

Proxy development: a new facet of morphological diversity in the marine diatom *Eucampia antarctica* (Castracane) Mangin

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ABSTRACT – The varied aspect ratios observed in the Antarctic marine diatom *Eucampia antarctica* are described and quantified. Data are compiled from detailed measurements of the gross morphology of winter stage specimens found in samples of modern marine sediments. Surface sediment samples come from a range of oceanographic settings spanning almost 20° of latitude from north of the Polar Front in the SW Atlantic to close to continental Antarctica in the southern Amundsen Sea. Results are compared with previously recorded morphological data ascribed to the polar and sub-polar varieties of *E. antarctica* (*E. antarctica* var *recta* and *E. antarctica* var *antarctica*) and reveal that the aspect ratio of both varieties responds independently of symmetry and colony structure. The discussion considers the likely basis of the observed aspect ratio distribution and whether the morphological diversity offers any potential for use as proxy evidence in Antarctic palaeoceanographic reconstructions. Although it requires further study, valve symmetry offers promising potential as a quantitative proxy for austral summer sea surface temperatures.

KEYWORDS: morphology, marine diatom, Antarctic, *Eucampia antarctica*, palaeoceanographic proxy

INTRODUCTION

Palaeoclimatic reconstructions are an essential component of climate research, revealing the Earth's varied climatic history and providing the empirical data for testing the validity of modelled climate systems. Developing our understanding of existing proxies and assessing the potential of new proxies is an important aspect of this research. In the Southern Ocean where carbonate preservation is scarce, diatoms are particularly useful for palaeoclimatic/palaeoceanographic reconstructions as they are diverse, abundant and well preserved. Although diatom-based reconstructions rely principally on species relative abundance data, previous studies have provided good evidence that infraspecific morphological variation ('polymorphism') can be used as an additional palaeoenvironmental proxy (Fryxell, 1988; 1994; Cortese & Gersonde, 2007).

Although few Antarctic diatoms produce true resting spores, summer/winter and cold/warm water forms appear to be common amongst Antarctic diatom species and are usually morphologically distinct. These growth forms are probably an important adaptation to survive the extreme seasonality of the polar regions and transitions between these growth forms (resting spores, winter/summer, cold/warm water forms) are likely to be environmentally triggered (Palmisano & Sullivan, 1983; Doucette & Fryxell, 1985; Ligowski *et al.* 2012). Studies have already shown the proxy potential of these growth stages in several Antarctic marine diatoms (Leventer *et al.* 2002; Taylor & Sjunneskog, 2002). Nitrogen depletion is suggested as an important resting state trigger for *Thalassiosira antarctica* Comber and *Chaetoceros* Ehrenberg subgenus *Hyalochaete* Gran (Peters & Thomas, 1996; Ishii *et al.* 2011) whilst in other species, temperature, salinity, nutrient availability and light intensity may be the principal controls over different growth forms. The warm- and cold-water forms of *T. antarctica* are morphologically distinct, with different areolae sizes, cell size-range and silicification, that have been related to water temperature and ice formation and yield additional proxy tools for Antarctic palaeoceanographic reconstructions (Villareal & Fryxell, 1983; Doucette & Fryxell, 1985; Buffen *et al.* 2007).

Morphological variety in the endemic Antarctic marine diatom *Eucampia antarctica* already provides a useful palaeoceanographic tool of relative temperature. Fryxell (1991) shows that the two morphologically distinct varieties *E. antarctica* (Castracane) Mangin var *antarctica* and *E. antarctica* var *recta* (Mangin) Fryxell & Prasad inhabit different oceanographic regions. The nominate variety, characterized by long chains (10+ cells) of asymmetrical valves, is found in the sub-polar plankton and sediments north of the Polar Front, whilst *E. antarctica* var *recta*, with short chains (typically 2–4 cells) of symmetrical valves, inhabits areas within the seasonal sea-ice zone and cold waters close to the Antarctic continent. Down-core variations in the ratio of the two varieties are used to infer relative temperature change. Fryxell (1991) also suggests that the aspect ratio of the *E. antarctica* valves is a feature of the same phenotypic response. Here I present morphological evidence from a range of sites throughout the Antarctic Peninsula (AP) and Scotia Sea to assess whether the aspect ratio varies in tandem with temperature and matches the changes in gross colony morphology.

Previous studies

Polymorphism is recognized in many diatoms and may reflect greater genetic diversity within a morphologically defined species (morphotype) (Beszteri *et al.* 2007; Pouličková & Hašler, 2007; Bruder & Medlin, 2008; Balzano *et al.* 2011). The most common and obvious changes occur in the valve structure and ornamentation, such as the valve shape and size, valve symmetry, silicification and areolation pattern. Changes in the cell morphology over time may be in response to environmental or evolutionary conditions. Morphological changes over long time periods ($\geq 10^5$ years) are attributed to evolutionary adaptation, whilst morphological transformations over short time frames ($\leq 10^4$ years) are more likely to be a response to environmental dynamics, e.g. variations in temperature, salinity, nutrient or light availability. Where an organism is able to alter its observable characteristics in response to a change in the environment, it is referred to as 'phenotypic

