Cold marine indicators of the late Quaternary: the new dinoflagellate cyst genus Islandinium and related morphotypes

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ABSTRACT: Round, brown, spiny dinoflagellate cysts characterise many modern high-latitude assemblages. Abundance is often highest where summer sea-surface temperatures seldom exceed 7 °C and where winter sea-surface temperatures are around 0 °C, making this morphological group important for reconstructing cold intervals within marine Quaternary sequences. Our analysis of modern sediments from the Beaufort Sea of Arctic Canada, the Kara and Laptev seas of Arctic Russia, and across the Arctic Ocean, allows us to recognise the new cyst genus Islandinium along with the extant species Islandinium minutum (Harland and Reid in Harland et al., 1980) new combination (basionym: Multispinula? minuta), Islandinium? cezare (de Vernal et al., 1989 ex de Vernal in Rochon et al., 1999) new status and combination (basionym: Multispinula? minuta var. cezare) sensu lato, and Echinidinium karaense new species. Of these, the generotype Islandinium minutum is a well-known but morphologically problematic species. We have re-examined the type material from the Beaufort Sea and studied specimens from across the Arctic, and our observations clarify ambiguities in the original description of this species. The archeopyle of Islandinium minutum results from the loss of three apical plates, an unusual style among peridiniphycidean dinoflagellates. The asymmetrical location of these plates around the apex is distinctive, and probably contributed to earlier misunderstandings of the archeopyle. Previous attributions to Multispinula? and Algidasphaeridium? are unsustainable. Maps showing the distribution of Islandinium minutum are given for the Northern Hemisphere and show this species to be polar to north-temperate, whereas Islandinium? cezare s.l. and Echinidinium karaense appear to be more restricted to polar environments. Copyright © 2001 John Wiley & Sons, Ltd.

KEYWORDS: Islandinium minutum; Multispinula; Algidasphaeridium; Echinidinium; Quaternary dinoflagellate cysts; modern Arctic distributions.

Introduction

Islandinium minutum and similar round brown spiny cysts are known to be important ecological indicators in high-latitude studies, yet they have always been of questionable biological affinity and taxonomic assignment. Indeed it had not been proven that the cysts were even of dinoflagellate affinity let alone assignable to one of the major dinoflagellate subclasses. A detailed history of research into this group of dinoflagellates spanning more than 20 years shows a persistent misunderstanding of their morphology. This account aims to clarify the situation by re-evaluating the type material of Islandinium minutum results from the loss of three apical plates, an unusual style among peridiniphycidean dinoflagellates. The asymmetrical location of these plates around the apex is distinctive, and probably contributed to earlier misunderstandings of the archeopyle. Previous attributions to Multispinula? and Algidasphaeridium? are unsustainable. Maps showing the distribution of Islandinium minutum are given for the Northern Hemisphere and show this species to be polar to north-temperate, whereas Islandinium? cezare s.l. and Echinidinium karaense appear to be more restricted to polar environments. Copyright © 2001 John Wiley & Sons, Ltd.

KEYWORDS: Islandinium minutum; Multispinula; Algidasphaeridium; Echinidinium; Quaternary dinoflagellate cysts; modern Arctic distributions.
Historical Perspective

The dinoflagellate cyst species originally named Multispinula minuta Harland and Reid in Harland et al., 1980 was described from a grab sample of assumed modern sediments at Dome Petroleum’s Kopanoar site in the Beaufort Sea, Canadian Arctic (Harland et al., 1980). At the time of its description, the distribution of dinoflagellate cysts in marine bottom sediments of low and middle latitudes was already known to be influenced by many environmental and taphonomic factors (Reid and Harland, 1977, Wall et al., 1977) including climate and surface water-mass characteristics. This knowledge could and was being applied to the interpretation of the Quaternary record (e.g. Gregory and Harland, 1978).

At that time modern cyst distribution in the higher latitudes was largely unknown, inevitably hindering the analysis and interpretation of cold-climate sequences within the Quaternary. The study of Harland et al. (1980) provided some initial data from the Canadian Arctic that helped redress this problem. It was hoped that publication of these authors’ distinctive arctic assemblage, including the species Islandinium minutum (as Multispinula minuta Harland and Reid in Harland et al., 1980) and Spiniferites trigidus Harland and Reid in Harland et al., 1980, would be useful for interpreting the climate signal throughout the Quaternary. Up to this time, the recognition of arctic environments within marine neritic Quaternary sequences had been based on somewhat negative evidence that required either an absence of dinoflagellate cysts or the presence of low-diversity assemblages (Harland et al., 1978). Unfortunately, two important factors were to complicate the recognition of Islandinium minutum elsewhere: an archeopyle had not been identified in the type material, and terminology used to describe the process morphology was to prove ambiguous.

Following the publication of Harland et al. (1980), the presence of Islandinium minutum was soon recognised in other modern Arctic assemblages from Canada and within the Pleistocene fossil record. Hence Mudie and Aksu (1984) used the species as an indicator of arctic conditions, Mudie (1989) as a zonal indicator, and Mudie (1992) as an important component for the reconstruction of circum-Arctic environments.
using multivariate statistical analysis and transfer function techniques. Extending this interest Matthiessen (1991, 1995) examined the distribution of dinoflagellate cysts within bottom sediments of the Norwegian, Greenland and Iceland seas and recognised Islandinium minutum (then as Algidaspheeridium? minutum) as an important component. Dale and Dale (1992) used sediment trap studies to demonstrate the presence of Islandinium minutum in the water column of the Nordic Seas; and based on its modern distribution in surface sediment samples Dale (1996) found Islandinium minutum to be the main diagnostic species of the polar–subpolar biogeographical zone. Records from southern Chile established Islandinium minutum as a bipolar species (Dale, 1996), and this distribution has been confirmed by records from the southern Indian Ocean (Marret and de Vernal, 1997) and Southern Ocean (Harland et al., 1998, 1999; Harland and Pudsey, 1999).

De Vernal et al. (1989) were the first to describe variation in the process morphology of Islandinium minutum, which they noted as having acuminated to capitate process tips, and proposed the variety cezare (as Algidaspheeridium? minutum var. cezare, later validated in Rochon et al., 1999) for specimens with capitate to bifurcate process tips. However, it was Matthiessen (1991, 1995) who first highlighted potential confusion over process morphology. Mudie and Deonarine (1983) were the first to document an archeopyle for Islandinium minutum, which they considered to be hexagonal in shape, and they proposed Protopерidinius pellucidum Bergh 1881 ex Loeblich Jr. & Loeblich III 1966 as the probable motile stage. Matthiessen (1991, 1995) drew further attention to the nature of the archeopyle, and Mudie (1992) illustrated specimens showing what she interpreted as being an intercalary archeopyle resulting from the loss of two plates. Dale (1996) tentatively accepted an intercalary archeopyle for Islandinium minutum and speculated that it was therefore likely to be the cyst of a Protopерidinius species presently unknown. Later Kunz-Pirrung (1998, 1999) also described this taxon and similar round, brown, spiny cysts from the Laptev Sea including illustrations of an archeopyle.

