigraphic and palaeoenvironmental interpretations purposes. In light of this, the peridinioid dinoflagellate cyst *Nucicla umbiliphora* gen. et sp. nov. from the Antarctic margin is formally described. *Nucicla* is dorsoventrally compressed, has a rounded pentagonal outline in dorso-ventral view, an epicyst that is only half as high as the hypocyst, an unusual archaeopyle formed by the loss of the three anterior intercalary plates, and a posterior sulcal plate that is positioned at the antapex. The species *N. umbiliphora* is characterised by a scabrate cyst wall and possesses undulated and/or crenulated folds/ridges. It has been so far exclusively found in Quaternary sediments obtained from the East Antarctic continental shelf and the Ross Sea. Although the dinoflagellate producing this cyst is as yet unknown, its brown color and the lack of autofluorescence suggest that the motile cell is likely a heterotrophic *Protoperidinium* species. As such, *N. umbiliphora* might benefit from the phytoplankton blooms occurring close to the Antarctic margin after seasonal sea-ice retreat.

**KEYWORDS**

protoperidinioid; dinoflagellate cyst; East Antarctic; Antarctic shelf; Quaternary

1. Introduction

Although the Oligocene to Quaternary sediments of the Southern Ocean and Antarctic margin had long been thought to contain no dinoflagellate cysts (McMinn 1995), several endemic and bipolar species have been discovered during the last two decades. They are important for both biostratigraphical purposes and reconstructing high-latitude climatic evolution (Bijl et al. 2018; Marret & De Vernal 1997; Montresor et al. 1999; Esper & Zonneveld 2002; Prebble et al. 2013; Clowes et al. 2016).

Here we formally describe *Nucicla umbiliphora* gen. et sp. nov. This species has already been reported without formal description from four localities around Antarctica (Figure 1). These dinoflagellate cysts are now included in *N. umbiliphora*. It was first depicted as Dinocyst sp. A from Quaternary samples from the Cape Roberts Project drill core 1 (CRP-1), Ross Sea (Wrenn et al. 1998). Storkey (2006) reported the species from shelf surface sediments in Prydz Bay. Furthermore, the dinoflagellate cyst is depicted in Warny et al. (2006) as ‘Lejeuneycysta cf. sp. 1 and 5 of CRP’ (i.e. cf. Hannah et al. 2000) from the Ross Sea shelf edge. Finally, the species has also been reported from a Holocene core from a small meromictic basin upstream Ellis Fjord, which lies at the eastern coastal margin of Prydz Bay (Boere et al. 2009). Here we add occurrences of this species in nine other East Antarctic marine sediment cores and surface sediments (Figure 1; Table 1).

2. Material and methods

Samples obtained from nine cores (Table 1; Figure 1) were freeze-dried and crushed manually to small fragments in a mortar, after which a *Lycopodium* tablet was added with Agepon (1:200). Agepon was used to expand the shrunken *Lycopodium* from the tablets, and the palynomorphs in general. A small amount of 30% cold hydrochloric acid (HCl) was added to remove carbonate, and to dissolve the *Lycopodium* tablet. Samples were treated with 38% cold hydrofluoric acid (HF) and shaken for 2 hours at 250 rpm. Thereafter, samples were diluted with tap water, allowed to settle for 24 hours, and decanted. Subsequently, 30% HCl was added to remove fluoride gels, tap water was added and the samples were centrifuged, after which the samples were decanted. No additional neutralisation steps were performed to remove excess HF. Tap water was added to the residue to prevent oxidation of the organic material. The treated material was sieved using a 10-µm mesh sieve and kerogen clumps were ultrasonically fragmented. Heavy minerals were removed by pouring the residue from the sieve into a porcelain dish that is kept floating in the ultrasonic bath, and by decanting this back into the sieve after 5 minutes. The fraction > 10 µm was concentrated into ~1 mL of glycerin-water mixture and a fraction thereof was mounted on a microscope slide using glycerine jelly.

