THE TEMPERATURE RELATIONS AND BI-POLAR BIOGEOGRAPHY OF THE CILIATE GENUS *Colpoda*

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ABSTRACT. Between 1968 and 1971 studies were made on the Protozoa occurring in 68 sites covering a wide range of terrestrial habitats on maritime Antarctic islands. No species of the ciliate genus *Colpoda* was observed—a surprising result because *Colpoda* spp. have been frequently recorded from soils in temperate and Arctic regions. Previous work suggests that resting cysts of *Colpoda* could certainly survive maritime Antarctic winters. In order to explain the absence of this genus, it is suggested that Antarctic summers are too cool and short for *Colpoda* spp. to maintain active multiplication phases long enough to establish themselves in terrestrial habitats, whereas the Arctic areas from which *Colpoda* has been recorded have longer warmer summers. This hypothesis is supported by experiments with single-species cultures in which *Colpoda cucullus* showed poorer ability to survive at 0° and 4° C than three species of Protozoa which do occur in the maritime Antarctic, and by comparative meteorological data which show that Arctic localities from which *Colpoda* has been recorded have warmer summers than do maritime Antarctic islands from which it has not, even though they may have colder winters.

Colpoda Ehrenberg is the most abundant and most widespread of soil ciliate genera. *Colpoda cucullus* Muller and *Colpoda steini* Maupas were recorded by Sandon (1927) from 103 soils in the tropics, northern and southern temperate zones and the Arctic. They have also been recorded from many parts of the world by other investigators (Dixon, 1939; Horvath, 1949; Gellert, 1955; Nickolyuk, 1963; Stout, 1963; Chardez, 1967; Bamforth, 1969). A survey of ciliates and testates in North American by Bamforth (1971) indicated that, in most of the soils and litters investigated (which extended from Alaska to sub-tropical Louisiana), more than half the ciliate population belonged to these species. Less frequently recorded than these two species but still common in soils are *Colpoda maupasi* Enriques (Sandon, 1927; Horvath, 1949; Nickolyuk, 1963; Chardez, 1967) and *Colpoda inflata* Stokes (Horvath, 1949; Gellert, 1955; Chardez, 1967; Stout, 1970).

Studies by Stout (1955) suggested that *Colpoda* spp. have exceptionally good adaptation to soil habitats: small size, capacity to multiply rapidly under favourable conditions and ability to encyst rapidly in response to adverse conditions. The cysts can withstand extreme temperatures (Taylor and Strickland, 1936) and can remain viable for years (Goodey, 1915; Dawson and Mitchell, 1929).

Between 1968 and 1971 extensive studies were made on the terrestrial Protozoa in the maritime Antarctic. Samples from 68 sites in the South Orkney Islands, South Shetland Islands, Argentine Islands and islands in Marguerite Bay were analysed for Protozoa, the sites covering a wide range of habitat types including grass soil, moss peats, glacial moraines and excreta of birds and seals. Before the studies were begun, it was confidently expected (in view of the observations reviewed above) that, if any ciliates at all were to be found in terrestrial habitats in the Antarctic, *Colpoda* spp. would be prominent members of the fauna. In the event, 37 species of ciliate were recorded but none of the genus *Colpoda*. Nor have any other investigators (with one exception) observed *Colpoda* in the Antarctic. The exception was Sudzuki (1964), who recorded "*Colpoda* sp." from moss water at Langhovde (lat. 69°13′S.; long. 39°45′E.); however, many of his identifications are uncertain and this record must be regarded as doubtful. The remarkable absence of *Colpoda* from the maritime Antarctic was all the more surprising because *C. steini* was observed in peat samples from the cool-temperate Falkland Islands, and both *C. cucullus* and *C. steini* in peat samples from sub-Antarctic South Georgia.

The absence of a species from a particular locality may be attributable either to restrictions imposed by geographical barriers or to the unsuitability of the local environment. As far as species of *Colpoda* are concerned, geographical barriers do not seem to be the cause; the maritime Antarctic islands are certainly remote, but this has not prevented their acquiring a fauna of many Protozoa species and other taxa; also *C. cucullus* and *C. steini* are present in the soils of Tristan da Cunha and St. Helena (Sandon and Cutler, 1924), which are islands equally remote. It seems likely therefore that some environmental factors are responsible for the absence of *Colpoda* from the Antarctic. There is evidence from laboratory studies that *Colpoda*

may be particularly sensitive to low temperatures. In the course of experiments using *Colpoda steini*, Darbyshire (1972) was unable to detect any *Colpoda* cells in cultures which have been incubated at +5° C for 1 month, although they grew and multiplied in identical cultures incubated at 15° and 20° C. However, *Colpoda* spp. have been recorded in nature from several Arctic localities where annual mean temperatures are as low as, or lower than, those in the maritime Antarctic.