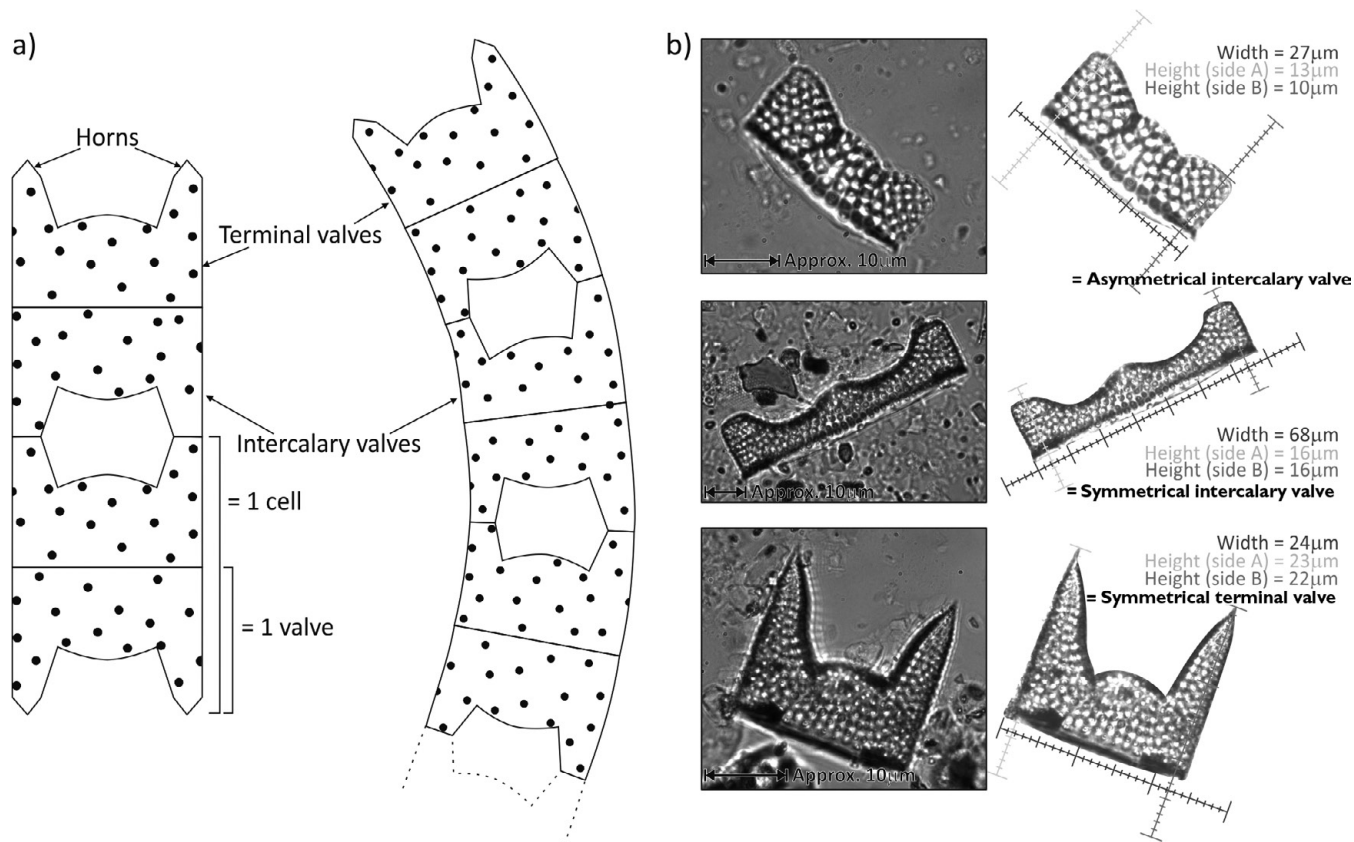


Fig. 1. Morphological structure and measurements. (a) Schematic drawing of colony structures of *Eucampia antarctica* indicating position of terminal and intercalary valves. The straight colonial form with symmetrical valves (left) is *E. antarctica* var. *recta* and the curved form comprised of asymmetrical valves (right) is *E. antarctica* var. *antarctica* (after Whitehead *et al.* 2005). (b) Illustration of valve measurements taken from light microscope images from different shaped *Eucampia antarctica* valves.

plasticity' and it is this type of polymorphism that holds the most potential for developing morphological proxies.

Several studies show that environmental conditions exert control over various aspects of valve morphology. In one of the early culture studies, Paasche *et al.* (1975) show that changing salinity causes variation in osmotic pressure that affects the length of siliceous processes in *Skeletonema subsalsum* (A. Cleve) Bethge. Similarly, Cattaneo *et al.* (2004) note a strong statistical relationship between valve length and metal contamination in diatoms from Lac Dufault (Québec, Canada). More recently, Balzano *et al.* (2011) investigated the impact of variable salinity across ten strains of *Skeletonema* and found evidence of morphological responses and diverse tolerances, even within species. These studies are usually concerned with monitoring water quality and understanding the potential legacy of pollution, so rarely include Antarctic diatom species.

Eucampia antarctica

E. antarctica exhibits heteromorphy related to both cell position within the colony and environmental responses (Fryxell & Prasad, 1990). Fryxell (1991) summarizes observations of *E. antarctica* prior to 1991 and describes the two morphological variants of *E. antarctica* (var *antarctica* and var *recta*) in the context of their distribution in the waters and sediments of the Kerguelen Plateau

and Prydz Bay. *E. antarctica* var. *recta* has symmetrical valves that create straight chains, short colonies (Fig. 1a), and is considered the 'true polar' variety associated with extremely cold, ice-covered waters and areas close to the continent. *E. antarctica* var. *antarctica* is characterized by asymmetrical valve shapes that produce spiralling chains (Fig. 1a) that tend to have many more cells than the colonies of the 'recta' variety. *E. antarctica* var. *antarctica* is found in association with warmer waters of the Polar Front Zone (PFZ) and Subantarctic Zone (SAZ). In both varieties the terminal valves are distinguished by pointed 'horns' in contrast to the flattened horns found on the intercalary valves (Fig. 1a). The ratios of terminal and intercalary valves of the summer and winter forms are used to estimate colony length and rates of cell division and are found to be consistent with the environmental associations inferred from the cell symmetry (Fryxell, 1991; Kaczmarek *et al.* 1993). Fryxell (1991) also calculates valve volumes for the two samples and notes that, together, the valve widths and volumes form a continuum rather than two independent populations, with valves from Prydz Bay expanded in the upper size range. Fryxell (1991) suggests that the larger cell size of the polar variety is another distinctive feature of the *E. antarctica* var. *recta* morphotype. Although the ratio of *E. antarctica*'s valve symmetry and colony structure is now used in palaeoceanographic studies as a proxy for relative sea surface temperature (SST) (Leventer *et al.*

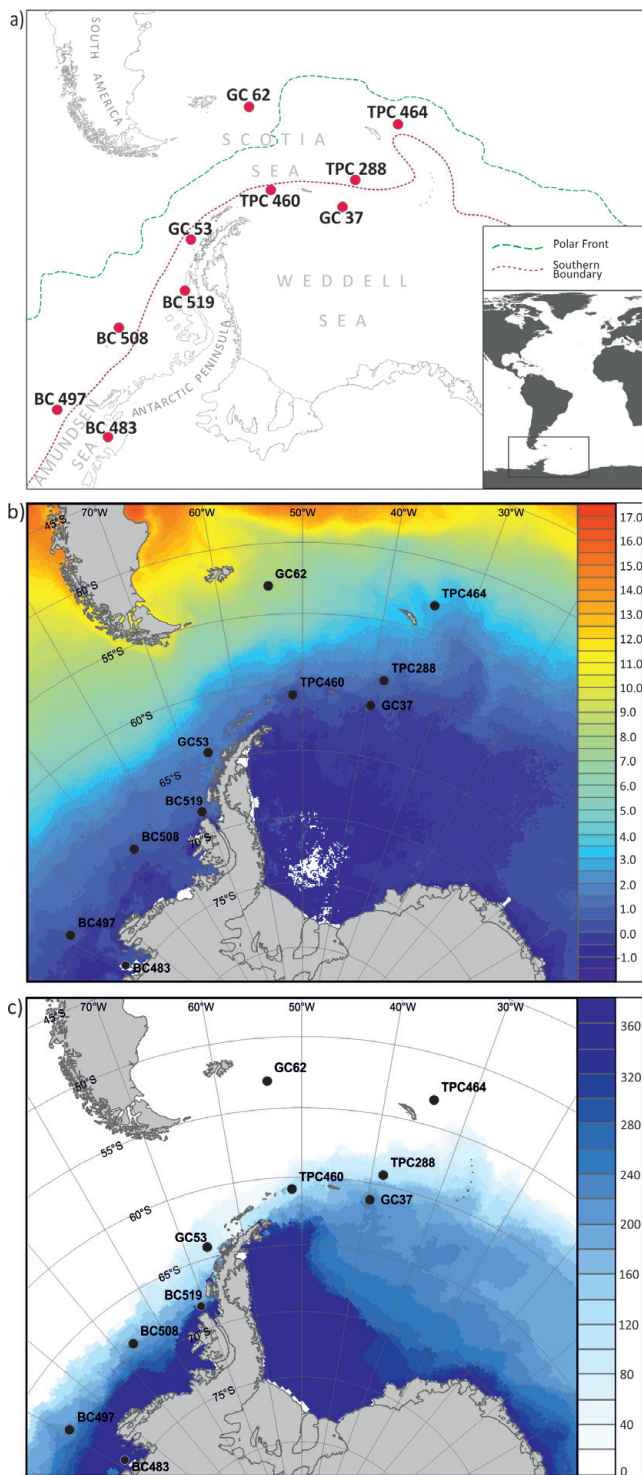


Fig. 2. Location maps. (a) Map of sample sites for *Eucampia antarctica* morphometric study. (b) Average summer sea surface temperatures (SST) for the Antarctic Peninsula region compiled from MODIS SST data. The seasonal climatology comprises daily averaged data for the months of mid-December to mid-March for the years 2002 to 2012 (Feldman & McClain, 2012). (c) Mean sea-ice duration data (days per year) are calculated from daily remote-sensed readings that have been averaged into monthly mean values and then into a single grid for the period 1979–2007.

