Morphology and infraciliature of some soil ciliates (Protozoa, Ciliophora) from continental Antarctica, with notes on the morphogenesis of *Sterkiella histriomuscorum* Wolfgang Petz and Wilhelm Foissner

Universität Salzburg, Institut für Zoologie, Hellbrunnerstrasse 34, A-5020 Salzburg, Austria

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ABSTRACT. The morphology of seven soil ciliate species from continental Antarctica was investigated using live observation and protargol impregnation. Observations on two populations of *Protospathidium serpens* corroborate the view that this species usually has a single, more-or-less nodular, macronucleus distinguishing it from *P. muscicola*, which possesses 10–30 nodules. The Antarctic specimens of *Protospathidium terricola* differ inconspicuously from the type population in that they are slightly larger, have fewer ciliary rows (17 vs 21), and the fragments of the circumoral kinety are less distinctly separated from each other. *Spathidium seppelti* nov. spec. resembles *S. bavariense*, but has 100–200 macronuclear nodules and a conical depression in the dorsal third of the oral bulge. *Odontochlamys wisconsinensis* nov. comb. (basionym: *Chilodonella wisconsinensis* Kahl, 1931) has four right field kineties and an oral basket consisting of 14 rods; the dorsal brush is near the anterior margin and usually consists of four cilia. The Antarctic population) pharyngeal rods. *Oxytricha opisthomuscorum* has six dorsal kineties with long cilia and a buccal cirrus near the anterior end of the paroral membrane. The Antarctic specimens of *Sterkiella histriomuscorum* have five transverse cirri. Their morphogenesis differs slightly from that of a population having four transverse cirri in that the daughter's anlagen are more distinctly separated and some temporal sequences are different.

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Introduction

Studies of the terrestrial ciliate fauna of continental Antarctica are rare, often dated, and rely almost entirely on stored (dried or frozen) samples (Flint and Stout 1960; Sudzuki 1964, 1979; Thompson 1965, 1972; Sudzuki and Shimoizumi 1967; Thompson and Croom 1978; Broady 1989; Ryan and others 1989; Bamforth and others 1993; Foissner 1996; Petz and Foissner 1996). It was only recently that more detailed data became available. Foissner (1996) recorded 16 carefully determined species in 37 moss and soil samples from the Antarctic Peninsula and 14 taxa, including one new species, in 14 samples from southern Victoria Land. Petz (1997) identified 26 taxa in 19 fresh samples, while enumerating the active ciliate fauna in the area of the Australian Casey Station (Wilkes Land), where one of the most extensive and best-developed plant communities of continental Antarctica occurs (Lewis Smith 1986). Some new and insufficiently known species, which were found in the course of this in situ investigation, are described in the present paper.

Materials, methods, and type slides

Specimens were found in soils collected from the environs of Casey Station, Budd Coast, Wilkes Land, continental Antarctica, 66°17'S, 110°31'E, 15–40 m above sea level (Fig. 1; Table 1). The ice-free surface was mainly fellfield, that is, a cold-desert soil consisting of weathered granitoidic

debris with very little organic material (Paul and others 1995); soil types included regosols, leptosols, and lithosols (Blume and Bölter 1993, 1996). Samples were usually collected from regions lacking macroscopic vegetation. Moss cushions grew locally between larger boulders; soil type under moss was histosol (Blume and Bölter 1993, 1996). Parts of ice-free coastal areas and inshore islands were often occupied by Adélie penguin (Pygoscelis adeliae) rookeries. Accumulated guano covered the stony ground forming ornithogenic soil. Algal ornithogenic soil, which was densely overgrown with the nitrophilic, membranous green alga Prasiola crispa, was collected from the edge of the penguin colonies. It was nutrient-rich due to bird excreta and run-off from the rookeries and had a considerably lower pH (about 4.8) than soil within colonies (pH 7.2; Roser and others 1993). During daytime, the temperature was generally distinctly higher in soil than in air, that is, frequently above freezing; it was usually below zero at night, when soils often refroze. In winter, the area is covered with snow and ice.

The ciliates described in this paper were found not only at the sites mentioned below, but also at some other locations of the study area (Table 1).

Protospathidium serpens: found in algal ornithogenic soil on 28 January 1994 in the 0–2 cm layer, Whitney Point, Clark Peninsula (population I); and on 4 January 1994 in 0–3 cm, Beall Island, Windmill Islands (population II).

Protospathidium terricola: found on 28 January 1994 in the 0–2 cm layer of algal ornithogenic soil, Whitney Point, Clark Peninsula; on 16 December 1993 in 0–3 cm, Beall Island, Windmill Islands; and on 2 December 1993 in 0–3 cm, north coast of Shirley Island, Windmill Islands:



Fig. 1. Map of study area, Casey Station, Wilkes Land, East Antarctica.

Spathidium seppelti: discovered on 29 November 1993 in 0–3 cm depth of algal ornithogenic soil, north coast of Shirley Island, Windmill Islands.

Odontochlamys wisconsinensis: found on 30 January 1994 in 0–3 cm depth of algal ornithogenic soil, Beall Island, Windmill Islands; and on 27 December 1993 in the topmost 0–3 cm layer of mineral soil under moss, Reeve Hill, Casey Station.

Pseudochilodonopsis mutabilis: found on 29 November 1993 in 0–3 cm depth of algal ornithogenic soil, north coast of Shirley Island, Windmill Islands.

Oxytricha opisthomuscorum: occurred on 25 November 1993 in Grimmia antarctici and Bryum pseudotriquetrum moss, Casey Station.

Sterkiella histriomuscorum: occurred between 27 November 1993 and 9 February 1994 in 0–3 cm depth of fellfield, southwest of Casey Station.

Immediately after collection, raw cultures were established by saturating soil samples with deionized water in glass Petri dishes of 20 cm diameter. Morphogenesis of *S. histriomuscorum* was studied in specimens from pure cultures initiated with a few individuals from raw cultures; indigenous soil bacteria grown on crushed wheat grains were provided as food.

