Six new taxa of subarctic Parmales (Chrysophyceae)

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Abstract The Parmales are an enigmatic group of marine phytoplankton, with siliceous plates of varying morphology surrounding their 2-5µm-diameter cells. Although rarely found in sediment traps or underlying sediments, in oceanic surface-waters they often outnumber even the diatoms during the spring months. Since their discovery, several decades ago, in the Antarctic and subarctic Pacific, the Parmales have been found in temperate and tropical regions. Despite the publication of several significant taxonomic papers, a number of Parmales remain without formal description. Here we provide descriptions of six new taxa from subarctic waters: Tetraparma catinifera sp. nov., T. gracilis sp. nov., Triparma columacea f. convexa f. nov., T. columacea f. fimbriata f. nov., T. laevis f. inornata f. nov. and T. laevis f. longispina f. nov. In addition, an annotated checklist of all Parmales, including undescribed taxa, is presented for the first time. Distribution maps of all subarctic taxa are also provided for the North Pacific and its marginal seas.

Keywords Bering Sea, Chukchi Sea, Japan Sea, Parmales, Sea of Okhotsk, subarctic Pacific, taxonomy

1. Introduction

Probably due to their small size (2-5µm), the Parmales escaped detection for most of the 20th Century. However, with the advent of the electron microscope, scientists began to record the presence of ‘siliceous cysts’ in marine water samples (Iwai & Nishida, 1976; Nishida, 1979, 1986; Booth et al., 1980, 1981, 1982; Silver et al., 1980; Takahashi et al., 1986) and of incomplete cysts and isolated siliceous plates in zooplankton faecal pellets (Urban et al., 1993), sediment traps (Ohyama & Jordan, 2002, unpubl. data) and marine sediments (Stradner & Allram, 1982; Franklin & Marchant, 1995; Ziehlemski, 1997; Thorn, 2004). Booth & Marchant (1987) formally identified these siliceous cysts as belonging to a new order, the Parmales, and assigned them to the Class Chrysophyceae. The previous year, Marchant & McEldowney (1986) had sectioned several of these siliceous cysts and demonstrated that they were algae. However, their assignment to the Chrysophyceae remains speculative, since no one has succeeded in cultivating them or conducting genetic studies on them directly. Recently, Lovejoy et al. (2006) analysed the genetic diversity of Arctic waters, using 18S rRNA, and noticed several novel sequences. One such cluster was a sister group to the Bolidophyceae, a group closely related to the diatoms (Guillou et al., 1999). Lovejoy et al. (2006) speculated that this cluster represented the Parmales, although clearly more evidence is needed before we can be sure. But if it is true, then Mann & Marchant (1989) may have been right to suggest that a Parmales-like ancestor gave rise to the diatoms, presumably some time after the Permian/Triassic mass extinction event (Medlin et al., 1997). However, some of the oldest Parmales fossils are reportedly those in Late Eocene to Early Oligocene (ODP Leg 188, Hole 1166A, 148.11 mbsf) and Middle to latest Miocene (ODP Leg 188, Hole 1165B, 169.58-291.28 mbsf) sediments from Prydz Bay, Antarctica (Thorn, 2004). Unfortunately, the author did not provide photographs to support the findings, and so micrographs of Parmales specimens from the Middle America Trench slope (DSDP Leg 66, Site 490-1-4, 25-26 cm), thought to be Middle to Late Quaternary (NN20) in age, are currently the oldest piece of evidence from the fossil record (Stradner & Allram, 1982).

The exclusively marine Parmales are now well known from polar waters, however, their occasional presence in tropical waters (Silver et al., 1980; Kosman et al., 1993; Bravo-Sierra & Hernández-Becerril, 2003) suggests that their distribution may be worldwide, albeit in restricted habitats. Despite this, the ecology of the Parmales is very poorly known. Several workers had noticed that the Parmales remained covered in plates all year round (e.g. Booth & Marchant, 1987), but Komuro et al. (2005) were perhaps the first to show this clearly, and to mention that they behaved like diatoms, ‘blooming’ in spring, sinking to the pycnocline/nutricline in the summer. A few years earlier, Tanimoto et al. (2003) had shown that, where subarctic Pacific waters entered the Bering Sea (i.e. through...
the shallow straits of the Aleutian Islands), the Parmales were present at the surface during the summer, but away from the Aleutian Islands the Parmales were almost absent from the subarctic surface-waters. The data of Komuro et al. (2005) clearly explains why some of the earlier workers found them at deeper depths, while others found them at the surface. Their seasonal dataset also confirms Marchant & McEldowney’s (1986) observation that the Parmales are not cysts at all, but the vegetative stage of an alga with a presumably high growth-rate (i.e. higher than that reported by Taniguchi et al. (1995) from their bag experiments) and high silica uptake rate.

Bravo-Sierra & Hernández-Becerril (2003) provided a list of extant Parmales taxa, including three genera, eight species, four subspecies and one forma. They proposed that, in the future, the status of the four subspecies be changed to forma or variety, since phytoplankton workers on other algal groups rarely used subspecies in this way - that is, when only morphological features are used as separation criteria, and life-cycle or interbreeding information is not known. Although we support this proposal, we did not encounter any of the four subspecies in this study, and so hesitate to make the changes here. However, some of the new taxa herein are assigned forma status, in recognition of their suggestion.

It is now known that the Parmales are a significant component of the phytoplankton community, especially in high latitudes, however their enumeration at the species or subspecific level is currently hampered by an underestimation of their diversity. Until this problem is addressed, ecological and biogeographic studies will be difficult to undertake with any confidence. Therefore, in this first taxonomic paper, we describe most of the subarctic taxa that are presently without formal names.

2. Material and methods
Samples were collected on three cruises undertaken at various times of the year and in different years: KH99-3 (July-August, 1999) of the R/V Hakuho Maru, MR00K01 (January, 2000) and MR06-04 (August-September, 2006) of the R/V Mirai. Figure 1 shows the station locations from which water-samples were collected and specimens photographed. The Kyodo North Pacific Ocean Time-Series (KNOT; Kyodo = cooperative in Japanese) station was established in 1997 as part of the Joint Global Ocean Flux Study, and was visited on 16th August, 1999 during KH99-3 and 17th January, 2000 during MR00K01. During the first visit, several hydrocasts were carried out over a short time-interval. Samples from two of these hydrocasts, referred to in the plate captions simply as Stations 1 and 2, have been analysed for this study. Samples were also collected from hydrocasts at Stations 16 and 17 during KH99-3, and from Stations 3, 4, 6, 7 and 12ex on MR06-04. In addition, two surface-water samples (Stations 23 and 24) were obtained while underway on MR06-04. Vertical water-samples were acquired on shallow hydrocasts (5-300m) using a Conductivity Temperature Depth (CTD) rig equipped with a rosette of water bottles. Surface-waters were collected either by bucket, or using the onboard continuous sea-water supply. For each CTD sample, a suite of hydrographic parameters was normally measured, while for those taken with the onboard sea-water supply, only temperature and salinity measurements were available from instruments connected to the continuous flow of sea-water.

Water-samples were filtered, prepared for scanning electron microscopy (SEM), and photographed as detailed in Konno & Jordan (2006). All filter samples, SEM stubs, negatives and scanned images used in this study (including those associated with the holotypes) are presently curated in the Department of Earth & Environmental Sciences, Faculty of Science, Yamagata University, Yamagata, Japan.

