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.

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 ‘Lejeunecysta 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 shrivelled Lycopodium from the tablets, and the palynomorphs in general. A tablet was added with Agepon (1:200) to the LiveImage 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

Table 1

<table>
<thead>
<tr>
<th>Sample Core</th>
<th>Location</th>
<th>Age Range</th>
<th>Cyst Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRP-1</td>
<td>Ross Sea</td>
<td>Oligocene</td>
<td>100</td>
</tr>
<tr>
<td>MC170</td>
<td>Prydz Bay</td>
<td>Quaternary</td>
<td>500</td>
</tr>
<tr>
<td>CRP-2</td>
<td>Ross Sea</td>
<td>Quaternary</td>
<td>200</td>
</tr>
<tr>
<td>CRP-3</td>
<td>Ross Sea</td>
<td>Quaternary</td>
<td>300</td>
</tr>
<tr>
<td>CRP-4</td>
<td>Ross Sea</td>
<td>Quaternary</td>
<td>400</td>
</tr>
<tr>
<td>CRP-5</td>
<td>Ross Sea</td>
<td>Quaternary</td>
<td>500</td>
</tr>
<tr>
<td>CRP-6</td>
<td>Ross Sea</td>
<td>Quaternary</td>
<td>600</td>
</tr>
<tr>
<td>CRP-7</td>
<td>Ross Sea</td>
<td>Quaternary</td>
<td>700</td>
</tr>
<tr>
<td>CRP-8</td>
<td>Ross Sea</td>
<td>Quaternary</td>
<td>800</td>
</tr>
<tr>
<td>CRP-9</td>
<td>Ross Sea</td>
<td>Quaternary</td>
<td>900</td>
</tr>
</tbody>
</table>

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Downloaded from https://pubs.geoscienceworld.org/palynology/article-pdf/43/1/94/4638881/tpal_a_1430070_o.pdf
Figure 1. Previously published sites and the sites presented in this study from which samples are derived that contain Nucleus 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.

<table>
<thead>
<tr>
<th>Core</th>
<th>Locality</th>
<th>Latitude (S)</th>
<th>Longitude (E)</th>
<th>Core length (m)</th>
<th>Water depth (mbsl)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>AS05-10</td>
<td>Western Ross Sea</td>
<td>70° 59.11'</td>
<td>173° 03.91'</td>
<td>7.50</td>
<td>2377</td>
<td>This study</td>
</tr>
<tr>
<td>ANTA02-AV43</td>
<td>Western Ross Sea</td>
<td>74° 08.45'</td>
<td>166° 04.97'</td>
<td>2.20</td>
<td>218.5</td>
<td>Del Carlo et al. (2015)</td>
</tr>
<tr>
<td>BC22</td>
<td>Southwestern Ross Sea</td>
<td>76° 41.59'</td>
<td>169° 04.68'</td>
<td>0.37</td>
<td>790</td>
<td>This study</td>
</tr>
<tr>
<td>IODP U1357B</td>
<td>Adélie Basin</td>
<td>66° 24.7990'</td>
<td>140° 25.5705'</td>
<td>172.44</td>
<td>1017</td>
<td>Exp.318 Scientists (2011)</td>
</tr>
<tr>
<td>NBP0101-JPC41</td>
<td>MacRobertson Shelf</td>
<td>67° 07.817'</td>
<td>62° 59.436'</td>
<td>24.12</td>
<td>563</td>
<td>Leventer et al. (2001)</td>
</tr>
<tr>
<td>NBP0101-JPC42</td>
<td>MacRobertson Shelf</td>
<td>67° 07.479'</td>
<td>63° 00.195'</td>
<td>24.95</td>
<td>850</td>
<td>Leventer et al. (2001)</td>
</tr>
<tr>
<td>NBP1402-KC14</td>
<td>Sabrina Coast</td>
<td>66° 52.3691'</td>
<td>118° 14.4022'</td>
<td>2.63</td>
<td>643</td>
<td>Domack &amp; Leventer (pers. comm.)</td>
</tr>
<tr>
<td>NBP1402-KC27A</td>
<td>Sabrina Coast</td>
<td>66° 11.092'</td>
<td>120° 30.2403'</td>
<td>2.952</td>
<td>544</td>
<td>Domack &amp; Leventer (pers. comm.)</td>
</tr>
<tr>
<td>NBP1402-KC27B</td>
<td>Sabrina Coast</td>
<td>66° 11.0907'</td>
<td>120° 30.2385'</td>
<td>2.71</td>
<td>547</td>
<td>Domack &amp; Leventer (pers. comm.)</td>
</tr>
</tbody>
</table>
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, NBPO101-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 40Ar/39Ar dating (Del Carlo et al. 2015).