Field material and raw cultures were used for live observation and *in vivo* measurements at 100–1000 times magnification. Although these measurements provide only rough estimates, it is worth giving such data because specimens usually contract or shrink during preparation. Biomass was estimated from biovolume using a conversion factor of 1 μ m³ = 1 pg protoplasm (Finlay 1982); volume was calculated from *in vivo* dimensions and apply-

ing standard geometric figures to cells. Specimens from raw cultures were impregnated with protargol according to Wilbert (1975) and used for morphometric analyses; counts and measurements were performed at 1000 times magnification (one measuring unit = $1.3 \ \mu$ m). Drawings of impregnated cells were made with a camera lucida, whereas the live aspect was based on free-hand sketches. All figures are oriented with the anterior end of the organism directed to the top of the page. Terminology mainly follows Kahl (1932), Corliss (1979), and Berger and Foissner (1997).

Abundances of active ciliates were estimated in fresh soil samples using a direct counting method (for details, see Petz 1997). Soil temperature and pH (in deionized water) were measured electrometrically; water content and loss on ignition (unsifted soil) were assessed after airdrying and, respectively, by combustion at 550°C in a muffle furnace.

Two protargol-impregnated type slides of Spathidium seppelti, one neotype each of Odontochlamys wisconsinensis and Oxytricha opisthomuscorum, and voucher slides of Pseudochilodonopsis mutabilis, Protospathidium terricola, and Sterkiella histriomuscorum have been deposited in the Oberösterreichische Landesmuseum (LI), A-4040 Linz, Austria. Relevant specimens are marked by a black ink circle on the cover glass.

Description of species

Protospathidium serpens (Kahl, 1930) Foissner, 1981

The macronuclear configuration is apparently rather variable in *P. serpens* and other small spathidiids. Thus, Foissner (1996) concluded that detailed data are required from several populations to decide whether *P. serpens* and *P. muscicola* Dragesco and Dragesco-Kernéis, 1979 are distinct species. Accordingly, we provide a comprehensive morphometry of two Antarctic populations of *P. serpens*. The following description is mainly based on population I and mentions only supplementary or slightly differing observations.

Additional observations (Figs 2–5; Table 2)

Size highly variable, *in vivo* 43–117 x 8–25 μ m, however, usually about 65–90 x 15–20 μ m (Table 2). Macronuclear shape also highly variable (Figs 2–5): nodular in 60% (n = 92), rather widely wound in 38%, and rod-like in 2% of interphase specimens of population I; narrowly tortuous in 58% (*n* = 106), nodular in 34%, rod-like in 5%, U-shaped in 2%, and ellipsoidal in 1% of population II. Micronuclei slightly more numerous but smaller in population I than II, often adjacent to or in shallow depression of macronucleus; position in population II more constant than in population I, that is, usually one micronucleus each near anterior and posterior ends of macronucleus (Figs 3-5; Table 2). Extrusomes rod-shaped, in living specimens about 5 μ m long. Food vacuoles about 10–20 μ m across, possibly containing heterotrophic flagellates. Movement slow, rotates about main body axis when swimming, glides between soil particles.

Table 1. Community composition at selected sites of Wilkes Land (1 = moss, Casey Station, $66^{\circ}17$ 'S, $110^{\circ}31$ 'E; 2 = mineral soil under moss, Reeve Hill, Casey Station, $66^{\circ}17$ 'S, $110^{\circ}31$ 'E; 3 = fellfield, southwest of Casey Station, $66^{\circ}17$ 'S, $110^{\circ}31$ 'E; 4 = algal ornithogenic soil, Whitney Point, Clark Peninsula, $66^{\circ}16$ 'S, $110^{\circ}32$ 'E; 5 = algal ornithogenic soil, Shirley Island, Windmill Islands, $66^{\circ}17$ 'S, $110^{\circ}29$ 'E; and 6 = algal ornithogenic soil, Beall Island, Windmill Islands, $66^{\circ}18$ 'S, $110^{\circ}28$ 'E), where the described ciliate populations were found. + present; – absent.

Species			Site	s		
	1	2	3	4	5	6
Ciliates						
Bryometopus sp.	+	-	_	_		-
Bryophyllum cf. loxophylliforme	+	-	-	-	-	-
Colpoda cucullus (Mueller, 1773)	-		+	_	+	_
Colpoda inflata (Stokes, 1884)	-	+	+	_	+	-
Colpoda maupasi Enriques, 1908		-	+	_		
Cyclidium muscicola Kani, 1931	+	_	_	-	_	_
Cyrtolophosis elongata (Schewiakoff, 1892)	+	-		_	-	-
Euplotes sp.	+	-		_	+	_
Fuscheria terricola Berger and others, 1983	+	+	+	-		+
Gastronauta derouxi Blatterer and Foissner, 1992	+	-		-		_
Halteria grandinella (Mueller, 1773)	-	-	+	-	_	-
<i>Holosticha sigmoidea</i> Foissner, 1982	+	-	_	-	+	+
<i>Homalogastra setosa</i> Kahl, 1926	-		-	_	+	+
<i>Lamtostyla edaphoni</i> Berger and Foissner, 1987	-	-	-		+	-
<i>Leptopharynx costatus</i> Mermod, 1914	+	+.				-
Litonotus sp.	-	_		-	+	-
<i>Nassula</i> sp.	-		-	_	+	-
Odontochlamys wisconsinensis (Kahl, 1931)	-	+	+	+	-	+
<i>Opercularia</i> sp.	-	-	-	—	+ ,	-
Oxytricha opisthomuscorum Foissner and others, 1991	+	-	_	-		-
Parafurgasonia sp.	+		-	-	-	-
<i>Paraholosticha muscicola</i> (Kahl, 1932)	+	—	-	+	+	+
<i>Plagiocampa difficilis</i> Foissner, 1981	-	-	_	-	+	-
Platyophrya vorax Kahl, 1926	+	+	+	+		+
Protospathidium serpens (Kahl, 1930)	-	-	-	+	-	+
Protospathidium terricola Foissner, in press	-	_	-	+	+	+
Pseudochilodonopsis mutabilis Foissner, 1981	-	-	—	-	+	-
Pseudocohnilembus sp.	+	+	+		-	+
Pseudoholophrya terricola Berger and others, 1984		-	-	-	+	+
Pseudoplatyophrya nana (Kahl, 1926)	+	+	+ '	-		-
Pseudoplatyophrya cf. saltans	-	+	_	_	-	-
Sathrophilus muscorum (Kahl, 1931)	+	_	+	_	+	+
Spathidium seppelti nov. spec.	-	-	-	-	+	-
Sterkiella histriomuscorum (Foissner and others, 1991)		_	+	_	-	-
Sterkiella thompsoni Foissner, 1996	+	-	+	_	-	-
Trithigmostoma sp.	+	-	-	—	-	-
Vorticella astyliformis Foissner, 1981	+	+	+	_	+	+
Vorticella infusionum Dujardin, 1841	+	_	-	-	-	-
Testate amoebae						
Assulina muscorum Greeff, 1888	+	+	÷	-	-	-
Corythion dubium Taranek, 1881	+	+	+	-	-	-
Euglypha rotunda Wailes and Penard, 1911	+	+	+	-	-	-
Pseudodifflugia gracilis var. terricola Bonnet and Thomas, 1960	-	+	-	-		-
Schoenbornia viscicula Schoenborn, 1964	-	÷	+	-	-	-
Trachelocorythion pulchellum (Penard, 1890)	+		_			-
Gymnamoebae	+	+	-	_	-	-
Flagellates	+	+	+	-	+	+
Algae (often Prasiola crispa)	-	_		+	+	+
Nematodes	+	+	+	_	-	_
Rotifers	+	+	+	+	+	-
Tardigrades	+	+	+	_	+	_
Mites	+	+	_	_	_	_
				-		