2002; Milliken *et al.* 2009), the ecological significance of *E. antarctica*'s relative abundance remains ambiguous. The down-core pattern of *E. antarctica*'s relative abundance is notably consistent throughout the Southern Ocean and Burckle (1984) shows how it provides a useful chronostratigraphic marker for glacial–interglacial time frames in Southern Ocean sediments where dating is often problematic. The temporal and spatial distribution of peak *E. antarctica* relative abundances led Burckle (1984) to propose that high abundances are associated with coastal conditions and melting icebergs, whilst Kaczmarek *et al.* (1993) and Whitehead *et al.* (2005) advocate a link with winter sea-ice extent. Burckle's (1984) assertion of a 'pseudoneritic' habitat for *E. antarctica* is gaining credence as authors recognize the potential links with nutrient (more specifically iron) availability and melt-water-induced buoyancy (Mohan *et al.* 2006; Armand *et al.* 2008; Salter *et al.* 2012). Although I will briefly discuss the ecological implications of *E. antarctica*'s pattern of relative abundance, the focus is primarily on assessing the morphological proxies.

In addition to the valve symmetry and colonial position of *E. antarctica* valves, the heights and widths of *E. antarctica* valves will be measured to assess whether or not the two morphological varieties exhibit distinct aspect ratios, as originally suggested by Fryxell (1991). Examining the data geographically, I will assess if there is a trend in the distribution of distinctively shaped valves and whether their distribution matches the trends of symmetry and colony structure already identified by previous authors or offers an independent facet of morphological diversity in *E. antarctica* valves.

MATERIALS AND METHODS

Box (BC), Trigger (TPC) and Gravity (GC) cores collected aboard the British Antarctic Survey vessel RRS *James Clark Ross* during research cruises to the Scotia Sea and AP between 1990 and 2008 were selected to represent a wide range of ocean and climate conditions in order to capture the greatest variability in morphological response. The ten core sites chosen for the study (GC 62, TPC 464, TPC 288, GC 37, TPC 460, GC 53, BC 519, BC 508, BC 497 and BC 483) span from north of the PFZ to the continental coast and cover a broad spectrum of temperature, light and sea-ice regimes (Fig. 2; Table 1).

Site GC 62 is in the SAZ at the western end of the Falkland Trough in waters 3000m deep and is located north of both the maximum extent of sea-ice and the PFZ. TPC 464 is also situated north of the maximum sea-ice limit but lies within the present day PFZ. The majority of the cores (TPC 288, GC 37, TPC 460, GC 53, BC 519; BC 508 and BC 497) are all south of the PFZ with varying exposure to seasonal sea-ice and covering a depth range from 495 m to 4229 m. BC 483 lies furthest to the south and closest to continental Antarctica (Fig. 2; Table 1). Sediments from the sites comprise diatom-bearing muds and diatomaceous muds, with varying contributions of foraminifera, radiolarians and sponge spicules. Terrigenous content is highest close to the continent at sites BC 483 and BC 519 and lowest at sites in the central Scotia Sea and NE Georgia Rise – TPC 288 and TPC 464.

Surface sediment samples from each of the cores were analysed for diatom assemblages and *Eucampia antarctica* morphometric data. Sediments were dried thoroughly in a warm oven at c.30 °C; then 5–200 mg of bulk sediment was sub-sampled into

Table 1. List of core samples with associated geographical and environmental data referred to in the text

Core	Latitude	Longitude	Water depth (m)	Core length (m)	Summer SST (°C)	Sea-ice cover (days per year)
GC 62	-52.925	-53.6833	3000	3.4	8.0	0
TPC 464	-53.0452	-34.0048	3028	9.27	3.5	0
TPC 288	-59.142	-37.96467	2864	1.16	1.5	100–120
GC 37	-61.105	-39.1783	4025	4.07	-0.5	200–220
TPC 460	-60.80914	-51.03374	2592	0.68	0.0	120–140
GC 53	-64.1367	-65.775	495	0.4	1.5	80–100
BC 519	-68.2375	-70.2035	697	0.135	0.5	280–300
BC 508	-68.3105	-86.0322	3560	0.295	0.0	200–220
BC 497	-69.2302	-108.3492	4229	0.385	0.0	220–240
BC 483	-73.9915	-107.3842	528	0.55	-1.5	340–360

30 ml vials; these samples were cleaned and disaggregated using hydrogen peroxide (30%), dilute hydrochloric acid and Calgon solution for a minimum of 12 h in a water bath at *c.* 50 °C. Quantitative slides were prepared following the method of Scherer (1994) and mounted using Norland Optical Adhesive (refractive index = 1.56). Assemblage and morphological counts were measured at $\times 1000$ magnification on an Olympus BH2 Light Microscope with $\times 10$ magnification eye pieces and an Olympus S Plan $\times 100$ oil immersion lens. Diatom concentrations (valves per gram of dry sediment) were calculated using the following equation after Scherer (1994):

$$T = \frac{(NB / AF)}{M}, \quad (1)$$

where N is the number of valves counted, B is the area of beaker (mm^2), A is the area of transect (mm^2), F is the number of transects counted and M is the mass of dried sample (g).

Assemblage counts ($n \geq 300$) were used to determine the relative abundance of *E. antarctica* in each sample. A minimum of 100 specimens of *E. antarctica* in each sample were categorized (intercalary or terminal) and the height of both ‘horns’ (sides) and the basal width measured on each valve for morphological analyses. Morphometric measurements were carried out only on complete winter stage valves of *E. antarctica* in broad girdle view to avoid any bias from different morphological responses between vegetative and winter form cells. As some discrepancy in measuring the diatom frustules in 2D is possible, all valves exhibiting a height difference between the two ‘horns’ (sides) of $\leq 2 \mu\text{m}$ were classed as symmetrical and only once a height difference of $> 2 \mu\text{m}$ was exceeded were valves considered asymmetrical. These criteria hopefully ensure that symmetrical valves lying askew were not miscounted as asymmetrical. It is unlikely that valves with $< 2 \mu\text{m}$ height difference are capable of producing the tightly spiralling colonies that characterize *E. antarctica* var *antarctica* and may represent an intermediate, transitional form. Even so, the number of ‘asymmetrical valves’ in each sample is likely to be under-represented and reflects the minimum contribution of asymmetrical valves to a sample.

In order to assess the changes in aspect ratio between the samples, the broad girdle (basal) width and valve volumes were used to explore the statistical significance of the aspect ratio variability. The valve volume (V) was calculated using the following equation:

$$V = \pi abh, \quad (2)$$

where a is half of the narrow girdle width, b is half of the broad girdle width and h is the averaged valve height.

Fryxell (1991) shows that the narrow girdle width is typically between 16 and 20 μm irrespective of the broad girdle width. As such, it is unlikely that this parameter has much influence on the changes in valve volume. As it is not possible to measure the narrow girdle width (a) with valves orientated in broad girdle view, I have assumed a set value of 18 μm as the narrow girdle width for all valves based on the measurements made by Fryxell (1991).