Hypothesis

From observations on the temperature relations and longevity of *Colpoda* (Dawson and Mitchell, 1929; Stout, 1955), it appears that resting cysts of *Colpoda* could certainly survive maritime Antarctic winters. Since any terrestrial organisms which survive polar winters do so under an insulating layer of snow, it may be the summer and not the winter temperatures that are of critical importance. It is suggested that Antarctic summers are too cool and short for *Colpoda* spp. to maintain active multiplication phases sufficient to establish themselves in terrestrial habitants, and that *Colpoda* has been detected in Arctic lands because they have longer warmer summers.

This hypothesis may be examined in two ways:

i. Compare the ability of *Colpoda* with that of other Protozoa, which do occur in the maritime Antarctic, to survive and grow in single-species laboratory cultures incubated at low temperatures.

ii. Compare the climatic temperature regimes of the Arctic localities where *Colpoda* has been recorded with those of the maritime Antarctic islands where it has not. Ideally, ground and soil temperatures (those actually experienced by the Protozoa) should be used but, because they are mostly unavailable, screen temperatures have been employed. However, areas with higher air temperatures than others will tend to have higher soil temperatures also, so air temperatures can be used for comparative purposes.

Culture Experiments

Materials and methods

A series of culture experiments was performed in order to compare the temperature relations of *Colpoda cucullus* (CCAP 1615/2) with those of three other species (a flagellate, *Bodo saltans* (CCAP 1907/2), a rhizopod, *Euglypha rotunda* (CCAP 1502/1) and a ciliate, *Philaster* sp. (original isolation)) which had been observed to occur in the maritime Antarctic.

Colpoda was cultured on lettuce infusion. 1·5 g. dried lettuce were soaked in 1 l. distilled water and boiled for 2 hr. After cooling, the infusion was filtered and its pH adjusted to 6·8–7·0 with $CaCO_3$. Test-tube cultures were prepared with 5 ml. medium per tube. The tubes were autoclaved, inoculated with *Aerobacter aerogenes* when cool and incubated at 20° C. Protozoa were inoculated after 24 hr.

Bodo and *Euglypha* were cultured on Erdschreiber medium. Stock solution was prepared by boiling 500 g. sterilized soil with 1 l. tap water for 2 hr. and, after settling, pipetting off the supernatant. This liquid was then centrifuged and the supernatant diluted: 50 ml. stock made up to 1 l. with tap water. This 5 per cent solution was pasteurized for 2 hr. at 80° C. To every 20 ml. of solution used, 0·05 ml. of 4 per cent $NaNO_3$ + 0·6 per cent Na_2HPO_4 solution was added.

For *Bodo*, test-tube cultures were prepared: 5 ml. aliquots of pasteurized Erdschreiber medium were poured aseptically into autoclaved test tubes and a wheat grain, surface sterilized in boiling water, placed in each tube.

For *Euglypha*, plate cultures were prepared using 36 mm. petri dishes; the bottom was covered with a thin layer of 1·5 per cent agar and a surface-sterilized wheat grain inserted just before the agar set; 5 ml. aliquots of Erdschrieber medium were poured aseptically on to the agar dishes when cool.

Immediately after preparation the tubes or plates of media were inoculated with *Bodo* or *Euglypha*.

Philaster was cultured on liver infusion medium prepared from:

Liver infusion (Oxoid L25)	20 g.
Bacteriological peptone	10 g.
NaCl	5 g.
Distilled water	1 l.

and used without filtration. Test-tube cultures were prepared with 5 ml. medium per tube. The tubes were autoclaved, inoculated with *Aerobacter aerogenes* when cool and incubated at 20° C. Protozoa were inoculated after 24 hr.