Figs 2–5. *Protospathidium serpens*, variability of macronuclear shape in population I (2) and population II (3–5) after protargol impregnation. Ma = macronucleus; Mi = micronucleus. Length of cells 65–105 μ m.

Population I more densely ciliated than population II (Table 2). Dorsal brush as specified by Foissner (1996), that is, row 3 extends almost to mid-body with anterior portion composed of paired bristles and with posterior portion consisting of monokinetids with cilia about 2 μ m long.

Specimens encysted within about 15 min when transferred from the raw culture to Eau de Volvic (French table water). Resting cysts about 25 μ m across, structured as described by Foissner (1996).

Occurrence and ecology in Wilkes Land

First record for continental Antarctica, but previously found on Signy Island, maritime Antarctic (Foissner 1996). Occurred in fresh as well as air-dried and remoistened samples (pH 5.5) at 8–20°C, together with various other organisms (Table 1). Wet biomass of 10⁶ individuals: 10 mg (population I).

Comparison with other populations and related species The populations of *P. serpens* from Wilkes Land are similar to those described from Signy Island (Foissner 1996) and Europe (Kahl 1930a; Foissner 1981). However, the European specimens have slightly fewer (about eight on average) somatic kineties than those from the Antarctic and sub-Antarctic ($\bar{x} = 11-13$, Table 2; Foissner 1996). Spathidium sp. found by Thompson (1972, fig. 6) and Thompson and Croom (1978) in meltwater pools and in a lake on Anvers Island off the Antarctic Peninsula is similarly sized and shaped as *P. serpens*, but possesses a very long and often loosely coiled macronucleus and 14-17 somatic kineties.

The specimens identified as *P. serpens* by Berger and others (1984) possess 15–30 macronuclear nodules and are thus very likely conspecific with *P. muscicola*, as

already supposed by Foissner (1996). Although the latter differs only by the fragmented macronucleus from P. *serpens*, it should be classified as valid species because P. *serpens* has a single, vermiform nucleus.

Protospathidium terricola Foissner, in press

As the original description is based on an African population, a detailed redescription is provided. Of the three populations found (Table 1), that from Whitney Point was studied in detail.

Description (Figs 6-15; Table 3)

Size highly variable, *in vivo* about $134 \times 31 \mu m$ (Table 3). Shape dependent on nutritional state, slenderly to rather broadly cylindroid with neck usually distinctly narrowed and curved dorsally (Figs 6, 11–14); cross-section circular, neck and oral bulge laterally somewhat flattened. Oral bulge slightly concave and short, but usually slightly wider than neck, often somewhat inclined to ventral side, packed with extrusomes. Macronucleus in living specimens about $30-38 \times 12-22 \,\mu\text{m}$, basically reniform but rather variable in detail (Figs 6, 7, 11–13): sausage-like (28%, n = 115), Cshaped (25%), ellipsoidal (24%) or helically wound (23%); contains spherical to ellipsoidal nucleoli 1.5–4 μ m across. Micronucleus globular to slightly ellipsoidal, adjacent to macronucleus. Contractile vacuole in posterior end, with up to nine excretory pores. Extrusomes rod-like with rounded ends, 4–8 μ m, usually about 5 μ m long in living specimens, in oral bulge and cytoplasm; fusiform extrusomes found only in cytoplasm are very likely developmental stages.

Cortex flexible and colourless, with four to five, rarely up to eight rows of minute (about 0.2 μ m), pale granules between each two ciliary rows; granules stain reddish with methyl green-pyronin but are not extruded. Cytoplasm with numerous small, colourless granules, some fat droplets up to 4 μ m across, and food vacuoles containing bright green globules (algae?, up to 13 μ m across), many pale green spherical to ellipsoidal (up to 6 x 3 μ m) cyanobacteria, flagellates, and ciliates (for example, *Odontochlamys wisconsinensis*). Rotates about main body axis when swimming with neck usually curved dorsally; glides between and on soil particles, often recoils and changes direction.

Circumoral kinety oval in frontal view, discontinuous, that is, composed of dikinetidal fragments adhering to anterior ends of somatic kineties and separated from each other by indistinct gaps, which are often difficult to recognize, especially on right side (Figs 9a and 9b). Dorsal brush three-rowed, rows 1 and 2 almost of same length (Table 3) and mainly composed of paired cilia; row 3 consists of a short, dikinetidal anterior portion and a long, monokinetidal tail with about 2.5 μ m long bristles terminating near mid-body; brush rows at posterior end often with one to six apparently unciliated basal bodies before continuing backwards as normal somatic kineties (Figs 9a and 10). Cilia of brush dikinetids highly differentiated, clavate, anterior cilium usually longer (about 2–4 μ m) than posterior (approximately 1–2.5 μ m), in rear portion of

Table 2. Morphometric characteristics from *Protospathidium serpens*, population I (upper line) and population II (lower line). Except where noted, based on randomly selected, protargol-impregnated and mounted specimens from raw cultures. Measurements in μ m. CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; n = number of individuals investigated; SD = standard deviation; \bar{x} = arithmetic mean.