Meanwhile, Zonneveld (1997) had described several new species of round, brown, spiny cysts from the Arabian Sea that she assigned to her new genus Echinidinium. The relationship between these species and the morphotypes found in the Arctic Ocean was not established by Zonneveld (1997), or subsequently until now.

Rochon et al. (1999) were the first to provide a clear distinction between Islandinium minutum and Islandinium? cezare (as Algidaspheeridium? minutum var. minutum and var. cezare), the former having acuminated process tips and the latter having minutely expanded process tips. Rochon et al. (1999) gave detailed distribution maps of these taxa based on surface sediments across the northern North Atlantic region.

Most recently contributors to two Workshops on Arctic Dinoflagellate Cysts held at GEOTOP-UQAM, Montreal in 1999 and 2000 recognised the importance of Islandinium minutum and similar morphotypes in the characterisation of the Arctic dinoflagellate cyst flora. The present account is derived from that interest and serves to clarify the taxonomy of this cyst species, originally named Multispinula? minuta, and similar round, brown, spiny cysts.

It was clear from the outset that Harland and Reid (in Harland et al., 1980) in proposing Multispinula? minuta were unsure as to its correct taxonomic assignment. Subsequent workers have accepted a questionable generic assignment, and indeed Matsuoka and Bujak (1988) questionably assigned the taxon to their new genus Algidaspheeridium, implying a gymbnodinalean affinity. Over the past 20 years, Islandinium minutum therefore has been considered under both the dinoflagellate subclasses Gymnodiniphyceae and Peridiniphyceae, and conclusive proof even of dinoflagellate affinity has remained elusive.

**Methods**

Modern samples from the Kara Sea were gently processed using cold HCl and HF following the method of Matthiessen (1995). Oxidising reagents were not used. Modern samples from the Laptev Sea had been processed similarly by M. Kunz-Pirrung (see Kunz-Pirrung, 1998, 1999). Residue for both the Kara and Laptev seas was mounted on microscope slides using glycerine jelly. Gentle chemical processing and the use of glycerine jelly leaves cysts uncompressed and with their protoplasm often preserved, this being necessary for detailed morphological study of the archeopyle.

The type material of Islandinium? cezare, from the late Pleistocene of Quebec, had likewise been processed without oxidation and mounted using glycerine jelly (de Vernal et al., 1989). The type slides are partially dried out but still usable. Specimens are all strongly compressed.

The type material of Islandinium minutum from modern sediments of the Beaufort Sea had been oxidised during processing (Harland et al., 1980), and this has apparently bleached the cyst walls and perhaps contributed to the compressed state of the holotype and paratype. The present colour is the result of staining with safranin-o prior to mounting.

Distribution maps (shown in Figs 3–5) are based on our own unpublished counts for the Kara Sea (full data available at the Alfred Wegener Institute’s databank PANGAEA: http://www.pangaea.de, and the GEOTOP website: http://www.units.uqam.ca/geotop), together with published counts for the Laptev Sea (from Kunz-Pirrung, 1998, 1999) using our updated nomenclature. The distribution of samples used to generate the maps is given in Fig. 2. All photomicrographs (Plates 1–3) were taken with a Leica DMR camera and DC300 digital camera.

This report uses standard morphological terminology for dinoflagellates, including the terms saphopylic (e.g. Islandinium) and theropylic (e.g. Echinidinium) for archeopyle with opercula that are either free or adnate, respectively (Matsuoka, 1988).

**Results and Conclusions**

Our analysis of spiny round brown cysts from across the Arctic region presently allows us to recognise three species: Islandinium minutum (Harland and Reid in Harland et al., 1980) new combination (basionym: Multispinula? minuta) (Plates 1 and 2a–j). Islandinium? cezare (de Vernal et al., 1989 ex de Vernal in Rochon et al., 1999) new status and combination, sensu lato (basionym: Multispinula? minuta var. cezare) (Plates 2k–m and 3a–h), and Echinidinium karaense new species (Plate 3i–o). The individual distributions of these species are given in Figs 1 and 3–5. These species are all assigned to the family Protoperidiniaceae Balech, 1988, which consists exclusively of marine non-photosynthetic species (Fensome et al., 1993). We therefore accept that our three
species are heterotrophic dinoflagellates; and note that none of our species has autofluorescence, a feature which when absent seems to indicate heterotrophy (Brenner and Biebow, 2001). The morphological characteristics, modern and fossil distribution, autecology and biological affinities of our species are discussed below.

Morphological subdivision of taxa

*Islandinium minutum*

Re-examination of type specimens of *Islandinium minutum* n. comb. from modern sediments of the Beaufort Sea, Arctic

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**Figure 2**  Bathymetry and sample distribution for Russian Arctic, based on Kunz-Pirrung (1998, 1999) for the Laptev Sea and this study for the Kara Sea. Dinoflagellate distributions based on these samples are given in Figs 3–5. The 1000-m isobath is labelled, and all other isobaths represent 500 m. The great Siberian rivers Ob, Yenisei, Khatanga, Lena and Yana are shown only by their estuaries. The positions of Kara Sea samples cited in the text are as follows: 17 = BP97-17 (72°41'19.2"N, 73°43'50.4"E, water depth 20 m); 21 = BP97-21 (74°00'02.4"N, 81°00'27.6"E, water depth 41 m); 39 = BP97-39 (73°32'09.6"N, 79°55'03.0"E, water depth 40 m); 50 = BP97-50 (73°36'39.6"N, 72°57'04.8"E, water depth 28 m); and 52 = BP97-52 (74°00'01.2"N, 72°39'43.2"E, water depth 30 m)

**Figure 3**  Modern distribution of *Islandinium minutum* in the Russian Arctic. Based on Kunz-Pirrung (1998, 1999) for the Laptev Sea, and this study for the Kara Sea. Shading from light grey to dark (in per cent) = 0–10, 10–50 and >50. Black lines = August sea-surface temperatures (in °C). Grey lines = August sea-surface salinity (in psu). Annual duration of sea-ice is usually more than 9–10 months; and the southern limit of 100% sea-ice is approximately along the 80° parallel in summer.
Canada, along with new material from modern sediments of the Kara and Laptev seas of Arctic Russia, and across the Arctic Ocean, have resulted in the following conclusions. The presence of an unequivocal archeopyle is demonstrated for the holotype (Plate 1a–c) and other specimens (Plates 1 and 2), and confirms the dinoflagellate affinity of this cyst morphotype. New morphological details including epitabulation have emerged, and these permit assignment to the subfamily Protoperidinoideae Balech, 1988 within the family Protoperidiniaceae. The archeopyle results from the loss of three apical plates (Fig. 6). This style is rare among protoperidiniacean dinoflagellates and requires the establishment of the new genus Islandinium. The apical plates in Islandinium minutum are arranged asymmetrically, an unusual feature within the Protoperidinoideae that prevents us from interpreting the epitabulation unequivocally. This asymmetry, which probably confused earlier attempts to understand the style of archeopyle, continues to hinder our interpretation of the intercalary and precingular plate series. Two, three or four anterior intercalary plates are possible, although we favour two or particularly
three (Fig. 6). The processes in Islandinium minutum are confirmed as narrowing distally to fine points; that is, they are acuminate, not aculeate as diagnosed originally.