Protozoa were inoculated into media at room temperature (18–20° C) and cultures subsequently transferred to incubators at experimental temperatures. The temperatures of cultures to be incubated at 12° C or less were decreased gradually from room temperature (at a rate of −2° C/hr.); similarly, they were increased gradually to room temperature at the end of the experimental period of incubation.

Test-tube cultures were stoppered with cotton-wool bungs which effectively prevented losses by evaporation. To keep the atmosphere around the plate cultures humid, they were placed inside larger petri dishes together with a small open dish of distilled water.

Stock cultures of *Colpoda*, *Bodo* and *Euglypha* were grown at room temperature. *Philaster* did not grow successfully at room temperature; stock cultures of this species were grown at 12° C.

The densities of Protozoa in cultures were determined by counting the numbers of cells in samples of cultured fluid of known volume. *Colpoda*, *Bodo* and *Philaster* were motile cells at densities of the order of 10^4/ml. or more. To kill the cells, 0·01 ml. Noland's stain-fixative (Noland, 1928) was added to a 0·05 ml. sample of culture fluid. A count of the cells was then made with a haemocytometer. *Euglypha* was more difficult to count as the cells in culture formed into clumps. Cells adhering to the agar base were first scraped clear with a microspatula so that they were suspended in the culture fluid. The fluid was pipetted into a Jorgensen bottle and shaken for 5 min. to break up the clumps and disperse the individual cells. Because the cells were at densities of 10^2 or 10^3/ml. (too low for haemocytometer counting), a sample of culture fluid, volume 0·05 ml., was taken with a calibrated pasteur pipette and the total number of cells in it counted. As the cells were virtually non-motile, it was not necessary to kill them before counting.

Nine replicate counts were made on each culture so that a mean figure with 95 per cent confidence limits could be obtained.

Experimental

Experimental cultures of each species were incubated at seven temperatures: 0°, 4°, 10°, 12°, 15°, 18° and 25° C. (The 10° and 18° C cultures of *Philaster* were omitted.) Each culture of 5 ml. was inoculated with 0·05 ml. of a growing stock culture of known density, so that the initial density of the experimental culture could be calculated. Three replicate cultures were established at each temperature. After 14 days' incubation, the densities of the cultures at each temperature were measured. (*Euglypha*, being a testate rhizopod and growing more slowly than the other species, was incubated for 25 days.) When no cells could be detected, or only cysts were observed, incubation of the culture was continued at room temperature (12° C for *Philaster*) and a sample of the culture inoculated into fresh medium. After a further 14 days, these were inspected for the growth of Protozoa, a positive result indicating that the original culture contained viable cells at the end of its experimental incubation period.

Results

The initial and final densities of the cultures of each species are shown in Table I. In the 0° C culture of *Colpoda* and the 25° C culture of *Philaster* no cells could be detected at the end of incubation, and no evidence of cells having survived was obtained from further incubation or from inoculation of samples into fresh media. In the 0°, 4° and 15° C cultures of *Philaster*, cysts were detected in numbers too low for a count to be made. Further incubation at 12° C showed these cysts to be viable. The survival of each species at each temperature at the end of incubation is summarized in Table II.

TABLE I. INITIAL AND FINAL DENSITIES OF FOUR SPECIES OF PROTOZOA IN EXPERIMENTAL CULTURES INCUBATED AT A RANGE OF TEMPERATURES

Species	*Incubation time* (days)	*Initial density* (cells/ml.)	*Final density* (cells/ml.) ± *95 per cent confidence limits after incubation at* (° C):						
			0°	4°	10°	12°	15°	18°	25°
Colpoda	14	$6{\cdot}8\pm1{\cdot}6\times10^3$	None detected	$2{\cdot}9\pm1{\cdot}1\times10^3$	$38\pm19\times10^3$	$48\pm17\times10^3$	$95\pm36\times10^3$	$340\pm87\times10^3$	$426\pm82\times10^3$
Bodo	14	$0{\cdot}9\pm0{\cdot}1\times10^4$	$0{\cdot}3\pm0{\cdot}1\times10^4$	$3{\cdot}6\pm0{\cdot}7\times10^4$	$31\pm3\times10^4$	$45\pm15\times10^4$	$50\pm15\times10^4$	$66\pm10\times10^4$	$109\pm19\times10^4$
Euglypha	25	$1{\cdot}4\pm0{\cdot}2\times10^2$	$0{\cdot}3\pm0{\cdot}1\times10^2$	$0{\cdot}6\times0{\cdot}2\times10^2$	$0{\cdot}8\pm0{\cdot}2\times10^2$	$1{\cdot}0\pm0{\cdot}3\times10^2$	$7{\cdot}3\pm1{\cdot}6\times10^2$	$24\pm2\times10^2$	$69\pm5\times10^2$
Philaster	14	$0{\cdot}8\pm0{\cdot}1\times10^3$	Cysts present	Cysts present	—	$419\pm61\times10^3$	Cysts present	—	None detected