Character	\overline{x}	М	SD	CV	Min	Max	n
Body, length <i>in vivo</i> (population I)	68.1	66.5	20.9	30.7	43.0	117.0	12
Body, width in vivo (population I)	12.8	12.0	4.9	38.2	8.0	25.0	11
Body, length	82.9	86.0	14.9	18.0	48.0	102.0	20
	72.2	70.0	17.9	24.8	38.0	114.0	31
Body, maximum postoral width	20.7	20.0	5.0	24.3	11.0	30.0	20
	14.9	14.0	2.8	16.0	11.0	22.0	31
Anterior end to macronucleus, distance	28.2	29.5	8.7	30.8	15.0	50.0	20
	22.1	22.0	5.0	22.7	10.0	34.0	31
Oral bulge, length	9.0	9.0	1.1	11.8	6.0	10.0	16
	7.9	8.0	1.3	16.3	5.0	11.0	31
Oral bulge, height	3.1	3.0	0.7	23.0	2.0	4.0	16
	2.5	2.5	0.5	19.2	1.5	3.0	31
Macronuclear figure, length	35.9	35.0	11.4	31.9	17.0	58.0	20
Management and the	34.2	34.0	6.5	19.1	20.0	48.0	31
Macronucleus, width	6.7	7.0	1.7	25.4	4.0	9.0	20
Minnervaleur dieventer	5.8	6.0	1.0	17.7	4.0	8.0	31
Micronucleus, diameter	2.1	2.0	0.3	14.3	1.5	3.0	28
Extructment length	2.7	2.5	0.4	13.3	2.0	3.5	31
Exitusomes, lengin	2.5	2.5	0.4	17.0	1.5	3.0	25
Nematodesmata longth	2.3	2.3	1.4	16.3	2.0	10.0	24
Nematodesmata, length	11.2	10.0	20	26.2	7.0	17.0	31
Macronucleus number	10	10.0	2.9	20.2	1.0	20	02
Macronucleus, number	1.0	1.0	_	_	1.0	2.0	106
Micronuclei number	29	3.0	11	36.9	1.0	5.0	20
	2.1	20	0.6	30.0	1.0	4.0	32
Somatic kineties, number	13.0	13.0	1.2	9.0	11.0	16.0	31
· · · · · · · · · · · · · · · · · · ·	11.1	11.0	0.8	7.4	10.0	12.0	32
Basal bodies in a lateral kinety, number	36.2	37.0	6.3	17.3	24.0	50.0	17
n no a si un la sense in lana de munacionenzador cario der a 7 militario den inte	22.4	22.0	5.1	22.8	12.0	34.0	30
Dorsal brush, number of rows	3.1	3.0		-	3.0	4.0	22
	3.0	3.0	-	-	3.0	4.0	32
Brush kinety 1, length	3.6	3.5	0.6	16.4	3.0	5.0	21
	4.6	4.3	1.6	34.7	2.5	8.5	26
Brush kinety 2, length	9.3	9.5	1.2	13.4	7.0	12.0	22
	9.0	9.0	2.4	26.4	4.5	12.5	31
Brush kinety 3, length	8.8	8.0	2.0	22.3	6.0	13.0	15
	7.1	7.0	2.4	34.2	3.5	12.0	28
Brush kinety 3, total length (including dikinetids	28.8	28.0	6.4	22.2	18.0	44.0	19
and single basal bodies with shortened cilia)	28.1	26.0	8.4	29.7	19.0	41.0	13
Dikinetids in brush kinety 1, number	3.4	3.0	1.0	27.5	1.0	5.0	23
	2.9	3.0	1.0	36.5	1.0	5.0	28
Dikinetids in brush kinety 2, number	9.2	9.0	1.5	16.3	6.0	12.0	29
Dillipstide in bouch binst of	6.9	7.0	1.6	23.5	4.0	10.0	31
Dikinetids in brush kinety 3, number	6.6	7.0	1.4	21.2	4.0	9.0	31
	4.5	4.5	1.2	25.9	3.0	7.0	30

brush gradually shortened; two to eight distinctly elongated cilia (6–8 μ m) in anterior portion of row 3 (Fig. 10).

Specimens may encyst rapidly, that is, the first cyst appeared 6 min after transfer from the raw culture to Eau de Volvic; after 30 min all (about 10) individuals were encysted. About one-week-old resting cysts 49–52 μ m in diameter ($\bar{x} = 50, n = 4$), wall about 1.5 μ m thick, smooth, vitreous. Cytoplasm with many about 1- μ m-sized granules and tortuous to C-shaped macronucleus containing spherical nucleoli (Fig. 15).

Occurrence and ecology in Wilkes Land

First record for Antarctica. Occurred in fresh as well as airdried and remoistened samples (pH 5.1–5.5) at 8–20°C, together with various other organisms (Table 1). Wet biomass of 10^6 individuals: 61 mg.

Comparison with type population and related species The Antarctic specimens match the original description by Foissner (in press) fairly well. They are, however, slightly larger ($\bar{x} = 101 \times 32 \times 81 \times 23$), have fewer ($\bar{x} = 17 \times 21$) ciliary rows, and the fragments of the circumoral kinety are



Figs 6–15. *Protospathidium terricola* from life (6, 10–15) and after protargol impregnation (7–9). 6: left lateral view of typical specimen; 7, 8: infraciliature of left and right side of same specimen. Arrowhead marks pores of contractile vacuole; 9a, 9b: infraciliature of left and right anterior side; 10: dorsal brush; 11–14: shape variability of body and macronucleus; 15: resting cyst. C = circumoral kinety; D = dorsal brush; Ma = macronucleus; Mi = micronucleus; S = somatic monokinetids with normal cilia. Scale bar division 10 μ m.

less distinctly separated from each other (Figs 9a and 9b; Table 3; Foissner, in press). Thus, impregnated specimens, particularly when not properly orientated, are easily confused with *Spathidium claviforme* Kahl, 1930. However, a reinvestigation of the neotype population of *S. claviforme*, which invariably has a continuous circumoral kinety and 10–13 ciliary rows (Foissner 1987), revealed that the Antarctic specimens belong to P. terricola.