Islandinium? cezare s.l.

Islandinium? cezare n. comb. is distinguished from Islandinium minutum principally on the basis of process terminations that are minutely expanded. It appears to have a saphopylic archeopyle, but as details are presently unclear the generic placement is tentative. The presence of several consistently recognisable morphotypes within our material implies that formal subdivision of this taxon may be warranted in the future. Pending such a revision, we refer to these morphotypes collectively as Islandinium? cezare sensu lato.

Echinidinium karaense

Echinidinium karaense n. sp. also is distinguished principally on the basis of process morphology and wall ornament. However, its archeopyle appears to be theropylic (Plate 3k), not saphopylic, requiring assignment to the genus Echinidinium Zonneveld 1997 ex Head et al. herein. We have examined the type specimens of species of Echinidinium described by Zonneveld (1997) from the Arabian Sea, and can confirm that Echinidinium karaense is different from these species.

Modern distribution and autecology

Islandinium minutum, Islandinium? cezare s.l. and Echinidinium karaense generally characterise the cold polar to subpolar waters of the high northern and southern latitudes. High percentages of these species (i.e. 35% and above) occur in regions with an extensive seasonal sea-ice cover, and summer (August) temperatures rarely exceeding 7 °C (Kunz-Pirrung, 1998, 1999; Rochon et al., 1999; de Vernal et al., this issue; this study). Summer (August) temperatures can be as low as −1° to 2° C (Kunz-Pirrung, 1998; Rochon et al., 1999; de Vernal et al., this issue; Figs 3–5) and high percentages are found in parts of the Laptev Sea (Kunz-Pirrung, 1998) and Kara Sea (this study) that experience more than 9 to 10 months of seasonal sea-ice cover. Freedom from the limitations of low light levels and the ability to feed on small diatoms, for example close to sea-ice,
Islandinium minutum

This species has been recorded in modern sediments of the Beaufort Sea, Canadian Arctic Archipelago, Baffin Bay, Labrador Sea, northwestern Atlantic Ocean, Iceland Sea, northern Norwegian Sea, Greenland Sea, Barents Sea, Kara Sea, Laptev Sea and into the Chukchi Sea (Harland et al., 1980; Harland, 1982; Mudie and Deonarine, 1983; Mudie, 1992; Dale, 1996; Kunz-Pirrung, 1998, 1999, this issue; Rochon et al., 1999; Mudie and Rochon, this issue; Radi et al., this issue; de Vernal et al., this issue; Rochon et al., 1999, text fig. 36; de Vernal et al., this issue). It is particularly associated with the Arctic Ocean and its adjacent seas. The distribution maps of Rochon et al. (1999), de Vernal et al. (this issue) and herein (Figs 1 and 3) clearly indicate its distribution throughout the Arctic and into the north temperate realm of the North Atlantic Ocean. Records in modern sediments of Chile (Dale, 1996), the southern Indian Ocean (Marret and de Vernal, 1997) and Southern Ocean (Harland et al., 1998; Harland and Pudsey, 1999) indicate its presence also within the modern polar regions of the Southern Hemisphere.

In northern latitudes, Islandinium minutum has a widespread distribution as far south as the Gulf of Maine and eastern Canadian Shelf and as far north as the Arctic Ocean (Dale, 1996; Rochon et al., 1999; de Vernal et al., this issue; study, Figs 1 and 3). It is a euryhaline species that occurs where surface-water salinities range from about 5 to 10 psu to 35 psu (Kunz-Pirrung, 1998; Rochon et al., 1999; de Vernal et al., this issue; Rochon et al., 1999, text fig. 35). This wide tolerance explains its particularly high abundance in estuarine environments of the rivers Ob and Yenisei and in the inner Kara Sea (this study, Fig. 3) as well as in the St Lawrence Estuary (de Vernal et al., this issue). Dale (1996, p. 1254) classified Islandinium minutum as a subpolar to polar taxon, with its present southern limit defining that of the subpolar zone. Rochon et al. (1999, text fig. 9a, 35) extended the known modern distribution of Islandinium minutum into the north temperate realm of the North Atlantic Ocean; and Islandinium cezare s.l. and Echinidinium karaense

Islandinium? cezare s.l. and Echinidinium karaense are widespread in polar waters, and have been recorded collectively in the Hudson Bay, Baffin Bay, the northern North Atlantic, offshore eastern Canada, and offshore eastern Greenland (as Algidasphaeridium? minutum var. cezare in Rochon et al., 1999, text fig. 36; de Vernal et al., this issue). They have been recorded separately from the east Greenland Sea (Matthiessen, 1995 and unpublished data, Fig. 1), the Iceland Sea (Matthiessen, unpublished data, Fig. 1), and from the Kara and Laptev seas of the Russian Arctic (Kunz-Pirrung, 1998, 1999; this study). Islandinium? cezare was described originally from late Pleistocene glaciomarine deposits of the Champlain Sea, Québec (de Vernal et al., 1989). In the Laptev Sea area, Islandinium? cezare s.l. and Echinidinium karaense both occur with similar abundances of about 10–30% of the total dinoflagellate cysts (as Algidasphaeridium? minutum var. cezare for Islandinium? cezare s.l. and Morphotype C for Echinidinium karaense; in Kunz-Pirrung, 1998, 1999; Figs 4 and 5). Our new results from the Kara Sea (Figs 4 and 5) show abundances of about 5–20% for Echinidinium karaense, and up to 8% for Islandinium? cezare s.l. Echinidinium karaense is particularly common in the inner Kara and Laptev seas where surface water salinities are less than 30 psu owing to large freshwater discharges from the Siberian rivers Ob, Yenisei and Lena. Because this species is presumably heterothropic, its elevated abundance may be a response to increased nutrients introduced by river discharge and hence increased abundance of potential prey such as diatoms. The same seems to be true of Islandinium? cezare s.l., although its distribution is more patchy (Fig. 4). This, along with the variable morphology we see in this taxon (see Systematic Palaeontology section), suggests that more than one biological species is represented.

Echinidinium karaense and Islandinium? cezare s.l. are apparently more restricted to polar conditions than Islandinium minutum, and therefore may be more sensitive indicators of cold environments and sea-ice cover. However, their distribution is probably more widespread than we have depicted. Specimens similar to the type material of Islandinium? cezare have been recorded rarely from Buzzards Bay, Massachusetts (V. Pospelova, personal communication to MJH, 2000), indicating a total range that extends beyond the Arctic realm.