3. Results
3.1 Terminology
In general, the terminology used in this paper follows that of Booth et al. (1981) and Booth & Marchant (1987), but also incorporates the recent findings and recommendations of Konno & Jordan (2007). The latter authors revealed that the cell-wall structures of Triparma and Tetraparma are more closely related than previously thought, with the same plate configuration; that is, three girdle plates, three shield plates, one dorsal plate and one ventral plate. The major differences between the two genera are the shape of the dorsal and girdle plates and the size of the ventral plate. In Tetraparma, the triradiate dorsal plate is notched, the girdle plates are also triradiate, and the ventral plate is smaller than the shield plates. In

![Figure 1](https://www.aquarius.ifm-geomar.de)
Triparma, the triradiate dorsal plate has rounded ends, the girdle plates are oblong, and the ventral plate is larger than the shield plates.

3.2 Systematic taxonomy
In this section, six new taxa are described from subarctic waters. To avoid taxonomic complications in the future, the bibliography for each taxon has been restricted to the subarctic Pacific and its marginal seas, although it is presumed that specimens occurring in the subarctic North Atlantic belong to one or more of the taxa below. For those species which are seemingly bipolar (i.e. morphologically identical), it is presumed that future studies will discover that they are actually cryptic species, as has been found in other plankton groups. An annotated checklist of the Parmales, complete with dates and authorities, is given in the discussion.

The cell and plate dimensions given in the descriptions below are of specimens photographed in the present study, while biogeographic references to water-samples with ‘NP’ and ‘B’ notations are from Tanimoto et al. (2003). Only one paper provides ultrastructural information on the Parmales. Marchant & McEldowney (1986) showed that the parmalian cell contains a large chloroplast and very little storage material, indicating its photosynthetic tendencies. Furthermore, they showed that it possesses a chloroplast endoplasmic reticulum, as found in diatoms and chrysophytes. Thus, it should be noted that the inclusion of the Parmales in the Class Chrysophyceae sensu lato is still tentative, pending detailed ultrastructural and genetic work.

Class CHRYSOHYCEAE Pascher
Order PARMALES Booth & Marchant emend.
Konno & Jordan

Family TRIPARMACEAE Booth & Marchant emend.
Konno & Jordan

Genus Tetraparma Booth in Booth & Marchant emend.
Konno & Jordan

Cells planktonic, solitary, non-motile, spherical to sub-spherical. Cells possess eight plates: three shield plates, three triradiate girdle plates, one triradiate dorsal plate and one circular ventral plate. Plate boundaries distinct. All plates are slightly to strongly convex in the central area, with or without papillae, and are radially veined with veins dichotomously branching and Anastomosing increasingly toward the margin, forming a wide inner ring of elongate areolae. Arms of triradiate dorsal plate with notched ends. Marine.

Tetraparma catinifera sp. nov.
Pl.1, figs 1-9; Pl.2, figs 1-2

1980 Siliceous cyst Booth et al.: fig.1(8).

1987 Tetraparma pelagica Booth & Marchant: fig.4.
2003 Tetraparma pelagica Booth & Marchant: Tanimoto et al., pl.3, fig.6.

Etymology: Catina (L.) meaning bowl, fero (L.) meaning to carry, in reference to the bowl-shaped shield plates.

Cellula solitaria, sphaerica, 2.7-3.3µm diametro. Laminae papillae praesentes, circa 6-12/µm. Papillae praesentes in seribus radiantis atque vel concentricis. Laminae processus centralis, sine umbonatae. Laminae parmae 1.7-2.4µm diametro, margines elevatos. Laminae triradiatae, brachii 1.3-1.5µm longitudo. Lamina dorsalis 1.0-1.4µm longitudo. Lamina ventralis, circa 1.6µm diametro. Species planctonica marina, ad 44˚N, 155˚E (Statio KNOT). Holotypus, hic designatus: EM Stub KNOTJ0030. Iconotypus: Lamina 1, Figura 2.

Description: Cells solitary, spherical, 2.7-3.3µm in diameter. Papillae usually present, ca.6-12 papillae/µm. Plates usually with radially arranged papillae between the slit-like areolae, and one or more concentric rows of papillae along the top of a raised marginal rim. Plates with small central papilla, but no central mound. Shield plates ca.1.7-2.4µm in diameter, with a wall-like plate margin. Triradiate girdle plates, arms ca.1.3-1.5µm long (measured along the dorso-ventral plane, from end to central papilla). Arms of dorsal plate, ca.1.0-1.4µm long. Ventral plate ca.1.6µm in diameter. Marine, in plankton at 44˚N, 155˚E (Station KNOT), 17th January, 2000 (30m).

Holotype: EM Stub KNOTJ0030 (specimen in Pl.1, fig.2).

Note: In Booth et al. (1981), this form was originally distinguished from T. pelagica (as Cysts VIII and IX, respectively), and when the latter species was formally described in Booth & Marchant (1987), the two forms were again distinguished in the text, but both appeared in the figure captions under the same name. Apart from a notable size difference, T. catinifera differs from T. pelagica by having wall-like shield-plate margins of variable height, lacking the triangular spines at the plate centre, and having a somewhat flattened central area. However, Booth & Marchant (1987, fig.5) showed an intriguing specimen (collected in May from surface-waters at 56°59′N, 141°27′W) that seemingly possesses a rimmed shield-plate in addition to typical T. pelagica plates. In the present study though, no such specimens have been seen. T. catinifera specimens show a significant amount of morphological variation, not just in wall height (compare Pl.1, fig.1 with Pl.2, fig.1), but also in the distribution and degree of papillation (compare Pl.1, figs 3, 4 with Pl.1, figs 6, 7), and the number of radiating slits in the central area (compare Pl.1, fig.5 with Pl.1, fig.7). It should be noted that the girdle and dorsal plates have less prominent walls than the shield and ventral plates (Pl.1, fig.2), and that, due to the curvature of the cell, all of the plates are actually convex (Pl.1, fig.9). This species has mostly been
Plate 1

*Tetraparma catinifera*

1. Cell wall, showing shield (s), girdle (g), dorsal (d) and ventral (v) plates. N Pacific, KNOT St.1, 100m

2. Specimen clearly showing juncture between girdle and dorsal (arrowed) plates. N Pacific, KNOT MR00K01, 30m. Holotype

3. Dorsal plate interlocking with three girdle plates. Note plates strongly papillate. Sea of Okhotsk, St.7, 30m

4. Specimen with clear plate junctures. Note papillae on inside of plate rims. Sea of Okhotsk, St.7, 30m

5. Specimen with less prominent papillae. Ventral plate at bottom of photo. Bering Sea, KH99-3, St.16, 50m

6. Note small ventral plate at bottom of photo (arrowed). Sea of Okhotsk, St.6, 30m

7. Specimen with more radiating slits, lacking papillae. N Pacific, KH99-3 St.17, 50m

8. Collapsed cell. Sea of Okhotsk, St.6, 30m

9. Collapsed cell. Note curvature of plates. Sea of Okhotsk, St.7, 30m
recorded in the subarctic Pacific, but also occurs in the Gulf of St. Lawrence, Canada (Bérard-Therriault et al., 1999, p.246, pl.113, figs a, c) and in the Chukchi Sea (this study).