Green autofluorescence of the cyst was tested on a Leica DM2500 LED fluorescence microscope. Images were taken using a Leica DM2500 LED microscope with mounted Leica MC170 HD camera, and for the images of Plate 1 the Live Image Builder (LIB) within the Leica Application Suite software 4.0 was used, which is a live z-stacking tool. Z-stacking constructs a two-dimensional image from a three-dimensional object by combining the areas in focus from...
Previously published sites and the sites presented in this study from which samples are derived that contain *Nucicla umbiliphora*. The positions of the summer sea ice edge (SSIE) and winter sea ice edge (WSIE) are indicated by dotted and interrupted lines, respectively. The positions of the SSIE and WSIE are based on the figure by Arrigo et al. (2008), which shows the averaged satellite-derived, annual sea-ice cover for the period 1997–2006. SSIE: < 20 days/year sea-ice cover, and WSIE > 320 days/year sea-ice cover.

**Table 1.** Coordinates, core length and water depth of the sampled cores.

| Core     | Locality          | Latitude | Longitude      | Core length (m) | Water depth (mbsl) | Reference                        |
|----------|-------------------|----------|----------------|-----------------|--------------------|----------------------------------|
| AS05-10  | Western Ross Sea  | 70°59.11'S | 173°03.91'E   | 7.50            | 2377               | This study                       |
| ANTA02-AV43 | Western Ross Sea | 74°08.45'S | 166°04.97'E   | 2.20            | 218.5              | Del Carlo et al. (2015)          |
| BC22     | Southwestern Ross Sea | 76°41.59'S | 169°04.68'E   | 0.37            | 790                | This study                       |
| IODP U1357B | Adélie Basin     | 66°24.7990'S | 140°25.5705'E | 172.44          | 1017               | Exp.318 Scientists (2011)        |
| NBP0101-JPC41 | MacRobertson Shelf | 67°07.817'S | 62°59.436'E   | 24.12           | 563                | Leventer et al. (2001)           |
| NBP0101-JPC42 | MacRobertson Shelf | 67°07.479'S | 63°00.195'E   | 24.95           | 850                | Leventer et al. (2001)           |
| NBP1402-KC14 | Sabrina Coast    | 66°11.092'S | 120°30.2403'E | 2.952           | 544                | Domack & Leventer (pers. comm.)  |
| NBP1402-KC27A | Sabrina Coast     | 66°11.0907'S | 120°30.2385'E | 2.71            | 547                | Domack & Leventer (pers. comm.)  |
multiple images, which is ideal for three-dimensional microscopic objects.

A scanning electron microscope (SEM) photograph was made using a JEOL NeoScope JCM-6000 Benchtop SEM, located at the ‘Gemeenschappelijk Milieu Laboratorium’ building at Utrecht University. For the SEM photo, dinoflagellate cysts were individually picked using a microinjection system, subsequently placed on a stub and coated with a thin (10 nm) layer of platinum.

Plate terminology follows the Kofoid tabulation system (see Kofoid 1911). Archaeopyle descriptive terms follow Bujak & Davies (1983).

3. Results

Nucicla umbiliphora was found in core-top samples of all the examined cores, with the exception of cores AS05-10, NBP0101-JPC41 and -JPC42 for which no core-top samples were available. Dinoflagellate cysts of *N. umbiliphora* were occasionally found with the operculum still attached (Plate 1, figures 1, 2, 6) and in one case also containing cell contents (Plate 1, figure 10–11). The cysts of *N. umbiliphora* did not autofluoresce under fluorescence microscopy (Plate 1, figure 12).