Plate 2 Photomicrographs and tracings of Islandinium minutum and Islandinium? cezare sensu stricto. (a–d) I. minutum from the Kara Sea (MPK12437; sample BP97-50, slide 1, N36/3; central body maximum diameter 40 µm); apical view of successively lower foci through upper surface showing archeopyle formed by loss of three apical plates and canal plate. (e and f) I. minutum from the Kara Sea (MPK12438; sample BP97-52, slide 4, O43/1; central body maximum diameter 42 µm); antapical view of lower surface showing all plates in place, but demarcated by folds and partial separation. (g–j) I. minutum from the Kara Sea (MPK12439; sample BP97-21, slide 1, P30/3; central body maximum diameter 41 µm); right-lateral view showing upper surface (g) with 4 folds and partial separation. (h) slightly lower focus, and (j) showing an enlarged view of 3 folds, which is suspended upside-down above the upper surface of the cyst at the position given in (i), demonstrating separate loss of all three apical plates during archeopyle formation. (k–m) Holotype of Islandinium? cezare from late Pleistocene deposits at Saint-Étienne, Québec: ISC 86-09, slide UQP199-38, B15/4; central body maximum diameter 28 µm); uncertain view of (k and m) upper surface and (l) lower surface showing rupture of wall (arrowed) perhaps part of incipient archeopyle formation.

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Stratigraphic distribution

*Islandinium minutum* has been recorded from the upper Pliocene through upper Pleistocene of the Labrador Sea (de Vernal and Mudie, 1989a) and lower through upper Pleistocene of Baffin Bay (de Vernal and Mudie, 1989b). Earlier records such as the middle Miocene of offshore New Jersey (unillustrated in de Verteuil, 1996) require confirmation owing to taxonomic uncertainties. *Islandinium? cezare* was described from the late Pleistocene of Quebec but, like *Echinidinium karaense*, its fossil record is essentially undocumented.

Biological affinity

The unequivocal possession of an archeopyle formed by the loss of three apical plates clearly confirms that *Islandinium minutum* is a dinoflagellate. We assign all our spiny round brown cysts to the dinoflagellate family Protoperidiniaceae based on the nature of their archeofoyles (saphopylic or theropylic, but not chasmic, hence indicating that they are armoured dinoflagellates), brown pigmentation of the cyst wall, lack of epifluorescence and non-tabular process distribution (Fensome et al., 1993, under Congruentidiaceae; Brenner and Biebow, 2001).

*Islandinium minutum*

*Islandinium minutum* most strongly resembles cysts belonging to several species of the extant motile-defined genus *Protoperidinium*, for which reason we assign our new genus. *Islandinium* to the subfamily Protoperidinoideae. In particular, the loss of three apical plates in archeofoyle formation suggests similarity to *Protoperidinium americanum* (Lewis and Dodge, 1987), although the topology of the apical plates differs from this species (Fig. 6). *Protoperidinium* is the largest dinoflagellate genus in the Arctic Ocean today, with nearly 50 species recorded in the plankton (Okolodkov and Dodge, 1996; Okolodkov, 1998). We have checked the literature in an attempt to identify an equivalent motile-stage species for *Islandinium minutum*, but without success despite the abundance and widespread distribution of this cyst in Arctic sediments. Either we have not recognised the motile-stage species in our literature search, or biologists have not yet found it in the plankton. The latter is possible because of very brief growing periods in the Arctic that may cause species to be missed in those surveys that do not continuously sample throughout the summer. In this respect it is worth noting the comments of Okolodkov (1999, p. 167) that the cysts of several species, such as *Pentapharsodinium dalei* Indelicato & Loeblich III 1986, *Protoperidinium avellanum* (Meunier 1919) Balech 1974 and *P. americanum* (Gran and Braarud 1935) Balech 1974, are persistently and sometimes abundantly reported in surface sediments of the Arctic (Matthiessen, 1991, 1995; Dale and Balech, 1992; Dale, 1996; Kunz-Pirrung, 1998, 1999) despite their corresponding motile stages being rarely present or even absent from records of the plankton (Okolodkov, 1998, 1999).

Mudie and Deonarine’s (1983) proposal that the motile equivalent of *Islandinium minutum* is probably *Protoperidinium pellucidum* is not supported by our analysis of the cysts. Unfortunately *Protoperidinium pellucidum* is one of the least well defined species of the genus, with a history of misidentification including that of Lebour’s often cited 1925 record (Abé, 1981, p. 226). Notwithstanding this complication, *Protoperidinium pellucidum* appears to have a symmetrical epizoical tabulation (Abé, 1981, fig. 21.144) in contrast to the asymmetrical epizoical tabulation of *Islandinium minutum*. It also may be noted that, whereas *Islandinium minutum* has a bipolar distribution, *Protoperidinium pellucidum* has not been found in the Antarctic (Y. Okolodkov, personal communication to JM, 2001). Attempts to germinate *Islandinium minutum* under laboratory conditions have not so far been successful (A. Rochon, personal communication to MJH, 2001).

*Islandinium? cezare* s.l.

*Islandinium? cezare* s.l. is less well understood than *Islandinium minutum* because details of the archeofoyle are unknown. However, some specimens of morphotype 2 (see Systematic Palaeontology section) from the Kara Sea apparently have saphopylic archeofoyles, suggesting that this morphotype belongs to the subfamily Protoperidinoideae.

*Echinidinium karaense*

The morphology of *Echinidinium karaense* and its similarity to the cyst of *Protoperidinium monospinum* (Paulsen 1907) Zonneveld and Dale 1994, as described by Zonneveld and Dale (1994), suggest an affinity with the genus *Protoperidinium*. However, there are also broad similarities with the subfamily Diplopsalioideae including the cysts of *Diplopsalta parva* (Abé 1941) Matsuoka 1988, as described by Matsuoka (1988). Unfortunately we have no incubation data for *Echinidinium karaense*.

Plate 3 Photomicrographs of *Islandinium? cezare* and *Echinidinium karaense*. (a) Paratype of *Islandinium? cezare* from late Pleistocene deposits at Saint-Césaré, Québec: (SC 86-09, slide UQP 199-3B, M49/0; central body maximum diameter 27 µm); uncertain view of upper surface. (b) *Islandinium? cezare* s.l. (morphotype 1) from the Kara Sea (MPK12440; sample BP97-52, slide 2, O41/3; central body maximum diameter 39 µm); uncertain view of upper surface showing long, uniformly slender process stems. (c,d and h) *Islandinium? cezare* s.l. (morphotype 2) from the Kara Sea (MPK12441; sample BP97-17, slide 3, J52/1; central body maximum diameter 51 µm); equatorial view of (c) upper surface showing incipient release of plates, and both acuminate and minutely expanded (recurved) process tips. (e) *Islandinium? cezare* s.l. (morphotype 2) from the Kara Sea (MPK12442; sample BP97-50, slide 1, N36/2; central body maximum diameter 41 µm); equatorial view of (e) upper surface showing archeofoyle suture, and (f) close-up of lower surface showing barbs (arrowed) on some process stems. (i–k) Holotype of *Echinidinium karaense* from the Kara Sea (MPK12443; sample BP97-52, slide 2, E40/2; central body maximum diameter 33 µm); uncertain view of (i) upper surface, (k) slightly lower focus on archeofoyle, and (l) mid-focus showing both acuminate and minutely expanded process tips. (l–o) Paratype of *Echinidinium karaense* from the Kara Sea (MPK12444; sample BP97-50, slide 3, L40/0; central body maximum diameter 31 µm); uncertain view of (l) and (m) upper surface showing characteristic polygonal breakage of cyst wall along faintly darker lines of weakness that are not plate boundaries, (n) lower focus, and (o) mid-focus.
Systematic Palaeontology

Division Dinoflagellata (Bütschli, 1885) Fensome et al., 1993
Subdivision Dinokaryota Fensome et al., 1993
Class Dinophyceae Pascher, 1914
Subclass Peridiniphycidae Pascher, 1914
Order Peridiniidae Haeckel, 1879
Suborder Peridinioidea (autonym)
Family Protoperidiniidae Balech, 1988 nom. cons.