**Biogeography (this study):** Sea of Okhotsk - MR06-04 St.4, MR06-04 St.6, MR06-04 St.7; NW Pacific - St. KNOT (August, 1999, KH99-3; January, 2000, MR00K01), KH99-3 St.17; NE Pacific - KH99-3 NP15; Bering Sea - MR06-04 St.24, KH99-3 St.16; Chukchi Sea - MR060-04 St.12ex.

**Tetraparma gracilis** sp. nov.

Pl.2, figs 3-7

1981 Cyst IX Booth et al.: fig.68?
2003 *Tetraparma pelagica* Booth & Marchant: Tanimoto et al., pl.3, fig.7.

**Etymology:** *Gracilis* (L.) meaning slender, in reference to the shape of the central process.

**Cellula solitaria, sphaerica, 2.3-2.5µm diametro. Laminae papillis carentes. Processus centralis, 0.7-0.8µm longitudo, in laminae sine umbonatae. Laminae margines laevi et leviter elevatiae. Laminae parmae 1.3-1.8µm diametro. Laminae triradiatae circa 1µm longitudo. Lamina dorsalis circa 1µm longitudo. Lamina ventralis, circa 1.2µm diametro. Specimen planctonica marina, ad 44˚N, 155˚E (Statio KNOT). Holotypus, hic designatus: EM Stub KNOTA9960. Iconotypus: Lamina 2, Figura 4.

**Description:** Cells solitary, spherical, 2.3-2.5µm in diameter. Plates without papillae. All plates lack a central mound, but have a central process 0.7-0.8µm long. Processes on girdle and dorsal plates slender, those on shield and ventral plates appear bifurcate. Plates with a smooth, slightly raised margin. Shield plates ca.1.3-1.8µm in diameter. Triradiate girdle plates ca.1µm long (measured along the dorso-ventral plane, from end to central structure). Arms of dorsal plate, ca.1µm long. Ventral plate ca.1.2µm in diameter. Marine, in plankton at 44˚N, 155˚E (Station KNOT), 16th August, 1999 (60m).

**Holotype:** EM Stub KNOTA9960 (specimen in Pl.2, fig.4).

**Note:** *T. gracilis* differs from *T. pelagica* by seemingly lacking papillae and having a long central process. A similar specimen was illustrated by Iwai & Nishida (1976, pl.II, fig.7), but the central process on at least some of the plates was cruciate. The processes on the shield and ventral plates of some of our specimens appear bifurcate, whilst those on the girdle and dorsal plates are slender (Pl.2, fig.4). Furthermore, in broken specimens, the central process cross-section appears circular (Pl.2, figs 6, 7), whilst that of *T. pelagica* (subarctic forms) is elongate (Pl.3, figs 12, 13). Another specimen featured by Nishida (1986, pl.1, fig.4), from the Southern Ocean, has an angled short spine on each plate. Both of these forms clearly belong to *Tetraparma*, but are in need of further observations and formal descriptions. *T. gracilis* has only been recorded in the subarctic Pacific.

**Biogeography (this study):** Sea of Okhotsk - MR06-04 St.7; NW Pacific - St. KNOT (August, 1999, KH99-3), KH99-3 NP30, KH99-3 St.17; Bering Sea - MR06-04 St.23.

**Tetraparma pelagica** Booth & Marchant

Pl.3, figs 1-13

1987 *Tetraparma pelagica* Booth & Marchant: p.248, figs 2 (holotype, from 64˚59.8’S, 83˚02’E; January, surface-water), 3, 5, non fig.4.
1976 Sp. indet. C Iwai & Nishida: pl.II, fig.3?
1979 Genus & species indeterminable Nishida: pl.1, fig.4.
1980 Siliceous cyst Booth et al.: fig.1(9).
1981 Cyst IX Booth et al.: figs 60-62, 69, non fig.68.
2003 *Tetraparma pelagica* Booth & Marchant: Tanimoto et al., pl.3, fig.5, non figs 6, 7.

**Description:** Cells 1.9-2.5µm in diameter. All plates with or without papillae, ca.12-15 papillae/µm, are radially veined, with veins dichotomously branching and Anastomosing increasingly toward the margin, forming a wide inner ring of elongate areolae. Plates with radially-arranged papillae between the slit-like areolae, and two concentric rows of papillae on top of a low marginals rim. Small triangular spine covered by papillae usually present at plate centre. Shield plates ca.1.3-1.6µm in diameter. Triradiate girdle plates ca.0.8-1.3µm long (measured along the dorso-ventral plane from end to central structure). Arms of dorsal plate, ca.0.8µm long. Ventral plate ca.1.1-1.8µm in diameter. Marine.

**Note:** *T. pelagica* was originally described from the Antarctic (Booth & Marchant, 1987), but smaller, seemingly indistinguishable, cells are also found in the subarctic Pacific and Bering Sea (compare with Findlay, 1998, pl.3, fig.6; Marchant & Scott, 2005, figs 7.5a, b). Our own unpublished data on Antarctic *T. pelagica* specimens also conform to the original dimensions given by Booth & Marchant (1987). A closer examination of specimens from both polar regions may reveal them to be two cryptic taxa in the future. In addition, some specimens lacking plate spines, but possessing the other characteristic features of this species, have been found exclusively in the subarctic Pacific (e.g. Iwai & Nishida, 1976, pl.II, fig.3, as Sp. indet. C; Nishida, 1979, pl.1, fig.4, as Genus & species indeterminable, and in text-figs 4 and 6 as Indet. B) and the Sea of Okhotsk (Pl.3, figs 10, 11). These non-spiny forms are rare, and presumed to represent the same species as the spiny forms. The large ventral plate (1.8µm) mentioned in the above description was measured in ventral view, and so one assumes that shield plates larger than 1.6µm were present on the other side of the cell. A disarticulated specimen of *T. pelagica* from Disko Bay, Greenland, clearly shows the size difference between...
Plate 2

1-2: Tetraparma catinifera; 3-7: Tetraparma gracilis

Note low-walled rims and less prominent papillae. Bering Sea, St.24, 75m

Note low-walled rims and plates with more radiating slits. N Pacific, KNOT St.1, 100m

Cell wall showing shield (s), dorsal (d) and girdle (g) plates. N Pacific, KH99-3 St.17, 50m

Cell wall showing all the plate types, including the ventral plate (v). N Pacific, KNOT St.1, 60m. Holotype

Note dorsal/girdle plate juncture (arrowed). Bering Sea, St.23, 10m

Note strong curvature of shield plate in upper left corner. Sea of Okhotsk, St.7, 30m

Note circular hole left by broken spine, and ventral plate on left-hand side. Sea of Okhotsk, St.7, 30m
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Plate 3

_Tetraparma pelagica_

Cell wall, showing shield (s), girdle (g), dorsal (d) and ventral (v) plates. Bering Sea, St.24, 0m

Specimen clearly showing dorsal plates (centre). N Pacific, KH99-3 St.17, 50m

Bering Sea, St.23, 0m

Bering Sea, St.23, 30m

Bering Sea, St.23, 10m

Bering Sea, St.24, 0m

N Pacific, KH99-3 St.17, 50m

Sea of Okhotsk, St.7, 30m

Note greater degree of ornamentation. Sea of Okhotsk, St.4, 30m

Note plates seemingly lack spines. Sea of Okhotsk, St.7, 30m

Note plates seemingly lack spines. Sea of Okhotsk, St.7, 30m

Note shape of aperture left by broken spine on girdle plate, and small ventral plate on left. Sea of Okhotsk, St.7, 30m