TABLE II. THE INFLUENCE OF INCUBATION TEMPERATURE ON THE PRESENCE OF VIABLE CELLS IN EXPERIMENTAL CULTURES OF FOUR SPECIES OF PROTOZOA

Species	*Incubation time* (days)	*Viable cells present or absent in cultures after incubation at* (° C): 0°	4°	10°	12°	15°	18°	25°
Colpoda	14	−	+	+	+	+	+	+
Bodo	14	+	+	+	+	+	+	+
Euglypha	25	+	+	+	+	+	+	+
Philaster	14	+	+		+	+		−
		(The 10° and 18° C cultures of *Philaster* were omitted)						

In order to make a graphical comparison of the performances in culture of the different species, the ratio final density : initial density was plotted against incubation temperature for each species. Graphs for *Colpoda*, *Bodo* and *Euglypha* are shown in Fig. 1. There were insuffi-

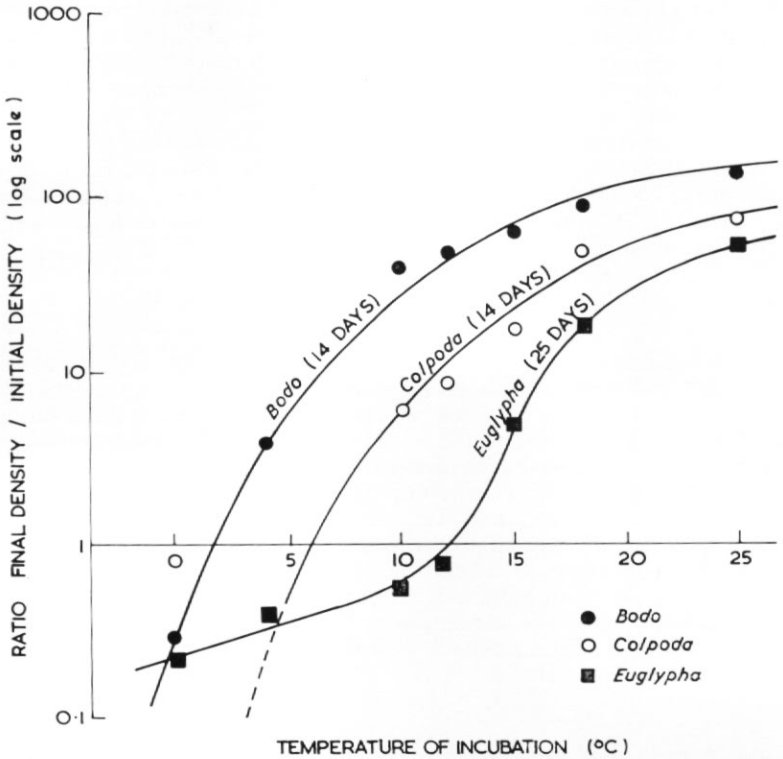

Fig. 1. Influence of incubation temperature on the growth and survival of three species of Protozoa in single-species culture.

cient numerical data on *Philaster* for a graph to be plotted. The parts of the graph below the line Final density/Initial density = 1 indicate the relative ability of the different species to survive at low temperatures. The parts of the graph above this line indicate their relative growth performances at more favourable temperatures. *Bodo* showed faster growth and better

survival than *Colpoda* at all temperatures; *Euglypha* showed slower growth than *Colpoda* above about 4° C but considerably better survival below this temperature. In all three species, increased temperatures resulted in increased growth rates, though these appeared to be levelling out at about 25° C.

Discussion

The results show that viable cells of the three species recorded from the maritime Antarctic could be recovered from cultures which had been incubated at 0° C for 14 days (25 days for *Euglypha*), but that none was recovered from *Colpoda* cultures at the same temperature.