Discussion. Fensome et al. (1998) proposed recently to conserve the name Protoperidiniidae, thereby significantly restricting the size of the family Congruentidiidae into which the large extant genus Protoperidinium had been placed (Fensome et al., 1993). This proposal, included in Report 6 of the committee for algae, which is to be published in an issue of the Journal of the Subcommission, was approved by the General Committee at the meeting in Saint Louis, Missouri during the nomenclature session and by the general assembly closing the 16th International Botanical Congress in 1999. Therefore, Protoperidiniidae is conserved against Congruentidiidae, Diplopsaliidae and Kolkwitziiellidae, and is included in Appendix II of the current International Code of Botanical Nomenclature (ICBN, ‘Saint Louis Code’; Greuter et al., 2000; p. 115).

The name Protoperidiniidae was first introduced by Bujak and Davies (1983), but these authors did not provide a Latin diagnosis and so failed to effect valid publication under the current International Code of Botanical Nomenclature (where a Latin diagnosis is not required). A Latin diagnosis was provided subsequently by Fensome et al. (1998), but there was actually no need to validate the name Protoperidiniidae as it had already been validly established by Balech in 1988.

Subfamily Protoperidinioideae Balech, 1988
Genus Islandinium new genus

Type of genus. Holotype of Islandinium minutum n. comb. (basionym: Multispinula? minuta), MPK 1306, fig. 2O in Harland et al. (1980) Plate 1a–c.

Included species. Islandinium? cezare n. comb.

Diagnosis. Cystae fuscae colore corpus spheroidale in medio habent, ciusus marus levis vel praecellere ornatus est. Processus numerosi, non tabulares sunt; terminantes in locis distallibus in cacumines acuminatos vel extentos, quibusdam divisis. Principales et aliquando adiectae archaeopyleae suturae solum indicium clarum tabulationis sunt. Archaeopyle saphopylica ICBN (Fensome et al., 1993). Balech (1988) was first to publish diagnosis and so failed to effect valid publication under the and Davies (1983), but these authors did not provide a Latin diagnosis was provided subsequently by Fensome et al. (1998), but there was actually no need to validate the name Protoperidiniidae as it had already been validly established by Balech in 1988.

Subclass Peridiniphycidae Fensome et al., 1993
Suborder Peridiniineae (autonym)
Family Protoperidiniidae Balech, 1988 nom. cons.

Comparisons. Islandinium compares most closely with the cyst genus Echinidinium Zonneveld 1997 ex Head et al., herein, which differs in possessing a theropylic archeopyle.

Multispinula Bradford 1975, now regarded as a taxonomic junior synonym of Seleneopexis Benedek 1972 emend. Head, 1993 (Matsuoka, 1987; Head, 1993), differs from Islandinium in being polar compressed, possessing an archeopyle formed by loss of a single intercalary plate (2a), and typically having a reniform ambitus.

Algidasphaeridium Matsuoka and Bujak 1988 differs from Islandinium in being nearly colourless and having a simple slit-like rupture of the cyst wall (Head, 1994). Algidasphaeridium has been treated as a dinoflagellate, because a chasmic (slit-like) archeopyle is characteristic of many gymnodiniphycidean dinoflagellates, but the type specimen offers no certainty of dinoflagellate affinity.

Of those modern, spherical, brown, spinose dinoflagellate cysts that do not have a palaeontological name, we are aware of none that would be contained within Islandinium. For example, the cysts of Pheopolykrikos hartmannii have a chasme archeopyle (Matsuoka and Fukuyo, 1986) and the cysts of Diplopetra parva have a theropylic archeopyle (Matsuoka, 1988).

Islandinium minutum (Harland and Reid in Harland et al., 1980) new combination
Plates 1 and 2a–j; Figs 1, 3, 6, 7

Cantiacidinium conicum (NS name) Reid, 1972, p. 119–120, pl. 16, Figs 16–19.

Dinoflagellate cyst E. Reid and Harland, 1977, pl. 2, fig. 11.


Figure 7 Islandinium minutum. Measurements of specimens (uncompressed) from modern sediments of the Kara Sea, Arctic Russia; and of the holotype (compressed) from modern sediments of the Beaufort Sea, Arctic Canada

Average process length (in μm)

Kara Sea

Holotype

Central body maximum diameter (in μm)


Original diagnosis. A small spheroidal cyst consisting of two wall layers carrying numerous, rigid to flexuous, solid, aculeate processes. Paratabulation and the archeopyle not observed (Harland and Reid in Harland et al. 1980, p. 216).

Emended diagnosis. Cystae fuscae colore, choratae, corpus spheroidale in medio habent, cuius murus granulatus est. Processus numerosi, erecti, nontabalares, tere solidi vel apiculocavati, fastigati in locis distalibus, terminant in cacumines acuminatos et rotundam transversam sectionem et levem superficiem habent. Principales et rara adspectae archaeopyleae sutureae solum clarum indicium tabulationis sunt. Archaeopyla acuminatos atque rotundam transversam sectionem et levem terminant in acuminate tips, and having circular transverse section and levem superficiem habent. Principales et raritae accedentiae archaeopyleae sutureae solum claram indicium tabulationis sunt. Archaeopylaria apicalis saphophyllica, generis A3, formatur laminis apicalibus amissis secundis terhis et quartis, plerumque etiam lamina canali et foramine apicali multiplici. Quarta lamina apicalis magna est, occupans paene omnis dexteri lateris regionis apicalis, paene quadrata forma; laminae apicales secundae et tertiae paene omnis sinistri lateris regionis apicalis occupant. Opeculum liberum est; fragmenta operculi separate soluta sunt. (Cysts brown in colour, chorated, having spheroidal central body whose wall is granulate. Processes numerous, erect, non-tabular, mostly solid to apiculocavate, tapering distally, terminating in acuminate tips, and having circular transverse section and smooth surface. Principal and rare accessory archeopyle sutures are only clear expression of tabulation. The archeopyle is saphoplytic, Type A3, formed by loss of three apical plates, 2′, 3′ and 4′, and usually also canal plate and apical pore complex. Fourth apical plate (4′) is large, occupying most of the right side of the apical region, and almost square in shape; apical plates 2′ and 3′ occupy most of the left side of the apical region. Opeculum free; opercular pieces released separately.)