Note shape of aperture left by broken spine on shield plate. Sea of Okhotsk, St.7, 30m
Plate 4

*Triparma columacea* f. *fimbriata*

Cell wall showing girdle (g), shield (s) and dorsal (d) plates (ventral plate not visible). N Pacific, KNOT St.1, 125m. Holotype

1. Ventral view showing ventral plate (v). Bering Sea, St.24, 10m

2. Ventral view showing ventral plate. Bering Sea, St.23, 30m

3. Cell wall with one shield-plate missing. Note ventral plate in bottom right corner. Bering Sea, St.23, 30m

4. Ventral view showing ventral plate. Bering Sea, St.23, 30m

5. Ventral view. Note upper girdle plates appear interlocked. Bering Sea, St.24, 30m

6. Ventral view showing ventral plate. Bering Sea, St.24, 50m

7. Girdle view. Bering Sea, St.23, 0m
the shield plates and the ventral plate (Kosman et al., 1993, fig.31).

**Biogeography (this study): Sea of Okhotsk** - MR06-04 St.4, MR06-04 St.7; **NW Pacific** - St. KNOT (August, 1999, KH99-3), KH99-3 St.17; **Bering Sea** - KH99-3 St.B5, MR06-04 St.23, MR06-04 St.24.

Genus *Triparma* Booth & Marchant emend. Konno & Jordan

Cells planktonic, solitary, non-motile, spherical to sub-spherical (excluding extensions). Cells possess eight plates: three shield plates, three oblong girdle plates, one triradiate dorsal plate, and one circular ventral plate. Plate boundaries distinct. Arms of triradiate dorsal plate with rounded or slightly squarish ends. Marine.

*Triparma columacea* f. *convexa* f. nov.  
Pl.5, figs 1-4

1979 Genus & species indeterminable (Indet. A) Nishida: text, figs 4, 6, pl.1, fig.3.
2003 *Triparma columacea* Booth: Tanimoto et al., pl.3, fig.4.

**Etymology:** *Convexa* (L.) meaning convex, in reference to the shape of the shield plates.

*Cellula 1.8-3.3µm diameter. Laminae parvae 1.1-1.7µm diametro, convexae. Laminae oblongae 1.6-2.1µm longitudo, carina fere conspicua et undulata in asceptu circularis, seriebus unabus areola elongatae in utraque latero et perpendicularibus carinam. Lamina dorsalis brachii 1.0-1.5µm longitudo, fere rotundis extremis. Lamina dorsalis cum foramina centrica, carina triradiata, areolae elongatae in unibus serie perpendicularibus ad quumque marginem et formantes latera carinam, atque seribus pluribus ex areolae parvae in extremum utraque bracho. Lamina ventralis incognita. Planctonica marina, ad 60˚N, 179˚W (Mare Bering). Holotypus, hic designatus: EM Stub BS062410. Iconotypus: Lamina 5, Figura 1.*

**Description:** Cells 1.8-3.3µm in diameter. All plates with coarse venation, without ornamentation. Shield plates *ca.1.1-1.7µm* in diameter, convex; radially veined, with veins dichotomously branching and anastomosing increasingly toward the margin forming a wide inner ring of elongate areolae and a narrow outer ring of compact areolae. Oblong girdle plates *ca.1.6-2.1µm* long, with keel more or less pronounced, undulating in girdle view, with a single row of elongate areolae on each side of the keel and perpendicular to it. Arms of dorsal plate, *ca.1.0-1.5µm* long with slightly rounded ends. Dorsal plate with central indistinct hole, triradiate keel with a single row of elongate areolae perpendicular to each margin forming the sides of the keel, and with several rows of small areolae at the end of each arm. Ventral plate unknown. Marine, in plankton at 60˚N, 179˚W, Bering Sea (St.24, 10m).

**Holotype:** EM Stub BS062410 (specimen in Pl.5, fig.1).

**Note:** Kosman et al. (1993) have already suggested that it would be reasonable to describe this taxon as a new form (their p.119). *T. columacea* f. *convexa* is clearly different from the type (and its currently described forms) as it possesses convex shield-plates rather than flattened ones (Pl.5, fig.1). Also, there appears to be a difference in the shape of the ends of the dorsal plate (more squarish in *f. convexa*, distinctly rounded in the type: Pl.5, fig.2). In the original description of *T. columacea*, the dorsal plate is described as having a hole in the middle, and with small holes at the end of each arm. Although not clear from our micrographs, it is possible to see these structures in some specimens. Furthermore, *f. convexa* appears to have only one row of areolae either side of the keel (as in *f. alata* Marchant and *f. fimbriata*), while there are two in the type. Booth & Marchant (1987, p.251) mentioned that similar forms had been seen in the Bay of Bothnia in waters of 5-6 PSU (H. Thomsen, pers. comm. in Booth & Marchant, 1987). In a later paper, Kosman et al. (1993) showed photographs of specimens of *T. cf. T. columacea* from Denmark and Finland, but this Baltic Sea form, although possessing convex shield-plates, had a much more bulky and less spherical cell shape, due to the strongly-keeled girdle-plates. In our opinion, the two forms are different, and both clearly deserve to be separated from the type.

**Biogeography (this study): Sea of Okhotsk** - MR06-04 St.7; **NW Pacific** - St. KNOT (January, 2000, MR00K01), KH99-3 NP30; **Bering Sea** - MR06-04 St.24.

*Triparma columacea* f. *fimbriata* f. nov.  
Pl.4, figs 1-7

1980 Siliceous cyst Booth et al.: fig.4.

**Etymology:** *Fimbria* (L.) meaning fringe, in reference to distal extension on the girdle plates.

*Cellula 2.3-2.7µm diametro. Laminae parvae non alatae, 1.3-1.5µm diametro. Laminae oblongae 2.7-3.0µm longitudo, carina cum fimbria ala fere undulata, una serie areolae elongatae in quoque latera et perpendicularis carinam. Lamina dorsalis brachii 1.2-1.5µm longitudo, dilute rotundis extremis. Lamina dorsalis cum foramine in centro obscuras, carina triradiate, striis elongatis in serie una perpendicularibus ad quumque marginem et formantes latera carinam, atque seribus pluribus ex areolae parvae in extremum utraque bracho. Lamina ventralis convexa, 2.3-2.7µm diametro, laminae parvae venae similis, sed annulum angustum exterior areolarum compactarum. Planctonica marina, ad 44˚N, 155˚E, Statio KNOT. Holotypus, hic designatus: EM Stub
Plate 5

1-4: *Triparma columacea* f. *convexa*; 5-9: *Triparma laevis* f. *laevis*

Cell wall showing girdle (g), shield (s) and dorsal (d) plates (ventral plate not visible). Bering Sea, St.24, 10m. Holotype

Cell wall with clear radial markings on plates. Bering Sea, St.24, 30m

Dorso-ventral view with ventral plate just visible (black arrow). Note notch of girdle plate (white arrow). Sea of Okhotsk, St.7, 30m