RESULTS

Bulk diatom concentrations and assemblage composition

Diatom absolute abundance in the surface sediments of the Scotia Sea and AP ranges from $< 10 \times 10^6$ valves per gram of dry sediment (v/gds) to $> 300 \times 10^6$ v/gds (Fig. 3a; Table 2). Highest diatom concentrations of 327×10^6 v/gds and 298×10^6 v/gds are found in the surface samples from TPC 460 & TPC 288, sites that lie within the seasonal sea-ice zone of the southern Scotia Sea and away from the continent. The next highest concentration of 222.2×10^6 v/gds occurs at site TPC 464, another site away from continental influences but north of the normal Scotia Sea seasonal sea-ice extent. Lowest diatom concentrations of 9.5×10^6 v/gds and 7.9×10^6 v/gds are found at sites GC 62 and BC 483, respectively. These sites are at opposite ends of the latitudinal range of this study and exposed to very different oceanographic conditions: GC 62 is from the southeastern flank of the Falkland Plateau in the SAZ whilst BC 483 is from Pine Island Bay, *c.* 230 km offshore from Pine Island Glacier. BC 508, from the deep Bellingshausen Sea, also contains relatively low diatom concentrations of 11.4×10^6 v/gds. Of the remaining sites, diatom concentrations at GC 37, GC 53 and BC 497 average $83.2 (\pm 3.7) \times 10^6$ v/gds and concentrations reach 108.5×10^6 v/gds at site BC 519 in Marguerite Bay, west AP.

Diatom assemblage compositions of the surface sediment samples are comprised of one or two dominant species or species groups and other minor taxa (Table 2). *Chaetoceros* resting spore is the most common dominant group present at all except the Amundsen Sea site (BC 497), with relative abundances ranging from 17.8–87.0%. *Fragilariopsis kerguelensis* (O’Meara) Hustedt has relative abundances $> 10\%$ at six of the study sites whilst *E. antarctica*, *F. curta* (Van Heurck) Hustedt, *Rhizosolenia antennata* (Ehrenberg)

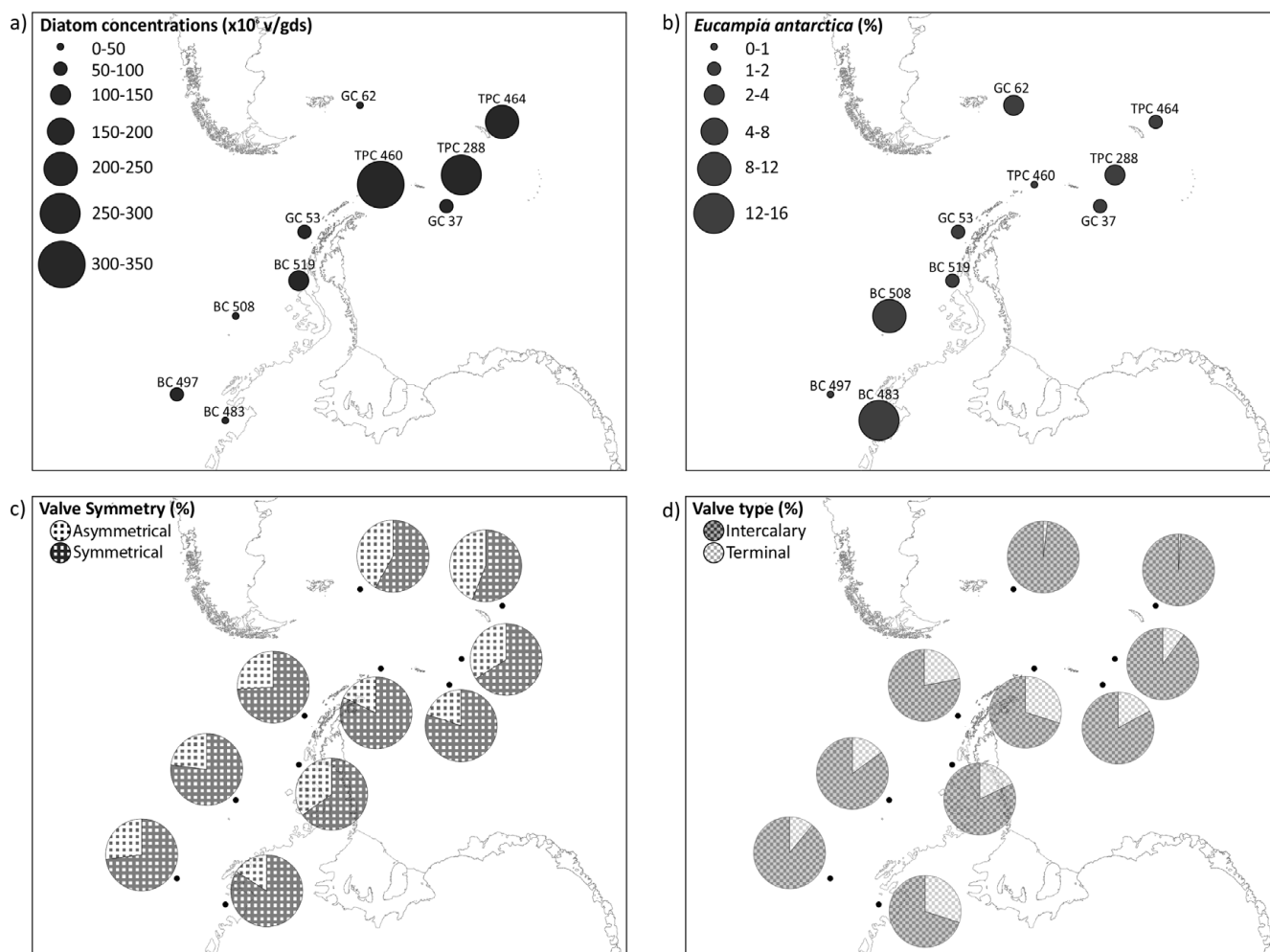


Fig. 3. Maps illustrating (a) diatom concentrations (b) relative abundance of *Eucampia antarctica* in surface sediment samples from the Scotia Sea and Antarctic Peninsula; and the relative contributions of (c) asymmetrical/symmetrical and (d) terminal/ intercalary valves to the *Eucampia antarctica* population in each sample.

Table 2. Diatom assemblage composition including total concentrations and relative contributions (%) by major species

Core	Diatom conc. ($\times 10^6$ v/gds)	EUA	CRS	FKG	FCU	FCY	FOB	RHIA	TLENT	TANT	OTHER
GC 62	9.4875	3.6	26.5	27.7	0.8	0.0	0.0	0.7	8.6	1.7	33.5
TPC 464	222.21	1.8	27.0	28.2	1.4	0.8	0.0	3.7	6.7	5.8	28.9
TPC 288	298.08	2.9	25.1	24.8	5.1	1.0	0.0	4.8	11.4	0.6	27.8
GC 37	81.969	1.6	46.8	11.9	2.0	3.1	0.5	10.4	3.1	1.3	23.9
TPC 460	327.85	<0.3	87.0	1.1	4.1	0.8	0.3	1.0	0.7	0.7	9.1
GC 53	80.648	2.0	53.1	7.2	4.2	0.0	0.0	1.3	4.2	5.9	26.1
BC 519	108.46	1.2	71.3	0.6	6.1	0.2	0.0	0.9	0.6	7.4	16.0
BC 508	11.361	8.9	17.8	36.1	2.5	0.0	0.0	0.0	2.5	1.0	37.1
BC 497	86.904	0.3	4.0	60.3	5.9	0.0	0.3	0.3	3.6	0.0	26.2
BC 483	7.9544	14.1	33.6	0.3	23.5	2.0	2.0	0.0	0.7	7.6	20.2

EUA, *Eucampia antarctica*; CRS, *Chaetoceros* resting spores; FKG, *Fragilariopsis kerguelensis*; FCU, *Fragilariopsis curta*; FCY, *Fragilariopsis cylindrus*; FOB, *Fragilariopsis obliquecostata*; RHIA, *Rhizosolenia antennata*; TLENT, *Thalassiosira lentiginosa*; and TANT, *Thalassiosira antarctica*. Bold type indicates relative abundances of >10%.