Description. Cysts are pale brown in the type material and have readily taken up the safranin-o stain; they are light to dark brown in the Laptev and Kara seas material. The wall surface is granulate, with raised elements being low verrucae or low confluent over 0.5 µm in diameter and separated by about 0.5 µm, as on the holotype (Plate 1c and j). The wall is thin (less than 0.5 µm) and there is no visible separation of layers between processes. Processes are numerous, non-tabular, erect, mostly solid to apiculocavate, tapering with a circular cross-section, terminating distally in finely acuminate tips. Process bases have a maximum diameter ranging from about 1.0 µm (as on the holotype) to 1.5 µm. Process bases are not distributed evenly but typically separated from one another by between 1.5 and 4.0 µm on each specimen (as on the holotype) although densities may reach between 1.5 and 2.5 µm per specimen. A small pericoel usually is present at process bases (apiculocavate condition sensu Evitt, 1985, p. 65 but not his fig. 4.1, O) and may occupy up to one-third of the process length (up to one-quarter of the process length on the holotype). All specimens have some apiculocavate processes, although fully solid processes also occur on some specimens. Process length is about one-seventh of the central body diameter in the holotype and paratype, these specimens being compressed, and about one-sixth to one-ninth of the central body diameter in the Kara Sea material, which is uncompressed. Principal and rare accessory archeopyle sutures are the only clear expression of tabulation. The archeopyle is saphoplytic, Type A3, formed by loss of three apical plates, 2′, 3′ and 4′. The first apical plate (1′) projects into the archeopyle, and the canal plate may remain attached to 1′ (Plate 1d–ii) or released (e.g. Plate 2a–d and g–j) during archeopyle formation. The fourth apical plate (4′) is large and occupies most of the right side of the apical region, whereas 2′ and 3′ are somewhat smaller and occupy most of the left side of the apical region. This results in an asymmetrical epitabulation. The contact between plates 1′ and 1″ is interpreted from a split (presumably an accessory archeopyle suture) seen in one specimen (Plate 1k–m). The contact between plates 1′ and 7″ is inferred, having not been seen. The ventral margin of plate 2′ is almost straight and suggests contact only with 1″ (Plate 1d–m; Fig. 6C). However, we do not exclude the possibility of contact with both 1″ and 2″ (Plate 2a–d; Fig. 6B). A small but distinctive pointed spur on the left-lateral side of the principal archeopyle suture (e.g. Plates 1j and k and 2b and c) marks the contact between plates 2′ and 3′, along what is otherwise a nearly straight line. In our material, the dorsal margin of 3′ appears curved rather than sharply angled; the triple-plate boundary shown in Fig. 6B and C therefore is inferred and not proven. The presence of two or three anterior intercalary plates is suggested (Fig. 6), but the paucity of secondary accessory sutures prevents a definitive interpretation of the epitabulation.

Measurements. Type material, Canadian arctic: Holotype; central body diameter, 50 × 35 µm, process length 5–7 µm. Paratype (Harland et al., 1980, fig. 2N); central body diameter, 36 × 25 µm, process length, 4–5 µm. Kara Sea: central body maximum diameter, 29 (38.8) 45 µm, standard deviation 4.1 µm; average process length 3.5 (5.42) 7.0 µm, standard deviation 0.9 µm; 44 specimens measured, all uncompressed and containing protoplasma; see also Fig. 7.

Holotype. Specimen MPK 1306, fig. 2O in Harland and Reid (in Harland et al., 1980) recovered from modern sediment, Dome Kopanoar, Beaufort Sea, Canadian Arctic; sample CSA 1780, specimen at G39/4 (label to right) (Plate 1a–c).

Epitype. Specimen MPK 12435. Sample BP97-39 (73°32′09.6″N. 79°55′03.0″E), slide 1; England Finder reference MS1/0; recovered from modern sediment, Kara Sea, Arctic Ocean (Plate 1d–i).

Repository. Holotype, other original type specimens, and epitype are deposited in the type collection of the British Geological Survey, Keyworth, along with all other interpretive types figured herein from the Kara Sea under the following numbers: MPK 12436 (Plate 1j–m), MPK 12437 (Plate 2a–d), MPK 12438 (Plate 2e and f) and MPK 12439 (Plate 2g–j).

Material examined. Type specimens from modern sediments of the Beaufort Sea, Canadian Arctic; and other specimens from modern sediments of the Laptev and Kara seas, Russian Arctic; east Greenland continental slope, Iceland Sea; and Holocene sediments from the continental shelf off Nova Scotia.

Discussion. Restudy of the type material has shown that the process tips are not aculate (pointed spines around a trumpet-shaped distal expansion) as stated originally, but acuminated, narrowing to a fine point. The confusion arose because both words are based on the same root (Latin, acus; meaning needle) although technically, as defined by Downie and Sarjeant (1966), these terms refer to distinct and separate
process morphologies. This uncertainty regarding the morphol-
ogy of the process tips led to some difficulty in the subsequent
literature, and is corrected in the emended description.

Our examination of type and other specimens from the
Arctic reveals the surface of the central body as being always
granulate, and not smooth to granulate as given in Harland
and Reid’s original description.

Our remeasurement of the type material shows that
dimensions given in Harland et al. (1980) are 20% too small.
Re-examination of one of the paratypes (fig. 2M in Harland
et al., 1980) shows it to be neither conspecific with the
holotype, nor assignable to the genus Islandinium.

A split in the cyst wall of the holotype was regarded originally
as possible damage. Our new observations of unequivocal
archeopyles in other Arctic material have prompted us to
reassess this feature. We now consider it to be a principal
archeopyle suture, with the loss of several opercular plates.
This suture is partially visible in fig. 2O of Harland and
Reid (in Harland et al. 1980) on the upper right-hand side
of the photomicrograph (see also Plate 1b). Because details
of the archeopyle are not discernible on the holotype, we
have chosen as an epitype (Plate 1d–i) a specimen with its
archeopyle clearly visible.

It is not possible to determine with certainty the number
of anterior intercalary plates present for Islandinium minutum,
as mentioned above. We have considered the possibility of
both two and three intercalary plates are shown in Fig. 6B
allow paratabulation or archeopyle to be distinguished. The
usual numbers for the genus Protoperidinium, if in a rather
asymmetrical pattern. Hypothetical tabulations incorporating
both two and three intercalary plates are shown in Fig. 6B
and C.

The ventral epitabulation of Islandinium minutum appears
to be of ortho style, judging from similarities between
its first apical plate and that of Protoperidinium americanum
(Lewis and Dodge, 1987). But Islandinium minutum has a much more asymmetrical arrangement of apical
plates than Protoperidinium americanum (Fig. 6D and E), and
this makes four plates difficult to configure. Consequently,
we favour a more conservative interpretation of three or
perhaps two intercalary plates for Islandinium minutum; the
usual numbers for the genus Protoperidinium, if in a rather
asymmetrical pattern. Hypothetical tabulations incorporating
both two and three intercalary plates are shown in Fig. 6B
and C.

Comparison. Islandinium minutum has acuminate process
tips whereas other species herein described differ in having
branched and/or minutely expanded process tips. Some
specimens of Islandinium? cezare s.l. from the Kara Sea have
mostly acuminate process tips but a few are always expanded
and processes are longer than for Islandinium minutum. Some
specimens of Echinidinium kaaraense from the Kara Sea have
mostly acuminate process tips, but the process bases are
usually broader; and ornament between the processes consists
of small spines or spindles and not low coni or low verrucae.