Dorsal view with strong keel on dorsal plate (arrowed). Sea of Okhotsk, St.7, 30m

Cell wall showing girdle (g), shield (s) and dorsal (d) plates (ventral plate not visible). Japan Sea, St.3, 50m

Ventral plate (v). Bering Sea, St.24, 0m

Ventral view. Bering Sea, St.24, 30m

Ventral view. Bering Sea, St.23, 0m

Ventral view of ventral plate. Bering Sea, St.24, 0m
**New taxa of subarctic Parmales**

**KNOTA99125. Iconotypus: Lamina 4, Figura 1.**

**Description:** Cells 2.3-2.7µm in diameter. All plates with coarse venation. Shield plates ca.1.3-1.5µm in diameter, flattened; radially veined, with veins dichotomously branching and anastomosing increasingly toward the margin, forming a wide inner ring of elongate areolae. Oblong girdle-plates ca.2.7-3.0µm long, with a keel bearing an undulating fringelike extension, with a single row of elongate areolae on each side of the keel and perpendicular to it. Arms of dorsal plate ca.1.2-1.5µm long with slightly rounded ends. Dorsal plate with central, indistinct hole, triradiate keel, with a single row of elongate areolae perpendicular to each margin forming the sides of the keel. Ventral plate somewhat domed, ca.2.3-2.7µm in diameter, similar venation to shield plates, but with a narrow outer ring of compact areolae. Marine, in plankton at 44˚N, 155˚E, Station KNOT (16th August, 1999, 125m).

**Holotype:** EM Stub KNOTA99125 (specimen in Pl.4, fig.1).

**Note:** *T. columacea f. fimbriata* differs from the type by having a projection on the girdle plates, rather than a mere keel (compare Pl.4, figs 1, 4-7 with Booth & Marchant, 1987, figs 8, 11), and from f. *alata* by the shape of the projection. In *f. fimbriata*, the projection extends along the entire length of the girdle-plate (Pl.4, figs 1, 4-7), whereas in f. *alata* it is located centrally (see Booth & Marchant, 1987, figs 15, 16). Two other forms of *T. columacea* are more similar to the type and lack extensions on the girdle plates (see above note on *T. columacea f. convexa*).

**Biogeography (this study): NW Pacific - St. KNOT (August, 1999, KH99-3); Bering Sea - MR06-04 St.23, MR06-04 St.24.**

**Triparma laevis Booth in Booth & Marchant f. laevis**

Pl.5, figs 5-9

1980 Siliceous cyst Booth *et al.*: fig.1-1.
1987 *Triparma laevis* Booth in Booth & Marchant: p.255, figs 31 (holotype, from 56˚45’N, 137˚27’W; May, surface-water, 32).

**Description:** Cells 2.4-2.8µm in diameter. Central area of plates smooth, without papillae or conspicuous areolation. Shield plates 1.3-1.6µm in diameter, with raised marginal rim and inverted cone or small arch at centre. Largest of the girdle plates about 1.8-3.7µm in length, with wing extending distally 2.0-2.5µm. Each girdle plate has a central spine or two spines, one near each end of the plate. Spines are buttressed on the dorsal side. Girdle plates interlock. Arms of dorsal plate, 1.4-1.5µm long, with slightly rounded or somewhat squarish ends and with a triradiate keel, bifurcate at one end. Ventral plate convex, ca.2.1-2.4µm in diameter, with an incomplete mid-radius circular ridge and a slightly raised central mound. Marine.

**Note:** This taxon has been recorded in various studies and it always appears to have one girdle wing longer than the others. However, whether the bifurcation at one end of the dorsal plate keel is always aligned in the same way is not known as yet. The type, *f. laevis*, has also been recorded from the Gulf of St. Lawrence, as *T. aff. T. laevis* (Bérard-Therriault *et al.*, 1999, pp.246-247, pl.113f). *T. laevis* now has a number of subspecific taxa affiliated to it, which share several key characters, but studies have shown that the ventral plate ornamentation is a good separation characteristic for this group.

**Biogeography (this study): NW Pacific - St. KNOT (August, 1999, KH99-3; January, 2000, MR00K01); NE Pacific - NP16; Japan Sea - MR06-04 St.3; Bering Sea - MR06-04 St.23, MR06-04 St.24.**

**Triparma laevis Booth in Booth & Marchant f. inornata**

f. nov.
Pl.6, figs 1-7


**Etymology:** *Inornatus* (L.) meaning unadorned, in reference to the relatively plain girdle plates and lack of plate spines.

**Cellula 2.2-2.7µm diametro. Laminae expolitae, areolae vel papillis carentes. Laminae parmae 1.4-1.8µm diametro, convexae, conicae, habens flabella alia centrica. Laminae oblongae 1.9-2.3µm longitudo, carinam ala similis, spinae carente. Laminae dorsi alae brachii i.5-1.6µm longitudo, fere rotundis extremis, carina triradiata non furcata. Laminae ventralis convexae, circa 2.1µm diametro, flabella alia centrica praeente. Planctonica marina, ad 60˚N, 179˚W (Mare Bering). Iconotypus: EM Stub BS062430. Iconotypus: Lamina 6, Figura 1.

**Description:** Cells 2.2-2.7µm in diameter. All plates smooth, without areolae or papillae. Shield plates ca.1.4-1.8µm in diameter, convex, conical with a raised flap at the centre. Oblong girdle plates ca.1.9-2.3µm long, with a single keel-like wing, lacking spines. Arms of dorsal plate ca.1.5-1.6µm long, with slightly rounded ends, triradiate keel not forked. Ventral plate somewhat domed, ca.2.1µm in diameter, with raised flaps in the centre. Marine, in plankton at 60˚N, 179˚W, Bering Sea (St.24, 30m).

**Holotype:** EM Stub BS062430 (specimen in Pl.6, fig.1).

**Note:** Until now, the other described subspecific taxa of *T. laevis* have all possessed some sort of ornamentation; f. *laevis*, f. *mexicana* (Kosman) Hernández-Becerril & Bravo-Sierra and f. *longispina* have wings, subsp. *pinatilobata* Marchant and subsp. *ramispina* Marchant have plate spines. However, a somewhat similar form was seen in Antarctica, but the specimen had “a slightly taller triradiate plate keel and heavier wings on the girdle plates” (Booth & Marchant, 1987, p.255, fig.33).
Plate 6

*Triparma laevis* f. *inornata*

1. Close-up of dorsal plate. Bering Sea, St.23, 30m. Holotype

2. Ventral view showing ventral plate (v). Sea of Okhotsk, St.7, 30m

3. Cell wall showing girdle (g), shield (s) and dorsal (d) plates (ventral plate not visible). Bering Sea, St.24, 30m.

4. Note plate junctions. Sea of Okhotsk, St.4, 30m

5. Note plate junctions. Sea of Okhotsk, St.4, 30m

6. Note plate junctions. Bering Sea, St.23, 10m

7. Note unusual shield plate. N Pacific, KH99-3 St.17, 50m
Biogeography (this study): Sea of Okhotsk - MR06-04 St.4, MR06-04 St.7; NW Pacific - St. KNOT (August, 1999, KH99-3), KH99-3 St.17; Bering Sea - MR06-04 St.23, MR06-04 St.24.