Table 3. Summary of morphometric data referred to in the text

Core	SYM	ASYM	TERM	INT	SYM ratio	Colony ratio	Mean basal width (μm)	Mean valve volume ($\times 10^3 \mu\text{m}^3$)
GC 62	58	42	2	98	0.72	0.02	30.7	7.49
TPC 464	56	44	1	99	0.79	0.01	31.3	10.66
TPC 288	66	34	10	90	0.52	0.11	37.9	11.05
GC 37	80	20	17	82	0.25	0.21	36.2	11.42
TPC 460	82	18	30	70	0.22	0.43	45.8	25.84
GC 53	74	26	22	78	0.35	0.28	38.2	12.06
BC 519	67	33	18	82	0.49	0.22	56.5	28.52
BC 508	77	23	15	85	0.30	0.18	35.1	11.07
BC 497	73	27	11	89	0.37	0.12	26.8	10.96
BC 483	84	16	30	70	0.19	0.43	52.4	19.93

SYM, symmetrical valves; ASYM, asymmetrical valves; TERM, terminal valves; and INT, intercalary valves.

Table 4. Correlation coefficient (r^2) values between environmental parameters and *Eucampia antarctica* valve characteristics

	Diatom conc. ($\times 10^6$ v/gds)	Latitude	Temperature (SST)	Sea-ice cover
Diatom conc. ($\times 10^6$ v/gds)	—	0.173	0.004	0.123
EUA %	*0.581	0.253	0.059	0.214
SYM ratio	0.016	0.532	0.696	0.500
Colony ratio	0.003	0.371	0.467	0.347
Mean basal width (μm)	0.004	0.239	0.207	0.364
Mean valve volume ($\times 10^3 \mu\text{m}^3$)	0.071	0.176	0.218	0.277

*Logarithmic regression (all others are linear). See Tables 2 and 3 for abbreviations. Bold type indicates the correlation with the highest significance.

Brown and *Thalassiosira lentiginosa* (Janisch) G. Fryxell all exhibit relative abundances $>10\%$ at one or more of the study sites.

Relative abundance of *Eucampia antarctica*

E. antarctica is not the most dominant species in any of the surface sediments of the Scotia Sea and AP, comprising between $<0.3\%$ and 14.1% of the total assemblage (Fig. 3b; Table 2). Although at first glance it appears that the pattern of *E. antarctica* relative abundances in the AP and Scotia Sea exhibits a north–south trend, low percentages of *E. antarctica* at sites BC 497 and TPC 460 and the third highest relative abundance at site GC 62 are inconsistent with a north–south gradient of increasing relative abundance. The low correlation coefficient ($r^2=0.25$; Table 4) reveals the disparity between *E. antarctica* relative abundances and latitude. Greater relative abundances of *E. antarctica* are, however, weakly correlated with decreasing valve concentrations ($r^2=0.58$) (cf. Fig. 3a and b; Table 4). Highest relative abundances occur at sites TPC 483, BC 508 and GC 62 where sediments contain only 11.3×10^6 v/gds or less and *E. antarctica* comprises 14.1% , 8.9% and 3.6% of the assemblage, respectively (Fig. 3a and b). In contrast, lowest *E. antarctica* relative abundances of $<0.3\%$ of the total diatom assemblage (being absent from the assemblage count of 300 valves) occur at site TPC 460 where diatom concentrations exceed 300×10^6 v/gds.

Morphology: symmetry and valve type

The relative contributions of symmetrical and asymmetrical valves to the *E. antarctica* assemblages are stated in Table 3 and plotted in Figure 3c. Highest numbers of the asymmetrical *E. antarctica*

var *antarctica* are found in the surface sediments from the Falkland Plateau and Northeast Georgia Rise (GC 62 and TPC 464) and the symmetrical *E. antarctica* var *recta* shows greatest dominance in samples of the northern Weddell Sea and southern AP (GC 37, TPC 460 and BC 483) (Fig. 3c). Asymmetrical valves comprise 42% and 44% of the *E. antarctica* assemblage in samples GC 62 and TPC 464, respectively, but only 16% , 18% and 20% in samples GC 37, TPC 460 and BC 483. Intermediate values between 20% and 40% asymmetrical valves occur in west AP and central Scotia Sea surface sediments at sites BC 497, BC 508, BC 519 and TPC 288. The highest proportion of symmetrical valves (84%) occurs in sample BC 483 in the southern Amundsen Sea. Agglomerative hierarchical clustering (AHC) on these valve symmetry data reveals four groups of statistically similar samples (Fig. 4a).

The relative numbers of intercalary and terminal valves (Table 3; Fig. 3d) yield useful information about the chain structures of the *E. antarctica* colonies. Although intercalary valves outnumber the terminal valves in every sample, the greater the number of pointed or ‘horned’ terminal valves, the more prevalent are the shorter colonies of the polar *E. antarctica* var *recta*. In sample TPC 483, 30% of the specimens are terminal valves, whilst in TPC 464 and GC 62 the samples have only 1 and 2 terminal valves, respectively, so are made up almost entirely of intercalary valves. AHC on these terminal versus intercalary valve form data reveals three significant groups of cores with the third group being split into two further (insignificant) sub-groups (Fig. 4b).

There is a good correlation between the ratios of valve symmetry and valve type ($r^2=0.706$) (cf. Fig. 3c and d) and the