Echinidinium euaxum (basionym: Algidasphaeridium? euaxum
Head, 1993, pp. 24 and 26, figs 16.1–8, 16.11 and
26.4) comb. nov., described from the upper Pliocene of
southwestern England, has hollow processes that taper to
minutely expanded tips (Head, 1993, p. 24), in contrast to
the processes of Islandinium minutum, which are mostly solid
and taper to pointed tips. Echinidinium delicaturn Zonneveld
(1997), from modern sediments of the Arabian Sea, has hollow
processes and a theropylic archeopyle, and is smaller (central
body diameter 17–25 µm) than Islandinium minutum.

Islandinium? cezare (de Vernal et al., 1989 ex de
Vernal in Rochon et al., 1999)
new status and combination, sensu lato
Plates 2k–m, 3a–h; Figs. 1, 4, 8.

Cyst-type B. Harland, 1977, p. 111, pl. 4, fig. 7.
Dinoflagellate cyst D. Reid and Harland, 1977, pl. 2, fig. 10.
Algidasphaeridium? minutum var. cezare de Vernal et al.,
1989, p. 2463, pl. 2, figs 5 and 10; ex de Vernal in Rochon
et al., 1999, p. 53, text figs 9b and 36 in part; not pl. 14,
figs 10–12.
Algidasphaeridium? minutum Morphotyp B. Kunz-Pirrung,
1998, p. 93, pl. 1, figs 9 and 10.
Algidasphaeridium? Typ B. Kunz-Pirrung, 1999, pl. 1, fig. 4.
Algidasphaeridium? minutum Morphotyp A. Kunz-Pirrung,
1998, p. 93, pl. 1, figs 7 and 11.
Algidasphaeridium? Typ A. Kunz-Pirrung, 1999, pl. 1, fig. 3.

Original description and dimensions. The cysts attributed
to A.? minutum var. cezare morphologically resemble a
species first described by Harland and Reid (in Harland
et al., 1980), but differing in the termination of processes. In
effect, A.? minutum var. cezare is spherical to subspherical,
consisting consistently of two wall layers, brown in colour, and
ornamented with numerous processes, generally flexible and
about 1/5 of the cyst diameter. Observed specimens do not
allow paratabulation or archeopyle to be distinguished. The
dimensions conform to those of specimens of A.? minutum:
total diameter 34 µm and on the average 25 µm (N = 8);
length of processes varies from 4.0 to 5.5 µm. The processes
are conical to subconical and hollow at the base. Process
terminations are not acuminate, as in the case of A.? minutum,
but possess a distal extremity that is capitate to buccinate, and
not bifurcate. (Translated from de Vernal et al., 1989, p. 2463).

Emended diagnosis. Cysts brown in colour, chorate, having
spheroidal central body with smooth to granulate surface.
Wall separation apparent only under process bases. Processes
numerous, non-tubular, erect, slender, unbranched, usually
solid with small pericoels at base. Process bases and
shafts circular in transverse section. Process tips minutely
expanded into platforms with recurved margins. Principal and
occasionally accessory archeopyle sutures are the only clear
expression of tabulation. Archeopyle saphophyl, principal
archeopyle suture revealing some tabulate margins but
otherwise not decipherable.

Material examined. Late Pleistocene Champlain Sea deposits
of Quèbec (type material). Modern sediments from the Kara
and Laptev seas, Russian Arctic.

Holotype. The specimen illustrated in de Vernal et al., 1989,
pl. 2, fig. 10, slide UQP 199-3B (not slide UQP 199-3 as
stated in de Vernal et al., 1989), specimen at 815/4 (slide label
to right), and subsequently designated as the holotype by
de Vernal in Rochon et al., 1999, p. 53, thereby validating the
name of this taxon (Plate 2k–m).

Repository. Holotype and paratype deposited in the paly-
nology type collection of GÉOTOP, Université du Quèbec à
Montréal. Other figured specimens are deposited in the type

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collection of the British Geological Survey. Keyworth under the following numbers: MPK12440 (Plate 3b), MPK12441 (Plate 3c,d,g and h), and MPK12442 (Plate 3e and f).

Description. Topotype specimens have a wall thickness of about 0.3 µm or less, and a finely granulate surface, granules being about 0.3 µm in diameter and spaced about 0.3 µm apart. Processes typically are hollow at their base with cavities extending usually from one-quarter to one-half of their length, although occasional processes on a few specimens were found to be solid along their entire length. Process bases are about 1.0 µm across (range, 0.8–1.8 µm) and slightly to moderately expanded. Adjacent process bases are separated from one another by about 2 to 3 µm on average. Process shafts are smooth, taper slightly, and the tips are minutely expanded to form platforms with recurved margins, appearing mushroom-like in longitudinal section. It is unclear from light microscopy whether these recurved margins are discrete aculeae or thin but entire platform margins. The entire distal expansion is no more than about 1.5 µm across. A clear archeopyle was not seen in these specimens, although a break in the wall of the holotype (Plate 2k and l) is possibly an archeopyle.

Specimens from the Kara Sea are considerably more variable in size and form than the type material, which is quite uniform in size (Fig. 8) and morphology. Although some overlap occurs, the Kara Sea specimens seem to fall into two main groups.

The first group (morphotype 1, Plate 3b) bears thin (0.5 µm), solid processes of even thickness throughout. Process bases are weakly expanded or not expanded, and are solid or minutely cavitating. The central body maximum diameter is 27 to 42 µm and the average process length is from 5 to 8 µm. These specimens have finely granulate surfaces similar to the type material. Process tips appear identical to the type specimens in longitudinal section.

The second group (morphotype 2, Plate 3c–h) has long and tapering robust processes that are solid except for the proximal 1 or 2 µm, with bases up to about 1.5–2.5 µm across. Processes may have one or several barbs or verrucae on otherwise smooth shafts. The barbs are directed mostly towards the cyst surface and are about 1.0 µm long. The central body maximum diameter is 31 to 51 µm and the average process length is from 7 to 11 µm. Specimens in this group have variable granulation on the central body surface, which may consist of granules, bacculae, or coni, with elements on some specimens varying in size from 0.3 µm to 1.0 µm (Plate 3g). One specimen was seen with a smooth wall. Process tips appear identical to the type specimens in longitudinal section, although discrete recurved aculeae were identified on some process tips. Some specimens were seen with mostly acuminate process tips, but damage or incomplete development is suggested by the presence always of some distal expansions on these specimens. An apparently saphopylic archeopyle, reminiscent of that seen on Islandinium minutum, was seen on some specimens (Plate 3c–h) but its tabulation could not be determined.

Dimensions. Type material. Holotype: central body diameter, 28 x 25 µm; process length 4.0–5.5 (average 5.0) µm. Range: central body maximum diameter, 23(26.1)28 µm; average process length, 4.0(4.8)5.5 µm. Thirteen specimens measured from the holotype slide. Other material: central body maximum diameter, 27(40.1)51 µm; average process length, 5(9.0)11 µm. Ten specimens measured from the Kara Sea. See Fig. 8.

Discussion. The presence of unbranched processes with tips that are minutely expanded into platforms with recurved margins distinguishes this species from others of the genus, and we consider their persistent expression to warrant the elevation of this taxon to species status. Even so, scanning electron microscopy will be necessary to determine whether the recurved margins of the distal platforms on the type material are aculeate (as seen on some specimens from the Kara Sea) or entire. The emended diagnosis nonetheless clarifies the morphology of the process tips, which are not capitate or buccinate (in the normally accepted sense; Williams et al., 2000) as diagnosed originally.