Protospathidium serpens is shorter (about 70–80 μ m on average) and has fewer ($\bar{x} = 8-13$) somatic kineties (Table 2; Foissner 1981, 1996). Protospathidium muscicola possesses a multinodular macronucleus and only 7–12 ciliary rows (Dragesco and Dragesco-Kernéis 1979; Berger and others 1984; see above).

Table 3. Morphometric characteristics from *Protospathidium terricola*, Whitney Point population (upper line) and *Spathidium seppelti*, type population (lower line). Except where noted, based on randomly selected, protargolimpregnated and mounted specimens from raw cultures. Measurements in μ m. CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; n = number of individuals investigated; SD = standard deviation; \bar{x} = arithmetic mean.

Character	\overline{x}	М	SD	CV	Min	Max	n
Body, length in vivo (P. terricola)	133.8	132.5	25.8	19.3	88.0	175.0	14
Body, width in vivo (P. terricola)	30.8	31.0	3.5	11.4	25.0	35.0	12
Body, length	101.0	91.0	23.6	23.3	68.0	150.0	31
	99.3	99.5	15.7	15.8	68.0	131.0	30
Body, maximum postoral width	32.3	33.0	5.6	17.3	23.0	44.0	31
	24.8	24.5	4.4	17.5	17.5	33.0	30
Anterior end to macronucleus, distance (P. terr.)	59.5	60.0	15.2	25.6	31.0	87.0	31
Oral bulge, length	17.2	17.0	3.5	20.3	10.0	26.0	31
	31.5	31.0	6.7	21.3	16.0	43.0	29
Oral bulge, height	3.9	4.0	1.0	24.9	2.0	6.0	30
	2.8	2.5	0.5	18.6	2.0	4.0	28
Macronuclear figure, respectively, macronuclear	33.6	33.0	4.7	13.8	24.0	43.0	31
nodule, length	4.5	4.8	1.7	36.8	2.0	8.0	30
Macronucleus, respectively, macronuclear	13.4	13.0	2.3	16.8	8.5	21.0	31
nodule, width	2.5	2.5	0.5	18.6	2.0	3.5	30
Micronucleus, diameter	3.1	3.0	0.5	15.9	2.5	4.0	6
	1.3	1.5	0.3	22.7	1.0	2.0	30
Extrusomes, length	5.8	6.0	0.8	13.6	4.0	7.0	31
	3.3	3.3	0.6	18.2	2.5	4.0	6
Nematodesmata, length	24.4	26.0	7.8	31.7	14.0	45.0	23
	50.2	47.0	11.8	23.6	34.0	71.0	13
Macronuclei, number	1.0	1.0	-	-	1.0	1.0	30
	-	-	-	about	100.0	200.0	10
Micronuclei, number	1.0	1.0	-	-	1.0	1.0	5
	12.1	12.0	4.3	35.7	6.0	20.0	17
Somatic kineties, number	17.4	17.0	1.2	6.6	15.0	19.0	31
	21.1	21.0	2.0	9.3	18.0	25.0	16
Basal bodies in a lateral kinety, number	42.3	43.0	6.6	15.7	31.0	60.0	24
	32.2	30.0	6.9	21.3	24.0	46.0	14
Dorsal brush, number of rows	3.0	3.0	-	-	3.0	4.0	31
	3.1	3.0	—	-	3.0	4.0	17
Brush kinety 1, length	15.2	14.0	3.8	25.1	9.0	23.0	31
	18.1	18.0	3.5	19.4	12.0	25.0	17
Brush kinety 2, length	18.7	19.0	3.9	20.8	12.0	30.0	31
	22.3	22.0	5.0	22.5	16.0	30.0	17
Brush kinety 3, length	9.9	9.0	2.6	26.0	6.0	15.5	28
	9.6	9.0	2.5	26.2	7.0	17.0	14
Brush kinety 3, total length (including dikinetids	52.8	48.0	10.7	20.3	34.0	72.0	31
and single basal bodies with shortened cilia)	61.0	61.0	14.1	23.1	47.0	95.0	9
Dikinetids in brush kinety 1, number	14.3	14.0	2.9	20.3	9.0	20.0	31
	14.0	13.0	4.0	28.8	8.0	21.0	17
Dikinetids in brush kinety 2, number	20.3	20.0	3.6	17.6	15.0	28.0	31
	17.6	18.0	4.5	25.8	12.0	30.0	17
Dikinetids in brush kinety 3, number	8.9	9.0	1.6	17.7	5.0	12.0	31
	8.2	8.0	2.1	24.9	5.0	13.0	13

Spathidium seppelti nov. spec.

Diagnosis

Size *in vivo* about 80–140 x 20–40 μ m, spatulate. Oral bulge about one-third longer than maximum postoral width, inclined to ventral side, with eccentric depression. 100–200 macronuclear nodules. On average 21 somatic kineties. Terricolous.

Type location

Algal ornithogenic soil near an Adélie penguin rookery,

north coast of Shirley Island, Windmill Islands, continental Antarctica (66°17'S, 110°29'E).

Dedication

Named in honour of Dr Rod D. Seppelt, Australian Antarctic Division, Kingston, Tasmania, in appreciation of his support of this investigation.

Description (Figs 16–26; Table 3)

Body narrowed behind oral bulge, posterior end more broadly rounded in impregnated than in living specimens



Figs 16–29. Spathidium seppelti (16–26) and related species (27–29) from life (16, 20, 21, 26–29) and after protargol impregnation (17–19, 22–25). 16: left lateral view of typical specimen. Arrowhead marks eccentric depression in oral bulge; 17–19: infraciliature of left and right side, as well as nuclear apparatus, extrusomes and nematodesmata of same specimen; 20: cortical granulation; cilia indicated by short lines; 21: frontal view of oral bulge; 22: dorsal brush; 23–26: shape variants; 27: *Spathidium* sp. from Signy Island (from Smith 1978); 28, 29: *Spathidium bavariense*, left lateral view and detail of oral bulge (from Kahl 1930a, 1930b). D = dorsal brush; E = extrusomes; Ma = macronucleus; Mi = micronucleus; N = bundles of nematodesmata; S = somatic monokinetids with normal cilia. Scale bar division 10 μ m.