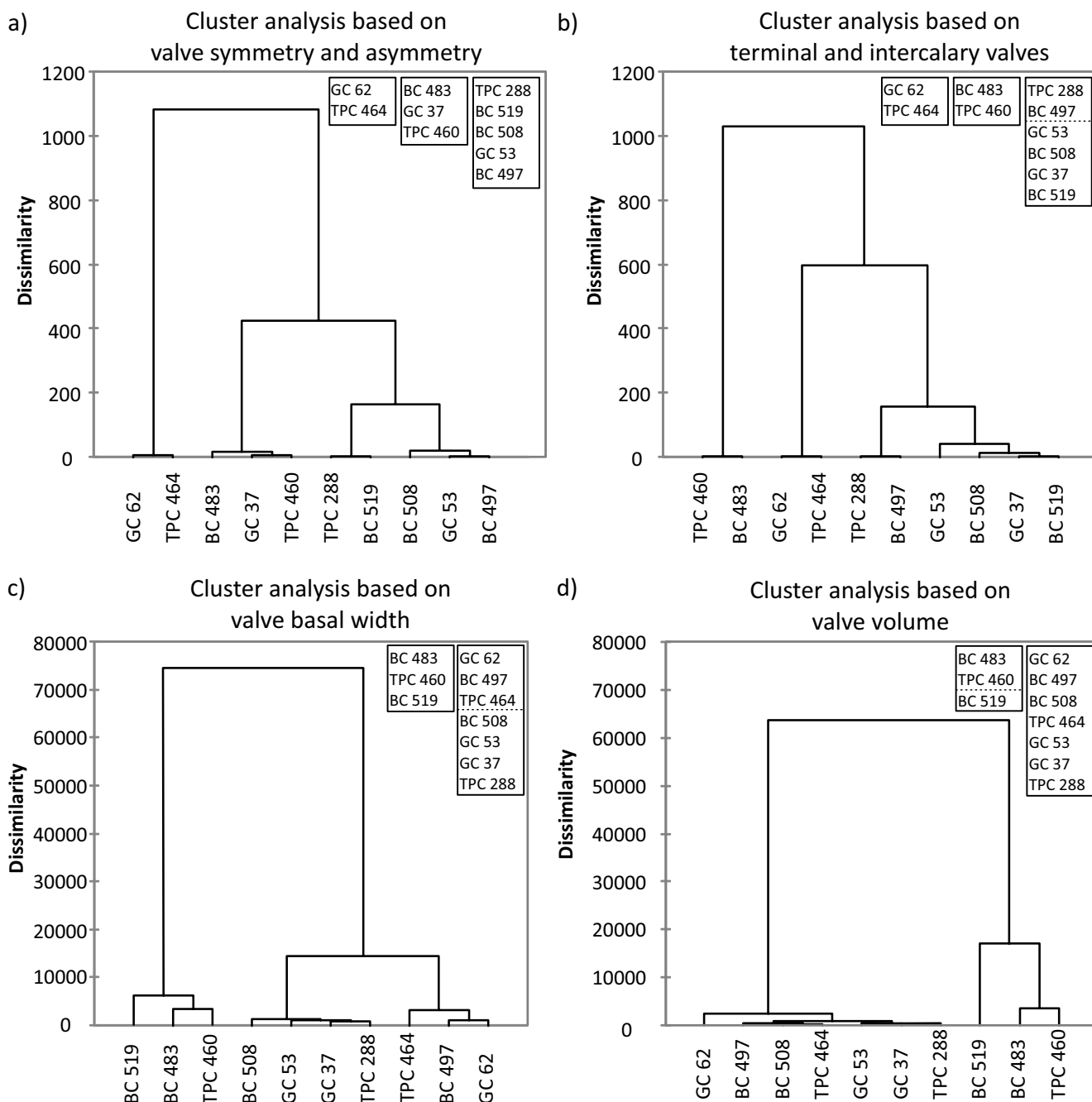


Fig. 4. Dendrograms presenting results of the agglomerative hierarchical clustering analysis on (a) the ratio of symmetrical versus asymmetrical *Eucampia antarctica* valves; (b) the ratio of terminal versus intercalary *Eucampia antarctica* valves; (c) the basal widths of *Eucampia antarctica* valves; and (d) the calculated volumes of *Eucampia antarctica* valves in surface sediment samples of the Scotia Sea and Antarctic Peninsula.

groupings revealed by the AHC on the two datasets are broadly consistent also (Fig. 4a and b).

Morphology: aspect ratio

The aspect ratio (width and average side height) of the 100 specimens measured in each sample are plotted as scattergrams (Fig. 5) to illustrate the morphological diversity within each sample. Cumulative frequency plots of the valve volumes are also included to illustrate the valve size distribution of each sample

(Fig. 6). All axes and plots are drawn at the same scale for ease of comparison.

There are clear differences in the valve shapes and in the range of sizes within a sample (Figs 5 and 6). Sample GC 62 exhibits the least variety in valve shape, with all valves measuring shorter than 30µm, narrower than 60µm and having volumes of less than 15×10³µm³ (Fig. 6). In contrast, BC 519 displays the greatest variety of shapes and sizes, with valve heights and widths ranging from 17–108µm, and 17–116µm, respectively, and with

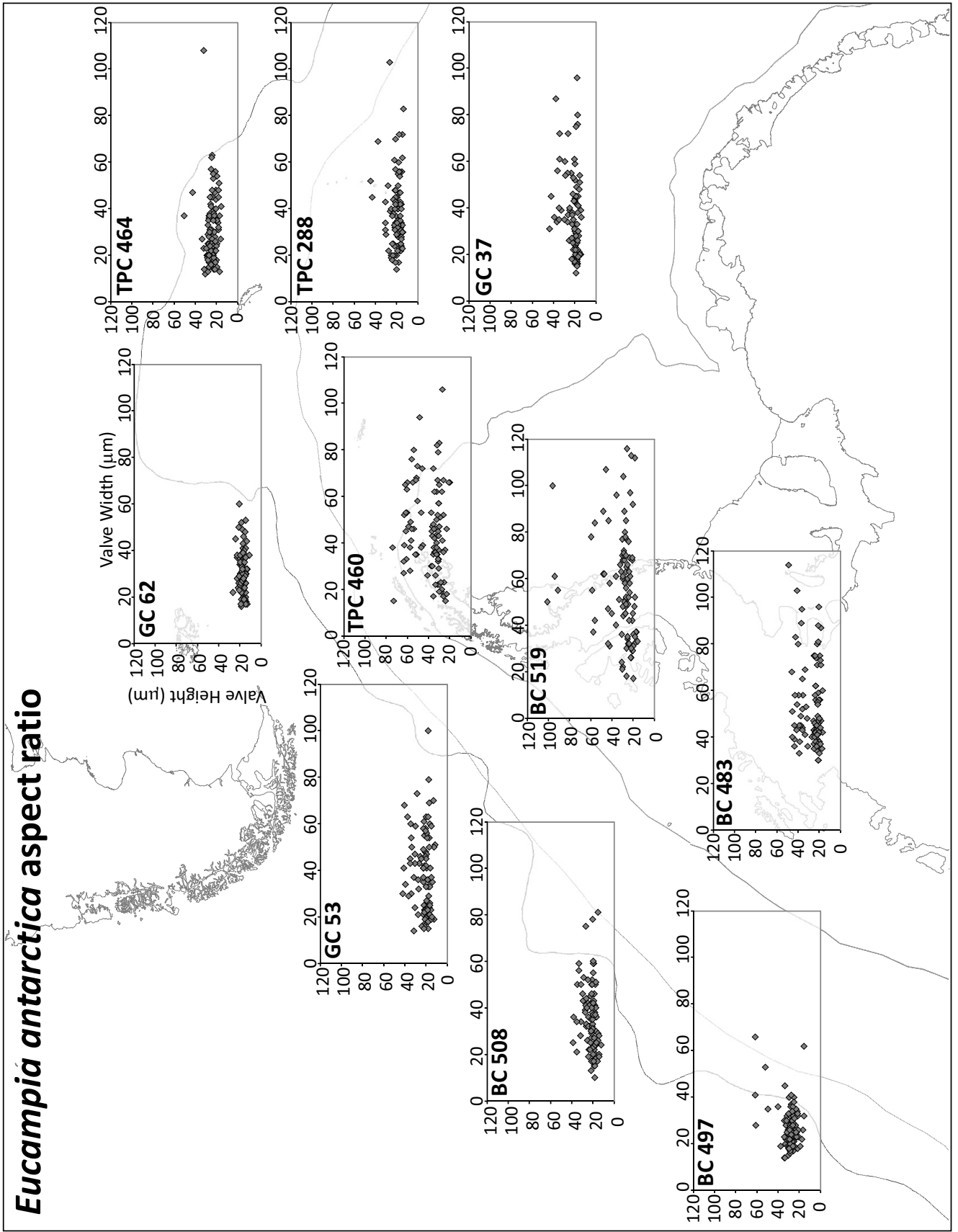


Fig. 5. Scattergrams of the valve width and averaged height (aspect ratio) for each sample of *Eucampia antarctica*.