Other aspects of morphology show considerable variation, and we foresee the likelihood that this taxon will be formally subdivided in future studies, although our material does not permit such separation at the moment. We note in particular the presence of barbs on process stems of some Kara Sea specimens: a feature we have not seen on the type material and are not aware of occurring in any other dinoflagellate species. Its purpose may be to promote flocculation of these cysts with other material in the water column in order to accelerate sinking to the bottom.

Similar variability within this taxon was reported for modern assemblages of the Laptev Sea (Kunz-Pirung, 1998) and might be a characteristic feature of polar estuarine environments, although detailed studies are needed to assess the distribution of individual morphotypes.

Despite the variability we see in this species, our emended diagnosis of Islandinium? cezare s.l. clarifies its process morphology and separates it from Echinidinium karaense: until now, all spherical brown spinose arctic dinoflagellate cysts with distally expanded and/or branched processes had been included in Islandinium? cezare (Rochon et al., 1999).

The generic attribution of Islandinium? cezare is tentative and reflects uncertainty as to which plates are involved in archeopyle formation.

Comparison. Echinidinium karaense differs in having a theropylic rather than saphopylic archeopyle, a smooth rather than granulate wall surface, and more hollow processes that may be branched and bear tips that are minutely flared and usually furcate but never recurved. Barbed process stems have not been observed on Echinidinium karaense.
Subfamily Protoperoiminioideae Balech, 1988
or
Subfamily Diplopsalioideae Abé, 1981
Genus Echinidinium Zonneveld, 1997 ex Head et al., here


Type of genus. Holotype of Echinidinium granulatum Zonneveld 1997 ex Head et al., herein.


Discussion. The type of the genus Echinidinium (the holotype of Echinidinium granulatum) is a specimen collected from a sediment trap suspended within the upper part of the water column in the Arabian Sea (trap MST-9E; Zonneveld, 1997; Zonneveld and Brummer, 2000). This is a modern specimen, not a fossil, and so a Latin diagnosis or description is needed for valid publication of both species and genus (ICBN Article 36.2). This requirement was not fulfilled in Zonneveld (1997) so Latin diagnoses are given here for both Echinidinium and its type Echinidinium granulatum.

The archaeopyle in Echinidinium is an angular split that follows plate boundaries but does not involve the release of plates (Zonneveld, 1997, fig. 4). It is therefore theropyle using the terminology of Matsuoka (1988), and not chasmic as diagnosed by Zonneveld (1997). The Latin diagnosis given above repeats Zonneveld’s (1997) English diagnosis except that ‘theropylica’ replaces the term ‘chasmic’.

Echinidinium granulatum Zonneveld 1997 ex Head et al., here

Echinidinium granulatum Zonneveld, 1997, pp. 325, 327 and 328; text fig. 4; pl. 2, figs 1–8.


Diagnosis. Cystae spheroidales spinis numerosis temere positis tectae sunt. Murus coloratus est cum tenai pedio luxuriae granularum secretarum. Cavae spinae separatione luxuriae et pedii formatur. Luxuriae et pedii transversae sono locis distalibus spinarum adesse possunt. Spiniae sunt acuminatas cum finibus clausis distalibus. Processi numerosi, nontabulares, robusti sunt, fastigati et forma coni, rare divisi, solidi in locis distalibus sunt, cum pericoels, qui secundum longitudine processus varia spatia extendunt. Processus in locis distalibus terminant in cavamina acuminatos vel minune extenso. Archaeopyla theropylica apertur fissura paene recta. (Cysts brown in colour, choratae, having spheroidal central body whose wall is smooth with scattered coni or spinules. Processes numerous, non-tabular, robust, conical to tapering, rarely branched, distally solid with pericoels extending variable distance along process length; terminating distally in acuminate or minutely flared tips. Archeopyle theropyle, opening by means of a nearly straight split.)

Description. Cysts have a brown wall that does not autofluoresce. The cyst wall is less than 0.5 µm thick, not visibly stratified between processes, and has a smooth surface bearing scattered small coni or spinules of variable length but up to 3 µm high on some specimens. In addition to spinules, slender solid or apiculocavate spines may occur on some specimens but they are somewhat shorter than the processes. Processes are numerous, non-tabular, and are separated from one another at their base by ca. 1.5–3.0 µm, this range of separation being present on most individual cysts. Processes are conical to tapering, and individual specimens show variable width at base, although usually this is not more than about 2.5 µm. Processes are apiculocavate to mostly hollow, with the extent of cavation varying on individual specimens, but most specimens have some processes with pericoels that extend for at least one-third of their length. Processes are solid distally, have a smooth surface, a circular transverse section, and are rarely branched (as on the paratype, Plate 3o). Process tips are either acuminate or minutely expanded and flared, and usually both types of tips are present on the same cyst, although in proportions that vary considerably from cyst to cyst. Where process tips are minutely expanded, aculeae are often discerned. These aculeae rarely exceed 1.0 µm in length, usually are directed away from the cyst wall and are never strongly recurved.

The acrobeyle is interpreted as being theropyle, opening by means of a simple, long, nearly straight split. Some slight angulations along its course suggest an opening along plate sutures. An acrobeyle was not clearly seen in most specimens, and this probably is a consequence of its indistinct nature. A few specimens have been found with polygonal openings (Plate 31 and m; and the holotype), but these are interpreted as damage to the cyst wall. There is no other evidence of tabulation, but some areas of the cyst wall on several specimens examined (including both holotype and
paratype) have slightly darkened lines (slight thickening?) that run between process bases and form a very faint and irregular reticulum. It is uncertain whether this is a preservational feature (a separation of wall layers?) but may be related to the polygonal openings noted above.

**Measurements.** Holotype: central body diameter, 32 × 32 µm, maximum process length, 6 µm. Range: central body maximum diameter, 29 (32.5)–36 µm; average process length, 5.0(6.1)–7.0 µm. Fifteen specimens measured from the Kara Sea (Fig. 9).

**Etymology.** Named after the Kara Sea, the type locality of this species.

**Holotype.** Specimen MPK 12443. Sample BP97-52 (74°00′01.2″N, 72°39′43.2″E), slide 2, EF E40/2 (label to left), from modern sediments of the Kara Sea, Arctic Ocean (Plate 3i–k).

**Repository.** The holotype (see above) and paratype (specimen MPK 12444; Plate 3l–o) are deposited in the type collection of the British Geological Survey.

**Material examined.** Modern sediments from the Kara and Laptev seas, Russian Arctic.

**Comparison.** *Echinidinium karaense* is most similar to the cyst of *Protoperidinium monospinum* (see Zonneveld and Dale, 1994), which appears to have more conspicuously branched processes. The cysts of *Diplopelta parva* (see Matsuoka, 1994), which appears to have a straight, slit-like opening interpreted to be part of the theropylic archeopyle (Zonneveld, 1997, fig. 5a; MJH personal observation).

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