(Figs 16 and 17); cross-section circular in mid-body, neck and oral bulge laterally distinctly flattened and rather flexible and hyaline. Oral bulge slightly to considerably inclined ventrally, with distinct conical depression in dorsal third (Figs 16 and 21); about one-third longer than maximum postoral width on average, anterior end thus distinctly set off from narrowed neck, appears obliquely truncate in living specimens but convex after protargol impregnation (Figs 16, 17, 23-26). About 100-200, usually 120-150 ellipsoidal to globular macronuclear nodules, each with one to two large (1-1.5 μ m in diameter) and some tiny (>1 µm) nucleoli (Fig. 19). Micronuclei globular, irregularly distributed, number variable and often difficult to determine because of many similarly sized cytoplasmic inclusions. Contractile vacuole in rear end, with one to four excretory pores in posterior pole area. Extrusomes rod-shaped, $3-4 \mu m \log in vivo$, found only in oral bulge (Figs 16 and 19). Pellicle colourless, slightly furrowed by ciliary rows; cortical granules 0.5 μ m in diameter, pale, arranged in two to three indistinct rows between each two kineties (Fig. 20). Cytoplasm rather hyaline, contains some fat droplets (about 5 μ m across) and food vacuoles with ciliates (for example, hypotrichs); well-fed and thus rather opaque specimens filled with 8-10 μ m-sized, ellipsoidal to roundish inclusions. Moves rather fast in straight lines, changing direction frequently.

Somatic kineties bipolar, rather loosely ciliated, those of right side abut to circumoral kinety at acute angles, while those of left side, which have three to five narrowly spaced cilia at anterior end, abut at right angles (Figs 17 and 18). Dorsal brush three-rowed, rows 1 and 2 almost of same length (Table 3) and composed of narrowly spaced dikinetids having 3–4 μ m long, rod-shaped cilia; row 3 consists of a short, dikinetidal anterior portion with 3–4 μ m long cilia and a long, monokinetidal posterior tail having 2–4 μ m long bristles and terminating behind midbody (Fig. 22); all brush rows continue posteriorly as normal somatic kineties.

Circumoral kinety continuous (not fragmented), composed of narrowly spaced dikinetids having long nematodesmata forming wedge-shaped bundles (Figs 17– 19).

Occurrence and ecology in Wilkes Land

Found together with various organisms (Table 1). Edaphic parameters: loss on ignition 7.8% of dry mass, pH 5.1–5.6. Occurred in the laboratory at room temperature (about 19° C). Wet biomass of 10^{6} individuals: 65 mg.

Systematic position and comparison with related species The anterior portion of the left lateral kineties of *S. seppelti* does not duplicate the circumoral kinety. Thus, it belongs to the genus *Spathidium* (Foissner 1984). However, the eccentric, conical indentation of the oral bulge is a very peculiar characteristic.

Spathidium sp. found by Smith (1978) on sub-Antarctic and maritime Antarctic islands is probably conspecific with *S. seppelti* because, as indicated by the figure given (Fig. 27), it is rather similarly sized and shaped and has, apparently, many macronuclear nodules. However, a definite identification is impossible because Smith's (1978) figure is not accompanied by a description.

At first glance, *S. seppelti* resembles a small *Epispathidium regium* Foissner, 1984, which has, however, considerably more ($\bar{x} = 41$ vs 21) and differently arranged somatic kineties (anterior ends strongly curved and thus duplicating circumoral kinety). With regard to the number of macronuclei, *S. seppelti* resembles *S. meloforme* Alekperov, 1983 (150–200 nodules) and *S. chlorelligerum* Kahl, 1930 (50–100 nodules). However, the former is broadly fusiform, has many more somatic kineties (75–80 vs 18–25), and was found in rearing ponds of a sturgeon hatchery. The latter is distinguished from *S. seppelti* by the larger size (200–400 vs 80–140 μ m), the longer extrusomes (10–12 vs 3–4 μ m), the number of somatic kineties (40–50 vs 18–25), and the possession of symbiotic algae (Kahl 1930a, 1930b; Vuxanovici 1959).

Spathidium seppelti greatly resembles S. bavariense Kahl, 1930. However, the oral bulge of S. bavariense turns back at the dorsal end and duplicates this section (Fig. 29), making the dorsal portion twice as thick as the ventral one (Kahl 1930a, 1930b; Wenzel 1953). Furthermore, S. bavariense has a distinctly lower number of macronuclear nodules (15–35 vs 100–200) and a relatively shorter oral bulge than S. seppelti (Fig. 28). The individuals found by Wenzel (1953) were only about 70 μ m long (his drawing indicates 95 μ m).

Spathidium sp. found by Vuxanovici (1962a) resembles S. seppelti in size, number of somatic kineties, and extrusomes. However, it is differently shaped (elongate drop-like), has only about 11 macronuclear nodules, and occurred in a lake.

Spathidium multinucleatum Gellért, 1955, described without figure, matches *S. seppelti* in body size and number of somatic kineties, but differs by having long extrusomes (exact length, however, not given), distinctly fewer macronuclei (30–32), and a short, very slightly ventrally inclined oral bulge.

Several other and sometimes very poorly described *Spathidium* species, such as *Spathidium ampulliforme* Srámek-Husek, 1954, *S. armatum* Vuxanovici, 1959, *S. inflatum* Vuxanovici, 1962b, *S. longicolum* Vuxanovici, 1962c, *S. metabolicum* Pomp and Wilbert, 1988, *S. nigrum* Vuxanovici, 1959, and *S. plurinucleatum* André, 1916, have a multinodular macronucleus, but differ considerably from *S. seppelti* at least in shape, size, extrusomes, and number of somatic kineties or macronuclear nodules.

Odontochlamys wisconsinensis (Kahl, 1931) nov. comb. Improved diagnosis

Size *in vivo* usually $40 \times 22 \,\mu$ m. Four kineties in right field, six in left. Dorsal brush near anterior end in midline of cell, consists of four narrowly spaced cilia on average. Oral basket composed of 14 rods on average. Dorsal hump regular.

Redescription (Figs 30-36; Table 4)

Size highly variable, in vivo about 25–60 x 12–30 μ m.