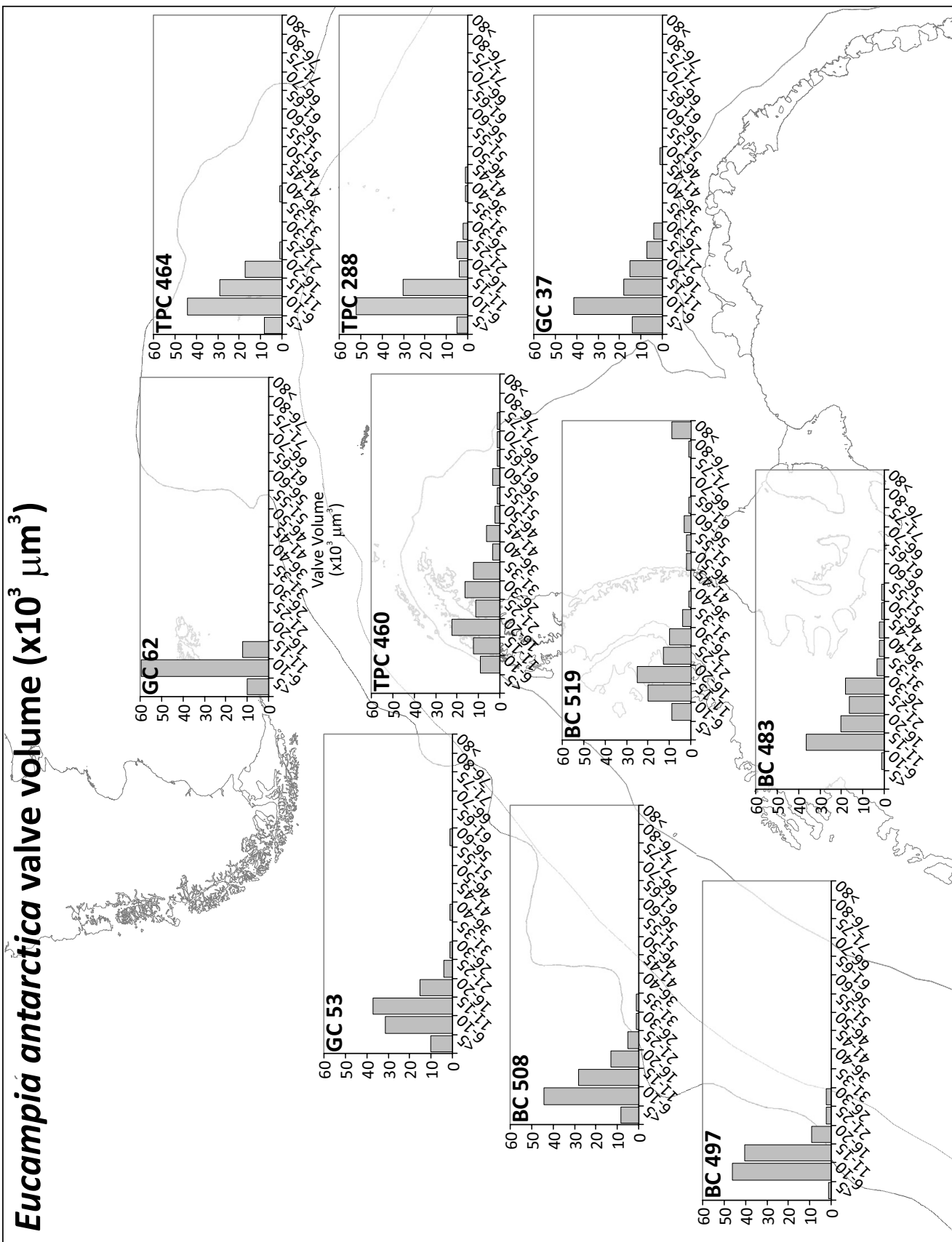


Fig. 6. Cumulative plots of valve volumes for each sample of *Eucampia antarctica*.

the highest valve volumes spanning from $5.91 \times 10^3 \mu\text{m}^3$ to $118.95 \times 10^3 \mu\text{m}^3$ (Fig. 6).

Across the Scotia Sea there is a north–south trend of increasingly diverse valve shapes from GC 62 to TPC 460. A similar trend is evident along the SW AP from BC 497, where valve shapes exhibit minimal diversity, to BC 519 where the wide range of valve shapes and sizes is on a par with TPC 460 (Fig. 5; Table 1). All the remaining samples contain assemblages that evince intermediate size and shape variability.

AHC analysis on the basal widths (Fig. 4c) and valve volume (Fig. 4d) sorts the samples into two identical clusters comprised of TPC 460, BC 483 and BC 519 in one and the other 7 samples (GC 62, TPC 464, TPC 288, GC 37, GC 53, BC 508 and BC 497) in the second. In the AHC of basal widths the second cluster can be further subdivided into two groups: the first containing GC 62, TPC 497 and TPC 464 and the second containing TPC 288, GC 37, GC 53 and BC 508 (Fig. 4c). The AHC of valve volumes exhibits greater divergence between BC 483, TPC 460 and BC 519 (Fig. 4d).

An interesting feature of the basal width data from *E. antarctica* specimens is a disparity between site BC 483 and all other sites. Of the 100 *E. antarctica* valves measured in BC 483 no basal widths are less than $30 \mu\text{m}$, whilst minimum basal widths measure between 10 and $17 \mu\text{m}$ at all the other sites presented here (Fig. 5).

DISCUSSION

Bulk diatom concentrations and assemblage composition

Diatom absolute abundances (concentration) in marine sediments are a function of production, preservation, dilution and lateral transportation. In surface sediments of the Scotia Sea and AP diatom concentrations are broadly consistent with the oceanographic setting at each of the sites. Low diatom concentrations at site GC 62 are probably due to its location north of the PFZ, beyond the Southern Ocean's 'opal belt' where exposure to silica-depleted waters inhibits diatom production and preservation. The position of site BC 483 in the southern Amundsen Sea results in low concentrations of diatoms in the sediment due to the short light-limited growth season at 74° south, episodic years of permanent ice cover as well as greater dilution from high inputs of glacial flour and ice-rafted debris.

The highest concentrations of diatom valves in the sediments of TPC 460 and TPC 288 reflect their position within the seasonal sea-ice zone and close to the Southern Boundary of the Antarctic Circumpolar Current (Fig. 2). High export production derives from sea-ice melt-induced spring blooms and long summer–autumn growth seasons supported by nutrient-rich upper circumpolar deep water (CDW) along the Southern Boundary (Tyman, 1998). These sites are too shallow to be exposed to the influence of Si-reduced bottom water and are located in bathymetrically sheltered positions protected from strong currents, allowing accumulating sediments to be preferentially preserved.

In contrast, GC 37 has much lower absolute valve abundance in the surface sediments, readily explained once the regional oceanographic setting is considered. Here sea-ice is more persistent owing to the northern limb of the Weddell Gyre transporting cold waters and sea-ice into the area from the NW Weddell Sea (Fig. 2b and c), and the absence of CDW which fails to penetrate through the south Scotia Ridge. Site GC 37 is also deep enough

to experience Si-depleted bottom waters exiting the Weddell Sea and may be exposed to winnowing currents (Carmack, 1973; Naveira Garabato *et al.* 2002).