For core ANTA02-AV43 all samples were taken above the interval 1.48–1.51 m below sea floor (mbsf), which has an age of 9.7 ± 5.3 ka based on $^{40}$Ar/$^{39}$Ar dating (Del Carlo et al. 2015). No age models have been published yet for cores U1357B, BC22, NBP0101-JPC41 or NBP0101-JPC42. However, the two latter are likely of Holocene age as the nearby core NBP0101-JPC43B (23.95 m long) shows bottom $^{14}$C ages of about 11.6 ka (Mackintosh et al. 2011). We encountered the species in JPC41 as deep as 17.52 m b.s.f. The new species has also been encountered throughout core BC22 (36.5 cm in length). Unpublished dinoflagellate cyst data from box core BC22 suggest a position for the Last Glacial Termination between 0.25 and 0.28 mbsf, from which the amount of dinoflagellate cysts per gram of dry sediment decreases strongly downward. It has also been encountered sparsely in Hole U1357B, to a depth of 55.06 mbsf. The new species has also been encountered in JPC41, which has an age of 31 ka based on $^{40}$Ar/$^{39}$Ar dating (Del Carlo et al. 2015). No age models have been published yet for cores U1357B, BC22, NBP0101-JPC41 or NBP0101-JPC42. However, the two latter are likely of Holocene age as the nearby core NBP0101-JPC43B (23.95 m long) shows bottom $^{14}$C ages of about 11.6 ka (Mackintosh et al. 2011). We encountered the species in JPC41 as deep as 17.52 m b.s.f. The new species has also been encountered throughout core BC22 (36.5 cm in length). Unpublished dinoflagellate cyst data from box core BC22 suggest a position for the Last Glacial Termination between 0.25 and 0.28 mbsf, from which the amount of dinoflagellate cysts per gram of dry sediment decreases strongly downward. It has also been encountered sparsely in Hole U1357B, to a depth of 55.06 mbsf. The $^{14}$C data from the nearby Hole U1357A provide an age of ~4.2 cal. kyr BP at 68.85 mbsf (Yamane et al. 2014). Samples from core AS05-10 have been retrieved from the interval with optimal dinoflagellate cyst preservation, which is associated with the onset of MIS5.5 (JD Hartman, pers. obs.). Apart from the CRP-1 core, for which the age model of the Quaternary section above 43 mbsf is not well resolved, the occurrence in core AS05-10 during MIS5.5 is the oldest record of *Nucicla umbiliphora*.

4. Systematic palaeontology

Division DINOFLAGELLATA (Bütschli 1885) Fensome et al. 1993

Subdivision DINOKARYOTA Fensome et al. 1993

Class DINOPHYCEAE Pascher 1914

Subclass PERIDINIPHYCIDAIE Fensome et al. 1993

Order PERIDINIALES Haeckel 1894

Suborder PERIDINIINAE Fensome et al. 1993

Family PROTOPERIDINIAEAE Bujak & Davies 1998 in Fensome et al. 1998

Subfamily PROTOPERIDINOIDEAE Bujak & Davies 1993

Genus *Nucicla* gen. nov.

**Type species.** *Nucicla umbiliphora* Hartman, Sangiorgi, Bijl & Versteegh sp. nov.

**Derivation of the name.** From the Latin *nucicla*, meaning small nut, in reference to the cyst resembling a nut.

**Diagnosis.** Acavate, dorsoventrally compressed cyst with a rounded pentagonal outline, a hypocyst that is twice the size of the epicyst, an archaeopyle formed by the loss of three anterior intercalary plates, and a large sulcus with the posterior sulcal plate positioned at the antapex.