Laboratory-cultured organisms are in a highly artificial environment, so these data do not give a precise indication of the ability of these protozoan species to survive or grow at various temperatures in their natural habitats. They do however allow inter-specific comparisons to be made, and the results show that *Colpoda* has less ability to tolerate low temperatures than the other three species. This result is consistent with the original hypothesis.

The fact that *Euglypha* grows less rapidly than *Colpoda* above 4° C (Fig. 1) might be thought to indicate that its numbers should, therefore, increase less rapidly than those of *Colpoda* during the Antarctic summer, and so the fact that it does occur in the maritime Antarctic in numbers sufficient to be detected requires further explanation. Data on the diurnal cycle of temperatures in moss peat on Signy Island (Longton and Holdgate, 1967) indicate that the temperatures of terrestrial habitats in the maritime Antarctic may oscillate very frequently above and below +4° C during the summer—perhaps once every 24 hr. If this is so, the balance between growth and mortality under such environmental conditions might result in a net gain in the numbers of *Euglypha* but a net loss in the numbers of *Colpoda*, so that *Colpoda* would never become established in the fauna.

The results for *Philaster* are incomplete. It was found impossible to grow stock cultures of *Philaster* at room temperature and viable cells could not be recovered from the experimental cultures incubated at 25° C, though they could be recovered from cultures at 0° and 4° C. This suggests that *Philaster* might be an obligate psychrophile but further investigation would be required to prove this.

Bi-polar Biogeography

Data collection

After a search of the literature, a list of Arctic sites in Spitzbergen, Greenland and Northwest Territories, Canada, and one cool-temperate site in the Faroe Islands, from which one or more species of *Colpoda* had been recorded, was prepared together with a list of meteorological stations, each being the nearest one to the site of the *Colpoda* for which weather records were available. The following data were abstracted from the published meteorological records of each station: annual mean temperature, monthly mean temperature (warmest month), monthly mean temperature (coldest month), and mean temperature of the four warmest months.

For comparison, a list of three maritime Antarctic areas, which had been examined for protozoan fauna but had failed to reveal the presence of *Colpoda*, together with the same meteorological parameters, was prepared in a similar way. In this list, data for one sub-Antarctic site (South Georgia) and one southern cool-temperate site (Falkland Islands), from both of which *Colpoda* had been recorded, were also included.

The lists are shown in Table III.

Discussion

Table III shows that the mean mid-summer temperatures for the Arctic areas from which *Colpoda* has been recorded are in the range +3° to +16° C, whereas those for the maritime Antarctic areas are below +1° C, in spite of some of the Arctic areas being at much higher latitudes. The annual mean temperatures of these Arctic areas are mostly similar to those of the maritime Antarctic, though Angmagssalik, Greenland, is milder throughout the year, and in summer is even milder than sub-Antarctic South Georgia. Scoresby Land, Greenland, the coldest of the Arctic areas investigated, has an annual mean temperature 3° to 6° C lower than that of the maritime Antarctic, but still has a summer about 2° C warmer.