No age models have been published yet for cores U1357B, BC22, NBPO101-JPC41 or NBPO101-JPC42. However, the latter two are likely of Holocene age as the nearby core NBPO101-JPC43B (23.95 m long) shows bottom 14C ages of about 11.6 ka (Mackintosh et al. 2011). We encountered the species in JPC41 as deep as 17.52 mbsf. 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 downcore. It has also been encountered sparsely in Hole U1357B, to a depth of 55.06 mbsf. The 14C 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 perhaps 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 PERIDINIOPHYCYDEA Fensome et al. 1993

Order PERIDINIALES Haeckel 1894

Suborder PERIDININAES Fensome et al. 1993

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

Subfamily PROTOPERIDINIOIDEAE Bujak & Davies 1983

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 *Trinovanteum* Drugg 1967 also has a 3I archaeopyle, but is cavate. *Vozzhennikovia* Lentini & 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 autophragm include *Votadinium* Reid 1977, *Lejeunecesta* 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 *Lejeunecesta* and *Trinovantedinium* may have a sulcus and/or cingulum, but have an I archaeopyle. In addition, *Trinovantedinium* has non-tabular proximochorate processes and *Lejeunecesta* 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.

*Lejeunecesta* 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 NBPO101, core JPC41, 108 cm depth, slide no. 1, England Finder (EF) coordinates: U29.2 down left corner.

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

Type stratum. Holocene.


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 3l 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. The autophragm has folds that form low, undulating or crenulating ridges, which are predominantly longitudinal and can be dentritic. With the exception of the cingulum and sulcus, these ridges have no relation to sutures. The cyst wall is scabrate and the degree of scabration varies between specimens (Plate 2, figures 4–6). The clearly distinguishable cingulum is level or very slightly descending and outlined by sutural ridges. Within the cingulum, low longitudinal ridges occur, but with no relation to cingular plate boundaries. The sulcus forms a clear depression, and is outlined by sinistral and dextral longitudinal sutural ridges. Some specimens also clearly show a posterior sulral ridge, which outlines the entire posterior sulcal plate (Sp; Plate 1, figures 6 and 8). The sulral ridge that outlines the Sp extends towards the dorsal side of the cyst, indicating the exceptional antapical position of the Sp. To our knowledge no other protoperidinioid cyst possesses an Sp that is positioned so far posteriorly, thereby pushing the antapical plates to the dorsal side. The sulcus shows a large flagellar scar, with low ridges converging towards it. Applying standard protoperidinioid tabulation to N. umbiliphora, low ridges within the sulcus seem to outline the right sulcal plate (Sd) and the left sulcal plate (Ss) (Plate 1, figures 3 and 9). In some specimens (Plate 1, figures 3 and 9) a low ridge is present at the anterior margin of the left and right sulcal plates, indicating the position of the anterior sulcal plate (Sa) (Figure 2).

The 3l archaeopyle is relatively large and spans almost the entire dorsal side of the epicyst. It has a consistent shape with clear angles marking plate junctions, except for the boundaries between the intercalary plates, which are smooth and subtle. Nevertheless, both archaeopyle and operculum outline suggest a 3l archaeopyle, for the following reasons: (1) the upper margin of the archaeopyle is concave; although in dinoflagellate cyst species with a 2a archaeopyle such a concave upper margin could be the result of the inward folding of the apical plates, we are certain that this is not the case for N. umbiliphora, because the outline of the operculum is also concave (Plate 2, figure 6); (2) the upper margin of the archaeopyle is three-sided (particularly visible in Plate 2, figure 3), strongly suggesting that these are the three sides of the third apical plate (3t) that border each of the anterior intercalaries (green, black and blue lines in Plate 2); and (3) in several instances the lower margin of the 2a intercalary appears slightly but nevertheless clearly elevated with respect to the lower margins of the 1a and 3a intercalaries (indicated by the ^ symbols in the figures of Plate 2). The position of the plate junctions in the lower margin of the archaeopyle suggests that the 1a and 3a intercalaries are very narrow, bordering a large latideltaform 2a intercalary. Although we cannot determine any further tabulation from the cyst of N. umbiliphora, the relatively low height of the epicyst in combination with the large 2a suggests that the height of the 3t, 4t, and 5t precingular plates is suppressed (Figure 2).