**Differential diagnosis.** This genus differs from all other peridinoid dinoflagellate cysts by its combination of (1) a consistent 3I archaeopyle, (2) a well-outlined cingulum and sulcus, (3) the absence of cavation, and (4) a large sulcus with a posterior sulcal plate at the antapex. The Late Cretaceous to Early Palaeocene genus *Trithyrodinium* Drugg 1967 also has a 3I archaeopyle, but is cavate. *Vozzhennikovia* Dent & Williams 1976 has an I or 3I archaeopyle, and is also cavate. Although the number of archaeopyle plates in *Brigantedinium* Reid 1977 is not determined and therefore can include species with a 3I archaeopyle, *Brigantedinium* is spherical/ovoidal and lacks tabulation other than the archaeopyle. Other genera with dorsoventral compression, a pentagonal outline and consisting of an autophagam include *Votadinium* Reid 1977, *Lejeunecysta* Artzner & Dörhöfer 1978, *Trinovantedinium* Reid 1977 and *Leipokatium* Bradford 1975. Like *Brigantedinium*, *Votadinium* and *Leipokatium* can have an archaeopyle consisting of any number of intercalary plates, but *Votadinium* differs from *Nucicla* in having a shallow or deep depression between the antapical lobes, and lacks a well-defined cingulum. *Leipokatium* has very distinct antapical horns and a hypocyst much smaller than the epicyst. Both *Lejeunecysta* and *Trinovantedinium* may have a sulcus and/or cingulum, but have an I archaeopyle. In addition, *Trinovantedinium* has non-tabular proximochorate processes and *Lejeunecysta* has an epicyst and hypocyst of approximately equal size. For all of the above-mentioned genera the position of the posterior sulcal plate is either unclear or not as posterior as in *Nucicla*.

*Nucicla umbiliphora* sp. nov.

Plate 1, figures 1–12 and Plate 2, figures 1–6

**Synonymy.**

Dinocyst sp. A. Wrenn et al. 1998, p. 595, fig. 5 a–d.

*Protoperidinium* sp. 2 Storkey, 2006, p. 49, plate 4, fig. 10–12.

*Lejeunecysta* cf. sp. 1 and 5 of CRP Warny et al. 2006, p. 163, plate 3, figs 3–4.

Cyst type 1 Boere et al., 2009, p. 273, fig. 5D, E, (F?)

**Holotype.** Plate 1, figure 1–2. Cruise NBP0101, core JPC41, 108 cm depth, slide no. 1, England Finder (EF) coordinates: U29.2 down left corner.
Repository. Stored in the collection of the Laboratory of Marine Palynology and Oceanography, Utrecht, The Netherlands.

Type locality. Iceberg Alley, MacRobertson Shelf, East Antarctica.

Type stratum. Holocene.

Paratype. Plate 1, figure 6. Core ANTA02-AV43, 2–3 cm depth, slide no. 2, EF: F19.2 bottom side. Stored in the collection of the Laboratory of Marine Palynology and Oceanography, Utrecht, The Netherlands.

Stratigraphical range. Marine Isotope Stage 5.5 to Recent.

Derivation of the name. From the Latin umbilicus (navel) and the Ancient Greek suffix -phoros (bearing), with reference to its large flagellar scar, which resembles a navel.

Diagnosis. A species of Nucicla with a scabrate wall structure and with low, undulating or crenulating ridges with no apparent relation to plate boundaries with the exception of the cingulum and sulcus. The sulcus shows a large flagellar scar. Apart from the cingulum and sulcus, tabulation is only indicated by the clear 3I archaeopyle, of which the 2a intercalary is large and latideltaform. In the holotype the operculum is still attached; specimens are usually found without operculum.

Dimensions. Holotype: Height = 70 μm; width measured along the cingulum = 62 μm. Other specimens (n = 10): Height = 57–70 μm, average = 64.5 μm. Width = 52–63 μm, average = 60.0 μm.

Description. A brown cyst with pentagonal outline, which is dorsoventrally compressed. Apical and antapical ‘horns’ are rounded and broad-based so that the cyst appears more rounded than pentagonal. A few specimens show a small acute apical horn (Plate 1, figures 3, 11). None of the specimens shows acute tips at the antapical ‘horns’. The hypocyst is twice the height of the epicyst in combination with the large flagellar scar, which resembles a navel.