Relative abundance of *Eucampia antarctica*

The weak inverse correlation between *Eucampia antarctica* relative abundance and diatom concentration may provide valuable clues to the ecology of *E. antarctica*. The highest relative abundance of 14.1% occurs in the surface sediments of BC 483 and suggests either that the oceanic setting is favourable for high production of *E. antarctica* or that production of other species is very poor at this southern site. The oceanographic conditions in the high latitude Amundsen Sea are dominated by sea-ice, icebergs and nearshore polynyas and are consistent with the initial concepts of *E. antarctica*'s ecological associations (Burckle, 1984; Kaczmarzka *et al.* 1993; Whitehead *et al.* 2005). Although the southern Amundsen Sea may support high production of *E. antarctica*, the low diatom concentrations at site BC 483 are evidence of low diatom production, poor preservation and/or dilution with other (glacial) sediment sources, such that taphonomic conditions may explain the higher relative abundance of heavily silicified *E. antarctica* valves at the site. Similarly, the 3.6% *E. antarctica* present in the assemblage of GC 62 may also be a result of taphonomic alteration in the reduced silica waters of the SAZ rather than a reflection of better growth conditions in the surface waters. It is difficult to reconcile the pattern of relative abundances without a better understanding of the flux of valves from the surface or the ecological preferences of *E. antarctica*.

Morphology: colony structure (symmetry and valve type)

The distribution of symmetrical and terminal valves versus asymmetrical and intercalary valves in surface sediments of the SW Atlantic and AP (Fig. 3c and d) follows a broad north–south trend that corresponds well with water temperature in the region (Fig. 2b). GC 62 and TPC 464 are both located within the SAZ and PFZ beyond the influence of seasonal sea-ice (Fig. 2c) and where summer SSTs are typically between 3 and 7°C (Fig. 2b). Consistent with the relatively warm SST at these sites, they contain the highest percentage of the asymmetrical valve forms and least number of terminal valves, reaffirming the association of long, spiralling chains of *E. antarctica* var. *antarctica* with the warmer conditions of the PFZ and SAZ as originally proposed by Fryxell (1991) and supported by Kaczmarzka *et al.* (1993) and Scherer *et al.* (2008).

In contrast, BC 483 and TPC 460 contain the highest ratio of symmetrical and terminal valves within these morphometric data, reflecting the cold summer SSTs of $<0.5^\circ\text{C}$ that characterize the Amundsen Sea embayment and the NW Weddell Sea (Fig. 2b).

TPC 288's valve morphological variety is consistent with its location within the seasonal sea-ice zone (Fig. 2c) but north of the South Boundary where circumpolar waters ($>1.0^\circ\text{C}$) of the Antarctic Circumpolar Current are prevalent (Fig. 2b) and probably represents a mix of the var. *recta* and var. *antarctica* valves or a transitional form.

BC 519's morphological assemblage differs from the other sites on the AP, having fewer symmetrical and terminal valves and suggesting a warmer environment than would be expected for its location on the AP inner shelf pattern. The pattern is consistent in both symmetry and colony length and may be explained by the

modern intermittent upwelling of CDW along the Marguerite Bay Trough and/or thermal stratification that would yield localized ocean warming.

The AHC analyses of valve symmetry and valve form yield very similar sample groupings in each to the two sets of data (Fig. 4a and b) adding weight to the premise that both valve symmetry and valve shape respond to the same forcing conditions. The distribution pattern of short, straight-sided colonies inhabiting colder, continental sites and the longer, spiralling colonies in the relatively warmer, permanently open Antarctic and sub-Antarctic waters is consistent throughout the Scotia Sea and AP and adds further legitimacy to this morphological change being a reliable proxy for relative temperatures. Linear regression between average summer SST and the ratios of symmetry and valve type delivers r^2 values of 0.696 and 0.467, respectively (Table 4), showing that the ratio of symmetrical to asymmetrical valves is a more accurate proxy for temperature than colony length. The strength of this relationship may be improved if it were possible to distinguish asymmetrical valves accurately, irrespective of their orientation on the slide. The regression analysis also suggests that with additional data points there is scope to develop a quantitative proxy based on the ratio of valve symmetry. A quantitative proxy for SSTs down to -1.5°C would be a valuable tool as most existing temperature proxies are either poorly calibrated for the Antarctic region or unable to resolve changes at low temperature.

Morphology: aspect ratio

The range of valve aspect ratios in the *E. antarctica* samples from the Scotia Sea and AP do not match the distribution pattern of valve symmetry. In particular, the three sites on the WAP outer-shelf – BC 497, BC 508 and GC 53 – exhibit a west–east trend of increasing diversity in *E. antarctica*'s aspect ratio (Fig. 5), whilst the ratio of symmetrical to asymmetrical valves are broadly consistent across all three sites (Fig. 3c). These inconsistencies in size and shape distribution suggest that temperature is not the principal factor driving changes in aspect ratio. The AHC results yield groupings for basal widths and valve volume which are noticeably different from those for valve symmetry and valve type (cf. Fig. 4a and d) and add weight to the suggestion that an alternative forcing mechanism (not temperature) lies behind the variety and distribution of valve shape evident in these aspect ratio data.

Linear regression analyses between mean basal width and mean valve volume against temperature and sea-ice cover yield fairly low r^2 values of 0.207, 0.364 and 0.218, 0.277 (Table 4) and provide further evidence that the aspect ratios are not sensitive to either temperature or sea-ice cover.

Although I show that temperature and sea-ice cover do not provide a straightforward explanation for the distribution of valve shapes found in the Scotia Sea and AP surface sediments, there are many other environmental parameters and biological responses that could account for changes in aspect ratio. Comparing the locations of the AHC-defined group of samples with the least-varied aspect ratios (GC 62, BC 497 and TPC 464; Fig. 4c and d), it is immediately apparent that these sites are located in open ocean sites, far from continental influences (Fig. 2). Oceanographically this translates as distance away from inputs of terrigenous material, greater water column mixing, potentially less

exposure to grazing pressures with distance north of the Southern Boundary (Tynan, 1998) and reduced iceberg concentration. These oceanographic conditions yield low nutrient inputs from terrestrial sources (iron?), increase mixed-layer depth and may flush cells beyond their irradiance limit. Alternatively, the AHC-defined group of three samples containing the most diverse valve shapes (BC 483, BC 460 and BC 519; Fig. 4c and d) are all within the seasonal sea-ice zone and much closer to the Antarctic continent (Fig. 2). These locations are likely to be characterized by high fluxes of glacial debris and icebergs, short growth seasons associated with stratified waters induced from sea-ice or glacier melt and episodic high productivity events associated with polynya or open-water formation driven by katabatic offshore winds.

From the descriptions of the broad oceanographic settings of the two groups (high and low diversity in aspect ratio), it is apparent that there are several environmental gradients that may potentially account for the observed variability in *E. antarctica* aspect ratio: input of terrigenous material; melt water flux; stratification and light intensity/availability. However, without better quantification of these parameters it is impossible to ascertain which, if any, of these environmental features may determine *E. antarctica* aspect ratio.

CONCLUSIONS

This paper expands on previously published data on *Eucampia antarctica* polymorphism and presents morphometric data covering the full range of cell structures and aspect ratio found in the surface sediments of the Scotia Sea and Antarctic Peninsula. Comparison of cell symmetry and colony length as proxies for temperature has shown that the ratio of cell symmetry is a more reliable temperature proxy than the ratio of terminal to intercalary valves. Augmenting the data presented here to include more samples from within the -1.5°C to 8°C temperature range would be useful in determining whether the match between valve symmetry and sea surface temperature is consistent enough to establish a new quantitative austral summer SST proxy for Antarctic waters.

As well as providing a more thorough grounding for existing proxies, the paper has also examined the aspect ratio as a new facet of *E. antarctica* polymorphism. Although the data show that the aspect ratio of the *E. antarctica* populations does not correlate with either temperature or sea-ice, this may be considered a positive result for proxy development. Comparison with other environmental data may reveal the factor controlling morphological divergence in *E. antarctica*'s aspect ratio and offer the potential for a novel proxy.

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