Triparma laevis Booth in Booth & Marchant f. longispina f. nov.
Pl.7, figs 1-9


Etymology: Longus (L.) meaning long, spina (L.) meaning spine, in reference to the long spine on one of the girdle plates.

Cellula 2.8-3.2µm diametro. Laminae expolitae, areolae vel papillis carente. Laminae parmae 1.6-2.2µm diametro, convexae, conicae, habens crater centrico. Laminae oblongae 2.8-3.2µm longitudo, cum ala 0.6-1.0µm latitudo, margines alam irregularis. Utraque ala cum spina anteride et flabella centrica. Laminae obscenta 1.3-2.2µm longitudo, fere rotundis extremis, carinae triradiatae et bifurcatae. Laminae ventralis convexa, 2.5-3.2µm diametro, habens una flabellum centra et alter in annulus. Planctonica marina, ad 59˚N, 179˚W (Mare Bering). Holotypus, hic designatus: EM Stub BS991650. Iconotypus: Lamina 7, Figura 3.

Description: Cells 2.8-3.2µm in diameter. All plates smooth, without areolae or papillae. Shield plates ca.1.6-2.2µm in diameter, convex, conical with a crater at the centre. Oblong girdle-plates ca.2.8-3.2µm long, with a single wing 0.6-1.0µm wide, wing margin irregular. Each wing with a buttressed spine, one of which is very long (up to 11µm), bifurcated at the end. Arms of dorsal plate ca.1.3-2.2µm long, with slightly rounded ends, triradiate keel forked at each end. Ventral plate somewhat domed, ca.2.5-3.2µm in diameter, with raised flaps in a mid-radius ring, and one flap in the centre. Marine, in plankton at 59˚N, 179˚W, (Sea of Okhotsk).

Holotype: EM Stub BS991650 (specimen in Pl.7, fig.3).

Note: This form was mentioned in Booth & Marchant (1987, p.256) as resembling the Antarctic taxon T. laevis subsp. pinnatifidobata, and in Booth et al. (1981) as being similar to Cyst V (= T. laevis). Whilst f. longispina is clearly related to T. laevis, it is quite distinct from the other subspecific taxa, with its single, long girdle-spine and unique ventral-plate ornamentation.

Biogeography (this study): Sea of Okhotsk - MR06-04 St.7; NW Pacific - St. KNOT (August, 1999, KH99-3), KH99-3 St.17; Bering Sea - KH99-3 St.16, MR06-04 St.23, MR06-04 St.24.

Triparma strigata Booth in Booth & Marchant
Pl.8, fgs 1-10

2003 Triparma strigata Booth: Tanimoto et al., pl.3, fig.3.

Description: Cells 2.2-2.8µm in diameter. All plates slightly convex with central area characterised by tubular processes, 0.2-0.3µm long, sometimes straight or forked, ca.6-7 processes/µm (Pl.8, fgs 4, 6). Plates lack central-area structure. Shield plates ca.1.3-1.9µm in diameter. Each girdle plate ca.1.5µm in length, with two straightish spines, one at each end of the plate, directed at a diverging angle. Spines ca.0.8-6.2µm long and bifurcate at the ends. Junction between adjacent girdle plates uncertain. Arms of dorsal plate ca.1.1-1.5µm long, with squared off ends. Dorsal plate without a keel, although some of the processes are aligned in an identical position to the keels of other species (Pl.8, fgs 1, 7, 9, 10). Other processes on the dorsal plate are arranged along the plate margin (Pl.8, fgs 7, 9, 10). Ventral plate ca.1.9-2.1µm in diameter. Plate boundaries sometimes indistinct. Marine.

Note: Although their cell and plate dimensions are smaller, the subarctic Pacific and Bering Sea specimens are otherwise indistinguishable from those illustrated from the Antarctic. However, our specimens exhibit a range of morphologies. In particular, the length of the girdle spines; some being very short (Pl.8, fig.3), others much longer (Pl.8, fig.5). In this study, all of the specimens appear to bear straight spines, although the spines were usually broken and so we did not see any spines with bifurcate ends (see Booth et al., 1981, fig.27). In contrast, specimens from the Gulf of St. Lawrence, Canada, exhibited either straight or twisted spines (Bérard-Therriault et al., 1999, p.246, pl.113b, c, respectively), while Kosman et al. (1993, figs 33-37, as T. cf. T. strigata) showed an Antarctic form, which bore shorter girdle-plate spines and shorter plate processes than those specimens attributable to T. strigata from both polar regions. Furthermore, an intriguing specimen from the subarctic lacked girdle-plate spines altogether (fig.42 in Booth & Marchant, 1987), while a specimen supposedly with mixed Tetraparma/Triparma features has also been illustrated (fig.30 of Booth et al., 1981; also shown as fig.43 in Booth & Marchant, 1987). Another area of variability is the central area. The holotype specimen (Booth & Marchant, 1987) has a shield plate with a centrally raised structure, as compared to our specimens, which have a more gradually-sloped central area (Pl.8, fgs 9, 10). The plate junctions of this form were clearly visible and showed that the ends of the dorsal plate were slightly rounded and fitted into a correspondingly-shaped notch on the girdle plate (Kosman et al., fig.33). On the other hand, the girdle plates seemingly abutted with each other (Kosman et al., fig.35).

Biogeography (this study): Sea of Okhotsk - MR06-04
Plate 7

*Triparma laevis* f. *longispina*

1. Cell wall showing girdle (g), shield (s) and dorsal (d) plates (ventral plate not visible). Bering Sea, St.24, 30m

2. Ventral view showing ventral plate (v). Bering Sea, St.23, 0m

3. Note one long, bifurcate girdle spine. Bering Sea, KH99-3 St.16, 50m. Holotype

4. Bering Sea, St.23, 30m

5. Note girdle plate with long spine. N Pacific, KNOT St.1, 125m

6. Bering Sea, St.24, 0m

7. Ventral view. Bering Sea. Ventral plate, girdle view. N Pacific, KNOT St.1, 100m

8. Ventral plate and junctions with girdle plates. Bering Sea, St.24, 100m
New taxa of subarctic Parmales

Plate 8

Triparma strigata

Cell wall showing girdle (g), shield (s) and dorsal (d) plates (ventral plate not visible). N Pacific, KNOT St.1, 100m

Ventral view showing ventral plate (v). Bering Sea, St.24, 30m

Ventral view showing ventral plate. Sea of Okhotsk, St.4, 30m

Cell wall with two long girdle spines (arrowed). Bering Sea, St.23, 30m

Close-up of Fig.5. Note plate processes are bifurcated

Cell wall with one shield plate missing. Bering Sea, St.24, 0m

Cell wall with one shield plate displaced. Note thinness of plates. Bering Sea, St.25, 30m

Cell wall with one girdle plate visible (arrowed). Bering Sea, St.24, 50m

Cell wall with two girdle plates visible (arrowed). Bering Sea, St.24, 30m
1980 Siliceous cyst Booth et al.: fig.1(5).
1981 Cyst I Booth et al.: p.63, figs 3-8, 63-64.
1987 *Triparma verrucosa* Booth in Booth & Marchant: p.258, figs 44 (= holotype, from 57°N, 141°W; May, surface-water), 45.