Differential diagnosis. This is currently the only species in the genus. Within the Protoperidiniaceae, 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-3, 1.5 cm depth, slide 2, EF: E18.3, antapical side up: antapical view; 4. JPC41, 108 cm depth, slide 1, EF: L35.4, dorsal side up: dorsal view, with clearly visible flagellar scar; 5. JPC41, 108 cm depth, slide 1, EF: L35.4, dorsal side up: ventral view, with clearly visible flagellar scar; 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: O41.2, antapical side up: apical view (mirrored), sulcus indicated by arrow; 8. JPC41, 556 cm depth, slide 1, EF: O41.2, antapical side up: antapical view, sulcus indicated by arrow, a low ridge can be distinguished at the posterior edge of the posterior sulcal plate; 9. JPC42, 295 cm depth, slide 2, EF: F52.4, ventral side up: ventral view, a low ridge within the sulcus may correspond to sulcal plate boundaries; 10. JPC42, 295 cm depth, slide 2, EF: N30.2, dorsal side up: ventral view (mirrored), cell contents visible; 11. JPC42, 295 cm depth, slide 2, EF: N30.2, dorsal side up: ventral 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 no autofluorescence.
its pentagonal outline, limited tabulation, rounded antapical horns, scabration and brown colour most closely resembles *Lejeunezysta rotunda* Clowes et al. 2016. Instead of erecting a new genus one might consider emending *Lejeunezysta* to include *N. umbiliphora*. However, *Lejeunezysta* differs from *Nucicla* in more than just one aspect. Most importantly, *Lejeunezysta* has a consistent 2a archaeopyle and closely defined archaeopyle shape. *Lejeunezysta* 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 2.** Schematic drawings of the plate boundaries of *Nucicla umbiliphora*. Top left: dorsal view. Top right: ventral view. Bottom left: apical view. Bottom right: antapical view. Uninterrupted lines indicate archaeopyle (thick), cingulum and sulcal outlines (thin). Dotted lines are hypothetical, based on the standard proteridinioid plate configuration and deduced from the archaeopyle outline and presumed sutural sulcal ridges. Archaeopyle plate junctions are marked by symbols. The upper archaeopyle margin is indicated by coloured lines. This coding of lines and symbols corresponds to that used in Plate 2.

**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.

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Plate 2. Light microscope photographs of the archaeopyle of *Nucicla umbiliphora*. Symbols and coloured lines correspond to plate junctions and the upper archaeopyle margin as indicated in Figure 2. Figure 1. JPC42, 295 cm depth, slide 2, EF: O35.4, ventral side up (archaeopyle mirrored); 2. JPC42, 953 cm depth, slide 2, EF: G28.4, ventral side up (archaeopyle mirrored), sinistral side is torn; 3. JPC41, 1752 cm depth, slide 1, EF: P41.1, ventral side up (archaeopyle mirrored), focus on the upper archaeopyle margin; 4. JPC41, 1752 cm depth, slide 1, EF: P41.1, ventral side up (archaeopyle mirrored), focus on the lower archaeopyle margin; 5. JPC41, 1004 cm depth, slide 1, EF: T40.3, dorsal side up; 6. Holotype, JPC42, 408 cm depth, slide 1, EF: U29.2, dorsal side up, operculum attached but outline of the archaeopyle visible.
et al. 1998 and Cryodinium meridianum Esper & Zonneveld 2002. Cryodinium meridianum also has low, sometimes dendritic ridges, but most of these crests reflect tabulation. Furthermore, C. meridianum lacks the pentagonal outline and dorsoventral compression, and has a 2I archaeopyle. Brigantedinium pynei 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, Lejeuneysta, Selenopemphix and Trinovantedinium (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; Pelouquin & 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 polyna 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, Protoperidinoideae) 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 Ascoli and Leonardo Langone (ISMAR Bologna); BC core – Lucilla Capotondi and Mariangela Ravaiol (ISMAR Bologna); NBP0101 and NBP1402 cores – Amy Leventer (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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