Figs 30–36. *Odontochlamys wisconsinensis* from life (30, 33–36) and after protargol impregnation (31, 32). 30: ventral view of typical specimen; 31, 32: infraciliature of ventral and dorsal side. Arrowheads mark pore of contractile vacuoles; 33: lateral view; 34: cilium from dorsal brush; 35, 36: ventral and lateral view of encysting specimen. D = dorsal brush; H = outline of dorsal hump; L = left kinety field; Ma = macronucleus; P = preoral kinety; R = right kinety field. Scale bar division 10 μ m.

Body flexible but acontractile, distinctly rostrate at anterior left, posteriorly usually slightly narrowed, right margin convex, left sigmoidal (Fig. 30). Dorsoventrally flattened about 1.5–2:1, ventral side sometimes slightly concave (Fig. 33). Dorsal hump projecting somewhat above ventral surface, outline regular elliptical to beanshaped, without lobes (Fig. 32), rarely with shallow, moreor-less longitudinal furrows (very likely beginning encystment) (Fig. 36). Macronucleus ellipsoidal, *in vivo* about 13 x 9 μ m, usually in posterior half of body, contains one central nucleolus, 4–5 μ m across, and several 1–2.5 μ m-sized, spherical nucleoli in periphery. Micronucleus globular, 2–2.5 μ m across, near macronucleus, usually not impregnated with protargol and indistinguishable from roundish cell inclusions. Two contractile vacuoles, one above mid-body with excretory pore usually between first and second innermost kinety of right field, the other slightly behind mid-body with pore close to posterior end of third kinety from left. Cytoplasm rather transparent, contains many tiny, colourless granules and food vacuoles with greenish contents and bacteria. Slowly gliding on substrate particles; thigmotactic.

Ventral ciliary rows (kineties) in two fields, cilia 4–5 μ m long, in anterior portion slightly longer than in poste-

Table 4. Morphometric characteristics from *Odontochlamys wisconsinensis*. Based on randomly selected, protargolimpregnated and mounted specimens from raw cultures. Measurements in μ m. CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; n = number of individuals investigated; SD = standard deviation; \bar{x} = arithmetic mean.

Character	\overline{x}	М	SD	CV	Min	Max	n
Body, length	37.9	37.0	5.9	15.5	30.0	57.0	31
Body, width	17.4	17.0	3.2	18.6	10.5	28.0	31
Macronucleus, length	12.7	13.0	2.2	17.3	8.0	17.0	31
Macronucleus, width	7.6	8.0	0.9	11.2	5.5	9.0	31
Oral basket, length	10.4	10.0	1.2	11.6	9.0	13.0	31
Oral basket, maximum diameter	4.0	4.0	0.2	5.9	3.5	4.5	27
Dorsal brush, length	2.5	2.5	0.5	21.4	2.0	3.5	8
Preoral kinety, length	5.4	5.0	0.8	14.8	4.5	8.0	31
Innermost kinety of left field, length	8.6	8.8	1.7	19.8	6.0	11.5	14
2nd innermost kinety of left field, length	11.0	11.0	2.3	20.8	8.0	16.0	14
Distance, anterior end to							
dorsal brush	1.9	2.0	0.3	13.1	1.5	2.5	19
oral basket	5.0	5.0	1.0	19.2	4.0	7.0	31
dorsal hump	4.9	5.0	1.0	20.9	4.0	8.0	31
anterior excretory pore	12.6	13.0	2.5	19.8	8.0	19.0	17
posterior excretory pore	24.6	23.0	3.6	14.5	21.5	33.0	11
Macronuclei, number	1.0	1.0	_	_	1.0	2.0	31
Kineties of left field, number	6.0	6.0	-	-	6.0	6.0	31
Kineties of right field, number	4.0	4.0	-	-	4.0	5.0	31
Basal bodies in dorsal brush, number	4.3	4.0	0.6	12.9	3.0	5.0	22
Basal bodies in preoral kinety, number	12.4	13.0	1.0	7.8	11.0	14.0	13
Oral basket rods, number	14.2	14.0	1.2	8.4	12.0	16.0	12

rior. Kineties of right field arched, innermost row terminates anteriorly at level of cytostome, others extend to preoral kinety; outermost kinety anteriorly rather loosely ciliated, terminates subequatorially while other rows extend further backwards. Kineties of left field of differing length: four terminate at preoral row while two are shortened and situated in subequatorial area (Fig. 31). Dorsal brush close to anterior cell margin, cilia about 5 μ m long and distally narrowed (Figs 32 and 34; Table 4).

Preoral kinety straight or very slightly curved, transverse to main body axis, rather short, covers left end of anterior circumoral kinety (Fig. 31). Circumoral kineties arched and Y-shaped, anterior row composed of 12–14, posterior of seven to nine cilia. Oral basket opening subapically in cell midline; oral basket bulbous in protargol-impregnated specimens, directed slightly rightwards and dorsally, cornucopia-shaped, that is, with thin posterior portion, but usually only anterior part recognizable in living (6–12 μ m long) and protargol-impregnated specimens (Figs 30 and 31; Table 4). Oral basket rods anteriorly without teeth.

Encystment as in congeners (Foissner 1981, 1988; Blatterer and Foissner 1992), conspicuously fast and also induced by cover-slip pressure (Figs 35 and 36).

Occurrence and ecology in Wilkes Land

Occurred together with various organisms (Table 1). Up to 19 ($\bar{x} = 8, n = 5$) active individuals per gram dry mass of soil were found, comprising up to 100% of the ciliate community. Edaphic parameters: temperature -1.6° to +12°C, water content 2.5-7.4% of wet mass, loss on ignition 0.8-1.8% of dry mass, pH 5.7-6.8. Occurred also at 21°C in the laboratory and in dried and rewetted samples at 5°C. Wet biomass of 10^6 individuals: 6 mg.

Systematic position and comparison with related species There are several insufficiently described chilodonellids that are similarly sized and shaped as the Antarctic specimens. Thus, instead of erecting a new species, this population was identified with the most similar of these, namely Chilodonella wisconsinensis, published by Kahl (1931) without figure. It differs only slightly from the current specimens by the reduced number of ciliary rows in the left field (four vs six), the non-curved oral basket, and the deformed dorsal hump. Since these characters are variable and/or difficult to recognize in living cells, they might have been overlooked or misinterpreted by Kahl (1931). The specimens in this study have the dorsal brush, not studied in detail by Kahl (1931), in an apical position and are able to encyst very quickly. These characteristics are typical for Odontochlamys, to which C. wisconsinensis is thus transferred: O. wisconsinensis (Kahl, 1931) nov. comb.