**Description:** Cells 2.7-3.1µm in diameter. All plates slightly convex with radiating papillae, ca.10-15 papillae/µm (Pl.9, fig.1). On the shield and ventral plates, a number of papillae are enlarged, some of which form a complete or incomplete mid-radius ring. The ventral plate may have another ring near the margin (Pl.9, fig.2). Circular plates lack central-area structure. Shield plates ca.1.7-1.8µm in diameter. Each girdle plate 1.7-2.1µm in length, with two straightish spines, up to ca.7µm long, one at each end of the plate, directed at a diverging angle. Narrow wing margin usually straight, occasionally crenulate. Girdle-plate papillae in rows perpendicular to the wings, adjacent plates interlock by alternating rounded and notched ends. Arms of dorsal plate ca.1.4-1.5µm long, with squared off ends. Dorsal plate with keel, both ends of keel forked (Pl.9, figs 1, 6). Dorsal plate papillae in rows perpendicular to plate arms. Ventral plate ca.2.3-2.8µm in diameter. Marine.

**Note:** In the original description of this species, Booth & Marchant (1987) mentioned that the spines on the girdle plates are ca.5µm long, however, those on one of our specimens shown here are considerably longer (see Pl.9, fig.3). Furthermore, a specimen from St. KNOT (collected in August, 1999), not shown here, had a girdle spine with a bifurcate end. However, this specimen photographed in ventral view had a different ventral plate morphology to those shown here. Our observations appear to be the first record of this species on the western side of the Pacific and in the Sea of Okhotsk.

**Biogeography (this study):** Sea of Okhotsk - MR06-04 St.6, MR06-04 St.7; NW Pacific - St. KNOT (August, 1999, KH99-3).

### 4. Discussion

#### 4.1 New taxa

In this study, a total of 10 taxa were encountered in our samples, six of which are formally described as new. As a result, most Parmales in the subarctic Pacific region can now be identified with a higher degree of confidence. However, some of these described taxa are in need of further observations (*e.g.* the appearance of the ventral plate of *Triparma columacea* f. *convexa* is currently unknown).

Also, several subarctic taxa previously featured by other workers were absent from our samples (*e.g.* *Triparma columacea* f. *columacea*, *T. retinervis* and *T. retinervis* subsp. *crenata*). Despite this, we believe that great progress is being made on the taxonomy of this understudied, yet significant, group of phytoplankton, and we are now in a better position to carry out detailed seasonal and biogeographic studies using our extensive sample collection. Additional studies are currently being undertaken in the Antarctic, where similar taxonomic uncertainty exists, and so it is hoped that the true diversity of this group may be realised in the near future. In an attempt to hasten this process, an annotated checklist of Parmales taxa is presented below, which includes undescribed taxa and those potentially cryptic taxa which are currently considered to have a bipolar distribution.

#### 4.2 Checklist of extant and fossil Parmales

Class Chrysophyceae Pascher, 1914


*Pentalamina* Marchant in Booth & Marchant, 1987

*P. corona* Booth & Marchant, 1987


*P. pelagica* Booth & Marchant, 1987


Siliceous microorganism *sensu* Nishida, 1987

Siliceous cyst *sensu* Silver et al., 1980, fig.38

Enigmatic siliceous cyst *sensu* Stradner & Allram, 1982


*Triparma columacea* subsp. *alata* Marchant in Booth & Marchant, 1987

*Triparma columacea* Booth in Booth & Marchant, 1987 f. *columacea*

*Triparma columacea* f. *convexa* Konno et al., 2007

*Triparma columacea* f. *fimbriata* Konno et al., 2007

*Triparma* Booth & Marchant, 1988

*Triparma* *laevis* subsp. *laevis* (Antarctic form) *sensu* Booth & Marchant, 1987

*Triparma* *laevis* Booth in Booth & Marchant, 1987 f. *laevis*

*Triparma* *laevis* Booth in Booth & Marchant, 1987 f. *laevis*


*Triparma* *laevis* subsp. *pinnatilobata* Marchant in Booth & Marchant, 1987

*Triparma* *laevis* f. *longispina* Konno et al., 2007

*Triparma* *laevis* f. *mexicana* (Kosman in Kosman et al., 1993)

Hernández-Becerril in Bravo-Sierra & Hernández-Becerril, 2003

*Triparma* *laevis* f. *laevis* Booth in Booth & Marchant, 1987 f. *laevis*

Hernández-Becerril in Bravo-Sierra & Hernández-Becerril, 2003

*Triparma* *laevis* f. *laevis* Booth in Booth & Marchant, 1987 f. *laevis*

Hernández-Becerril in Bravo-Sierra & Hernández-Becerril, 2003

*Triparma* *laevis* f. *laevis* Booth in Booth & Marchant, 1987 f. *laevis*

Hernández-Becerril in Bravo-Sierra & Hernández-Becerril, 2003

*Triparma* *laevis* f. *laevis* Booth in Booth & Marchant, 1987 f. *laevis*
New taxa of subarctic Parmales

Plate 9

_Triparma verrucosa_

1. Cell wall showing girdle (g), shield (s) and dorsal (d) plates (ventral plate not visible). Sea of Okhotsk, St.6, 30m

2. Ventral view showing ventral plate (v). Sea of Okhotsk, St.6, 30m

3. Specimen with long girdle spines. N Pacific, KNOT St.2, 60/70m

4. Ventral view with ventral plate inside collapsed cell. Note girdle-plate junctures (arrowed). Sea of Okhotsk, St.7, 30m

5. Collapsed cell in ventral view. Sea of Okhotsk, St.7, 30m

6. Cell in dorsal view. Note notch in girdle plate (arrowed). Sea of Okhotsk, St.7, 30m
T. laevis subsp. ramispina Marchant in Booth & Marchant, 1987

T. retinervis subsp. crenata Booth in Booth & Marchant, 1987

T. retinervis Booth in Booth & Marchant, 1987 subsp. retinervis

T. strigata Booth in Booth & Marchant, 1987

T. verrucosa Booth in Booth & Marchant, 1987

Sp. indet. F sensu Iwai & Nishida, 1976

Spined forms of Triparma spp. sensu Kosman et al., 1993

Cysts of uncertain affiliation

Unidentified species of Parmales sensu Tanimoto et al., 2003

Cyst 3D sensu Takahashi et al., 1986

Cyst 3A sensu Takahashi et al., 1986

Cyst 3B sensu Takahashi et al., 1986

Cyst 4C sensu Takahashi et al., 1986

Taxonomic notes

1 Pascher (1914) was the first person to erect the Class Chrysophyceae, and since then it has been emended many times as groups of taxa were removed or added (e.g. Christensen, 1962; Hibberd, 1976). Here, we follow the stance taken by Kristiansen & Preisig (2001), in which Chrysophyceae sensu lato is retained, and in which the Order Parmales can be included.

2 Previously recorded as ‘Cyst 4A’ by Takahashi et al. (1986, figs 17, 18), and also illustrated by Silver et al. (1980, figs 1C, E) and Buck & Garrison (1983, fig.35) from Antarctic waters.

3 Replaced original family name, Octolaminaceae Booth & Marchant, 1987, which was invalid since it was not based on a generic name (ICBN Art.18.17: Voss et al., 1983 Edition).