TABLE III. RECORDS OF GENUS *Colpoda* AND TEMPERATURE IN POLAR AND COOL-TEMPERATE REGIONS

Site	*Position* (lat.; long.)	*Habitat*	*Species of Colpoda recorded*	*Authority*	*Meteorological station*	*Position* (lat.; long.)	*Air temperatures*				*Period of observations*	*Source of data*
							Annual mean (° C)	*Monthly mean of warmest month* (° C)	*Monthly mean of coldest month* (° C)	*Mean of four warmest months* (° C)		
NORTHERN HEMISPHERE												
Faroe Islands, Nolsoy	62°00′N.; 6°40′W.	Peat	*C. cucullus*, *C. steini*	Original observation, 1967	Thorshavn	62°01′N., 6°44′W.	+7·1	+11·1	+3·9	+10·3	1931–60	(1)
Canada, Northwest Territories												
Fort Resolution	61°10′N.; 114°00′W.	Coarse soil with humus	*C. steini*	Sandon, 1927	Fort Smith	60°00′N.; 111°52′W.	−3·2	+16·2	−25·4	+12·8	1931–60	(1)
Mission Providence	61°22′N.; 117°59′W.	Soil deficient in humus	*C. steini*	Sandon, 1927								
Spitzbergen												
Prince Charles Foreland	78°30′N.; 11°00′E.	Black peat	*C. cucullus*	Sandon, 1924	Isfjord Radio	78°04′N.; 13°38′E.	−3·8	+5·0	−11·9	+3·3	1951–60	(1)
West Greenland												
Disko Island	69°30′N.; 53°35′W.	Soil	*C. cucullus*, *C. maupasi* *C. steini*	Sandon, 1927	Jacobshavn	69°13′N.; 51°02′W.	−3·8	+7·9	−14·3	+5·8	1921–50	(2)
East Greenland,												
Angmagssalik	65°40′N.; 37°40′W.	Peat	*C. steini*	Dixon, 1939	Angmagssalik	65°37′N.; 37°34′W.	−0·5	+7·3	−7·5	+6·0	1931–60	(1)
East Greenland, Scoresby Land												
Schaffhaverden	72°14′N.; 25°30′W.	Flushed soil, no vegetation	*C. cucullus*	Stout, 1970	Scoresbysund	70°25′N.; 21°58′W.	−7·3	+3·0	−16·5	+1·9	1948–60	(1) (2)
Kap Petersens	72°25′N.; 24°30′W.	Outwash sands	*C. inflata*	Stout, 1970	Myggbukta	73°29′N.; 21°34′W.	−9·7	+4·0	−20·4	+2·0	1932–39 and 1947–50	(2)
"Base Camp"	72°20′N.; 24°15′W.	Lichens and algae	*C. steini*	Stout, 1970								
Mestersvig	72°14′N.; 23°55′W.	*Salix* soil	*C. cucullus*, *C. inflata* *C. steini*	Stout, 1970								
SOUTHERN HEMISPHERE												
Falkland Islands												
Stanley Common	51°42′S.; 57°48′W.	Heath peat (*Empetrum rubrum*)	*C. steini*	Original observation, 1971	Stanley	51°42′S.; 57°52′W.	+5·5	+9·0	+2·2	+8·4	1951–60	(1)
South Georgia												
Hestesletten	54°17′S.; 36°30′W.	Tussock grass peat (*Poa flabellata*)	*C. cucullus*, *C. steini*	Original observation, 1969	Grytviken	54°16′S.; 36°30′W.	+2·0	+5·3	−1·5	+4·5	1951–60	(1)
South Orkney Islands	60°36′ to 60°45′S.;	Moraines, mineral debris,	Negative	Original observations,	Signy Island	60°43′S.; 45°36′W.	−3·6	+0·9	−9·9	+0·4	1948–70	(3)
29 sites	44°26′ to 46°07′W.	moss peats, grass soil, animal guano		1968–71	Orcadas	60°44′S.; 44°39′W.	−4·2	+0·4	−10·2	0·0	1931–60	(1)
Elephant Island	61°04′ to 61°14′S.;	Moraines, moss peats,	Negative	Smith, 1972	Elephant Island	61°12′S.; 55°09′W.	—	−0·1	—	−0·5	December 1970–March 1971	(4)
23 sites	54°40′ to 55°24′W.	grass soil, penguin guano										
Argentine Islands	65°15′S.; 64°16′W.	Moss peats	Negative	Original observations,	Argentine	65°15′S.; 64°16′W	−5·4	−0·1	−12·8	−0·6	1951–60	(1)
4 sites				1970	Islands							

Sources: (1) Climatic normals for climat and climat ship stations for the period 1931–1960. (WMO/OMM No. 117, TP.52, 1971).
(2) Clayton (1934); Clayton and Clayton (1947); Conover (1959).
(3) Records of British Antarctic Survey station at Signy Island.
(4) Observations of the Joint Services Expedition to Elephant Island, 1970–71 (personal communication from R. M. G. O'Brien).

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Fort Smith, situated in the middle of the continental land mass of Canada, has the greatest annual temperature range, its coldest month being 12° C colder than that in the maritime Antarctic, while its warmest month is about 15° C warmer. Its summer is even warmer than those of the cool-temperate islands in both hemispheres: Faroe Islands and Falkland Islands.

The data in Table III are fully consistent with the hypothesis that, despite having cold winters, Arctic areas have summers warm enough to permit *Colpoda* to be present in detectable numbers, while the maritime Antarctic summers are too cool for this to happen. The data suggest that the climatic temperature threshold for conditions to be suitable for *Colpoda* to become established is a mean for the four warmest months of between +0·4° and +1·9° C.

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