Differential diagnosis. This is currently the only species in the genus. Within the Protoperiophoraceae, Nucicla umbiliphora with

Plate 1. Light microscope photographs of Nucicla umbiliphora. Figure 1. Holotype, JPC42, 468 cm depth, slide 1, EF: U29.2, dorsal side up: dorsal view with operculum attached but archaeopyle outlined; 2, holotype, JPC42, 468 cm depth, slide 1, EF: U29.2, dorsal side up: ventral view (mirrored); 3, AS05-10, slice V-1, EF: L35.4, dorsal side up: ventral view (mirrored); 4, JPC42, 108 cm depth, slide 1, EF: L35.4, dorsal side up: dorsal view; 5, JPC41, 108 cm depth, slide 1, EF: L35.4, dorsal side up: ventral view (mirrored); 6, ANTA02-AV43, 2–3 cm depth, slide 2, EF: F19.2, ventral side up: ventral view; a low ridge indicates the position of the posterior sulcal plate; 7, JPC41, 556 cm depth, slide 1, EF: O42.1, antapical side up: apical view (mirrored), sulcus indicated by arrow; 8, JPC41, 556 cm depth, slide 1, EF: O42.1, antapical side up: antapical view, sulcus indiciated by arrow, a low ridge can be distinguished at the posterior edge of the poste- rior sulcal plate; 9, JPC42, 295 cm depth, slide 2, EF: G32.4, ventral side up: ventral view, some of the low ridges within the sulcus may correspond to sulcal plate boundaries; 10, JPC42, 295 cm depth, slide 2, EF: N33.3, dorsal side up: ventral view (mirrored), cell contents visible; 11, JPC42, 295 cm depth, slide 2, EF: N33.3, dorsal side up: dorsal view, cell contents visible, operculum still attached, but outline visible; 12, Holotype, JPC42, 468 cm depth, slide 1, EF: U29.2, viewed under fluorescence microscope showing autofluorescence.
its pentagonal outline, limited tabulation, rounded antapical horns, scabration and brown colour most closely resembles Lejeunecysta rotunda Clowes et al. 2016. Instead of erecting a new genus one might consider emending Lejeunecysta to include N. umbiliphora. However, Lejeunecysta differs from Nucicla in more than just one aspect. Most importantly, Lejeunecysta has a consistent 2a archaeopyle and closely defined archaeopyle shape. Lejeunecysta also differs in having the epicyst and hypocyst of approximately equal length, symmetrically located horns which are small pointed and solid, a laevigate or chagrinate wall, and tabulation only indicated near the archaeopyle and cingulum, whereas the sulcus is only marked by a shallow depression. Because of the number and clarity of the differences, we found it necessary to erect a new genus. It differs from most other peridinioid genera by its 3I archaeopyle. Other known genera with a 3I archaeopyle are the Cretaceous to Early Palaeocene Trithyrodinium and Palaeocene to Oligocene Vozzhennikovia, but both these genera are cavate. Typically, the apical and antapical horns of these genera are made up of the periphragm, while N. umbiliphora only has an autophragm (Figure 3). Other brown scabrate dinoflagellate cyst species from the present-day Southern Ocean are Selenopemphix antarctica Marret & de Vernal 1997, Brigantedinium pynei Hannah

Figure 3. Benchtop scanning electron microscope (SEM) photograph of Nucicla umbiliphora (dorsal view). No tabulation pattern is visible except for the archaeopyle and cingulum. The autophragm with its folded ridges can be seen both externally and internally.
et al. 1998 and Cryodinium meridianum Esper & Zonneveld 2002. Cryodinium meridianum also has low, sometimes dendritic ridges, but most of those crests reflect tabulation. Furthermore, C. meridianum lacks the pentagonal outline and dorsoventral compression, and has a 2I archaeopyle. Brigantidinium pynee is reminiscent of C. meridianum, but its rugulose surface does not reflect tabulation and it has an I archaeopyle (Clowes et al. 2016). Selenopemphix antarctica does not have ridges, has an I-type archaeopyle, and the width of the cyst is much larger than its height, so that it typically appears in (ant)apical view on microscope slides. Nucicla umbiliphora was found in Quaternary sediments of the Ross Sea together with the similar-looking Dinocyst sp. B (Wrenn et al. 1998). Because Dinocyst sp. B of Wrenn et al. (1998) has antapical ‘horns’ with acute tips, and the number of intercalary plates that comprise the archaeopyle is uncertain, it is not included in N. umbiliphora.