4 Only reported from the Gulf of Tehuantepec, Mexican Pacific (Bravo-Sierra & Hernández-Becerril, 2003).

5 Presently considered to be bipolar, however, some variation has been noted (Booth & Marchant, 1987). The holotype from the Antarctic has spines, as do most specimens in the subarctic Pacific (e.g. Iwai & Nishida, 1976, pl.II, fig.2, as Sp. indet. B; Tanimoto et al., 2003, pl.3, fig.5), while some specimens in the subarctic Pacific lack them (e.g. Iwai & Nishida, 1976, pl.II, fig.3, as Sp. indet. C; Nishida, 1979, pl.1, fig.4, as Genus & species indetiminable and Indet. B). Future studies may show that specimens from the subarctic belong to a cryptic species, but in the meantime the name T. pelagica should be used.

6 This form, illustrated by Iwai & Nishida (1976, pl.II, fig.7), resembles T. gracilis, but differs in possessing cross-shaped central spines. Clearly, more specimens are needed before this taxon can be formally described.

7 This form, illustrated by Nishida (1986, pl.1, fig.4) and Konno & Jordan (2007, fig.4), also resembles T. gracilis, but differs in having shorter, more pointed central spines.

8 This form slightly resembles T. insecta, but has highly-domed circular shields, with a small papilla on top. It was recorded in a towed net sample from 2800m water-depth in the eastern equatorial Pacific (Silver et al. 1980, fig.3). It appears to have a cell wall composed of shield and triradiate plates, and so belongs in the genus Tetraparma.

9 Specimens of an ‘enigmatic siliceous cyst’ found in Middle-Late Quaternary sediments off Mexico (Stradner & Allram, pl.1, figs 1-4) resemble the form found by Silver et al. (1980), but differ in having a raised structure with straighter edges, on top of which there is a papillate hump. This form appears to have a cell wall composed of shield and triradiate plates, and so should be placed in the genus Tetraparma.

10 The holotype specimen of T. columacea, and other specimens from the type material (subarctic Pacific), have flattened shield plates, while those from Finland and Denmark (Kosman et al., 1993, figs 17-23) have convex centres. Specimens of the latter differ from T. columacea f. convexa by having a much more bulky and less spherical cell-shape due to strongly keeled girdle-plates.

11 Booth & Marchant (1987, fig.33) showed a specimen of T. laevis subsp. laevis from the Antarctic. However, its girdle plates lacked the extended wings which characterise the holotype. Konno & Jordan (2007, figs 5, 6) showed two more specimens from the Antarctic, as T. laevis f., one of which possessed a different ventral plate than that of T. laevis f. laevis. This taxon (or taxa) needs to be examined more thoroughly.

12 Originally described from the Sea of Cortez as T. laevis subsp. mexicana Kosman (Kosman et al., 1993, figs 1-10).

13 T. strigata was originally described from the Antarctic (Booth & Marchant, 1987, figs 40, 41), although similar specimens had previously been recorded from the subarctic (Booth et al., 1980, 1981). A spineless form was also found in the subarctic (Booth & Marchant, 1987, fig.42), and a specimen with twisted spines was illustrated from the Gulf of St. Lawrence (Bérard-Therriault et al., 1999, pl.113c), but these are not considered here to be separate taxa. Also, it is not possible to separate the Northern and Southern Hemisphere specimens on purely morphological grounds, and so for the time being the name T. strigata should be used.

14 Iwai & Nishida (1976, pl.II, fig.6, as Sp. indet. F) illustrated a specimen from 50˚20’N, 178˚56’E that had an elongate central process on each shield plate.

15 Cyst II of Booth et al. (1981, figs 9-16, 21) included specimens with and without long girdle spines. Later, Booth & Marchant (1987, figs 23, 24, 27, 28) described T. retinervis subsp. crenata, based on the spineless forms, but noted that a “form of Triparma retinervis subsp. crenata with spines” also existed (p.253, fig.29). Kosman et al. (1993, figs 24-28) illustrated spine-bearing specimens of Triparma spp. from California and Antarctica, while isolated scales, called ‘pulvinate siliceous structures’, previously featured by Norris (1971, pl.2, figs 10-13; pl.3, fig.14) from the Indian Ocean, may belong to a similar taxon.
A spiny form first illustrated by Tanimoto et al. (2003, pl.3, fig.1) from NP38 (east of the Tsugaru Strait), was found in the surface-waters of the Soya Strait (MR06-04 St.3) in this study. Although Tanimoto et al. (2003, p.102, pl.3, fig.1) referred to it as an “unidentified species of Parmales”, it has overlapping monomorphic scales, and so lacks the dimorphic or polymorphic interlocking plates characteristic of all Parmales genera.

17 Cyst 3D, from the Kita-no-seto Strait near Syowa Station in Antarctica (Takahashi et al., 1986, pl.3, fig.14), appears to be related to the Parmales (Booth & Marchant, 1987). In particular, the bottom left specimen has lost one of its ‘shield’ plates, and the resulting view of the flange looks similar to that seen in specimens of Parmales.

18, 19 Cyst 3A and Cyst 3B, from the Kita-no-seto Strait near Syowa Station in Antarctica (Takahashi et al., 1986, pl.2, figs 9, 10 and 11, 12 respectively) may or may not be related to the Parmales (Booth & Marchant, 1987). This uncertainty is due to the fact that the ‘cysts’ comprise two hemispherical parts, supposedly with flattened bottoms (only their pl.2, fig.12 shows what appears to be a dimpled apex), and a narrow flange. Cyst 3B also has long, tapering spines associated with it. Clearly, more specimens are needed to elucidate the true nature of these ‘cysts’, but all the Parmales known so far have five or eight plates, with two to four plate types that are morphologically different.

20 Booth & Marchant (1987) believed that Cyst 4C of Takahashi et al. (1986, figs 22, 23) belongs to an undescribed species of Pentalamina, but since then no one has reinvestigated this form. The cell wall appears to be composed of three round plates and two triradial plates.

4.3 Biogeographic distribution of subarctic taxa

Photographic data from the subarctic Atlantic is rather sparse, limited to isolated sampling points in the Gulf of St. Lawrence (Bérard-Therriault et al., 1999), Gulf of Bothnia in Finland (Thomsen, 1986; Kosman et al., 1993), Great Belt in Denmark, and Disko Bay in Greenland (Kosman et al., 1993). Consequently, biogeographic maps encompassing only the subarctic Pacific and its marginal seas were compiled for each taxon, using data from the literature as well as that generated during this study (Figure 2). Although this dataset is also limited, it is clear that many of the taxa are distributed across the subarctic zone, whilst others appear poorly distributed due to their rarity and the paucity of samples analysed for Parmales.

5. Conclusions

In this study, ten taxa of Parmales have been recorded and illustrated from the subarctic Pacific and its marginal seas, including the descriptions of six new taxa. As a result of these additions, a checklist of all Parmales has been presented, with the aim of providing some stimulus for further taxonomic research. Using the data collected thus far, biogeographic maps of each taxon have been compiled for the study area. Perhaps from now on, detailed ecological studies can be carried out with greater taxonomic certainty.

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Figure 2: Biogeographic distribution of subarctic Parmales taxa in the North Pacific and its marginal seas, including taxa not reported in this study. Maps created using M. Weinelt’s ‘Online Map Creation’ site at www.aquarius.ifm-geomar.de
New taxa of subarctic Parmales

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