5. Discussion

5.1. Taxonomy

We placed N. umbiliphora within the family Protoperidiniaceae based on the visible tabulation, the absence of cavation and the brown colour. It lacks plate boundaries between the cingular plates, which hampers definite placement within Protoperidiniaceae. However, several modern cysts with a pentagonal outline and an intercalary archaeopyle but without plate boundaries between the cingular plates do produce Protoperidinium thecae, such as Votadinium, Lejeuneycysta, Selenopemphix and Trinovantidinium (Head 1996; Matsuoka & Head 2013; Mertens et al. 2017). In addition, N. umbiliphora does not show green autofluorescence, like many Protoperidinium cysts (Brenner & Biebow 2001; Anderson et al. 2003). Currently, the motile stage of N. umbiliphora is unknown.

5.2. Ecology

Nucicla umbiliphora occurrences are all near the Antarctic margin and, except for site AS05-10, only in sediments from the shelf or inland fjords. This strongly suggests it is endemic to the Antarctic shelf. All samples areas experience at least 9 months of yearly sea-ice cover (Figure 1; Arrigo et al. 2008). Considering that all modern dinoflagellates that produce brown cysts are heterotrophic, it is likely that the motile stage of N. umbiliphora is heterotrophic as well (Ellegaard et al. 2013). In the coastal waters of Antarctica, the phytoplankton blooms in the highly stratified surface waters after sea-ice retreat could be an important food source for N. umbiliphora (Kang & Fryxell 1993; Clarke & Leakey 1996; Arrigo et al. 1998; Smith Jr. et al. 2000; Hiscock et al. 2003; Smith Jr. et al. 2006; Peloquin & Smith Jr. 2007; Arrigo et al. 2008). At the Antarctic shelf, these conditions typically arise within the marginal ice zone in late summer (Fitch & Moore 2007; Arrigo et al. 2008) and within coastal polynyas (Arrigo et al. 1999; Arrigo & van Dijken 2003). Notably, the occurrence of N. umbiliphora in Hole U1357B confirms a preference for polynya environments, as U1357B was drilled directly downwind and downcurrent of the Mertz Glacier Polynya (Expedition 318 Scientists 2011).

6. Conclusions

Nucicla umbiliphora gen. et sp. nov. (Peridiniales, Protoperidiniidae) occurs in Quaternary sediments from the East Antarctic margin and the Ross Sea. It has a 3I archaeopyle, which is unique among protoperidinoids. Furthermore, it has a rounded to pentagonal outline with a hypocyst twice as large as the epicyst, a sulcus with a distinct flagellar scar and a posterior sulcal plate positioned at the antapex. It has a scabrate wall ornamentation with low, somewhat crenulating ridges. The species is probably endemic to the Antarctic shelf environment during the Holocene and may prove to be confined to the high primary productivity after spring sea-ice retreat.

Acknowledgments

We thank for sample material and core site details: AS05-0 core – Alessandra Asioli and Leonardo Langone (ISMAR Bologna); BC core – Lucilla Capotondi and Mariangela Ravaioli (ISMAR Bologna); NBP0101 and NBP1402 cores – Amy Lventer (Colgate University, USA); ANTA02-AV43 core – Paola del Carlo (INGV Pisa). We thank Natasja Welters for palynological processing of the samples, as well as Michiel Kienhuis and Linda van Roij for assistance with sample preparation for SEM imaging. This research used samples and data from the Integrated Ocean Drilling Program (IODP), which was sponsored by the US National Science Foundation and participating countries under the management of Joint Oceanographic Institutions Inc.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Nederlandse Organisatie voor Wetenschappelijk Onderzoek [grant number 866.10.110].

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