In vivo, O. wisconsinensis is easily confused with Chilodonella uncinata (Ehrenberg, 1838) due to its similar size and shape (Fig. 41). However, C. uncinata has the dorsal brush in a distinct subapical and left marginal position (Fig. 42), as is characteristic for this genus (Foissner and others 1991).

Odontochlamys wisconsinensis is also rather similar to O. alpestris Foissner, 1981 (Figs 37 and 38), but has fewer right kineties (four vs five), more oral basket rods (12–16



Figs 37–42. Chilodonellids similar to *Odontochlamys wisconsinensis*, infraciliature of ventral and anterior dorsal side after protargol impregnation. 37, 38: *Odontochlamys alpestris* (from Blatterer and Foissner 1992); 39, 40: *Odontochlamys convexa* (from Blatterer and Foissner 1992); 41, 42: *Chilodonella uncinata* (from Foissner 1988). D = dorsal brush. Scale bar division 6 μ m.

vs about six to eight), and the preoral kinety overlaps the circumoral kineties only slightly because it is composed of fewer cilia (11–14 vs 14–27 according to the figures in Foissner 1981 and Blatterer and Foissner 1992). Two populations of *O. alpestris* were previously studied, one each from soil and fresh water (Foissner 1981; Blatterer and Foissner 1992). Their main characteristics, the number of oral basket rods and somatic kineties, were very similar and hardly variable. Thus, the Antarctic specimens were separated from *O. alpestris* at species level.

Odontochlamys convexa (Kahl, 1931) Blatterer and Foissner, 1992 differs from O. wisconsinensis by having more (five) kineties in the right field, fewer oral basket rods (eight to nine), a very irregularly folded dorsal hump, and a longer preoral kinety, which is composed of more (about 17) basal bodies and thus distinctly overlaps the circumoral kineties (Fig. 39). Furthermore, the dorsal brush, although being composed, as in O. wisconsinensis, of four cilia, is considerably longer because the cilia are more widely spaced (Fig. 40).

Odontochlamys gouraudi Certes, 1891 is readily distinguished from *O. wisconsinensis* by its spiny dorsal hump, five to six right field kineties, and the distinctly longer brush and preoral kinety composed of 6–15 and about 19–27 cilia, respectively (Buitkamp 1977; Foissner 1988).

Pseudochilodonopsis mutabilis Foissner, 1981

The Antarctic specimens of *P. mutabilis* (*in vivo* 32–50 μ m long) correspond rather well to those from more temperate regions (Foissner 1981; Song and Wilbert 1989; Blatterer and Foissner 1992). However, they have slightly fewer oral basket rods (about 12–14 vs about 15) and a more regular dorsal hump (vs irregularly folded). Drawings are thus provided of the ventral and dorsal side (Figs 43 and 44).

Occurrence and ecology in Wilkes Land

Occurred together with various organisms (Table 1). 20 active individuals per gram dry mass of soil were found, comprising 15% of the ciliate community. Edaphic parameters: water content 26.6% of wet mass, loss on ignition 7.8% of wet mass, pH 5.1. Wet biomass of 10⁶ individuals: 7 mg.

Oxytricha opisthomuscorum Foissner and others, 1991 Improved diagnosis

Size *in vivo* about 55–80 x 20–40 μ m. Two macronuclei and one micronucleus in between. Buccal cirrus near anterior end of paroral membrane. Twenty adoral membranelles, 12 right marginal cirri, 13 left marginal cirri, five transverse cirri, and three caudal cirri on average. Six dorsal kineties with about 10 μ m long cilia.

Redescription (Figs 45–54; Table 5)

In vivo usually 65–70 x 25–30 μ m, outline ellipsoidal to

fusiform because ends often narrowly rounded or bluntly pointed (Fig. 45), dorsoventrally flattened up to 2:1 (Fig. 46). Flexible, especially in anterior portion. Macronuclear nodules ellipsoidal to almost globular, in vivo about 16 x 10 μ m, with nucleoli 0.5–2 μ m across. Micronucleus globular, in vivo about 4-5 μ m in diameter, in 71% of specimens (n = 31) between macronuclei or slightly displaced laterally, in 16%, respectively, 13% adjacent to anterior or posterior nodule; one specimen had two micronuclei (Figs 45, 48, 52-54). Contractile vacuole

Figs 43, 44. Pseudochilodonopsis mutabilis, infraciliature of ventral and dorsal side after protargol impregnation. D = dorsal brush; H = outline of dorsal hump; Ma = outline of macronucleus; P = preoral kinety. Scale bar division 10 μ m.







Figs 45-54. Oxytricha opisthomuscorum from life (45, 46) and after protargol impregnation (47-54). 45, 46: ventral and lateral view of typical specimen; 47, 48: infraciliature of ventral and dorsal side of same specimen. Arrow marks last, slightly postorally located frontoventral cirrus; 49-51: dorsal views showing more or less distinct connections between dorsal kineties 3 (arrows) and 4 (arrowheads); 52-54: variability of body shape and micronucleus position. M = hook-shaped anterior margin of buccal cavity; Ma = outline of macronucleus; Mi = micronucleus; numbers denote dorsal kineties. Scale bar division 10 μ m.

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Table 5. Morphometric characteristics from *Sterkiella histriomuscorum* (S; upper line) and *Oxytricha opisthomuscorum* (O; lower line). Based on randomly selected, protargol-impregnated and mounted specimens from raw cultures. Measurements in μ m. CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; *n* = number of individuals investigated; SD = standard deviation; \bar{x} = arithmetic mean.

Character	\overline{x}	М	SD	CV	Min	Max	n
Body, length	83.7	83.0	8.4	10.1	66.0	102.0	31
	60.8	61.0	5.3	8.6	49.0	74.0	31
Body, width	44.3	44.0	6.0	13.6	35.0	57.0	31
	26.6	26.0	3.1	11.7	21.0	38.0	31
Anterior macronuclear nodule, length	20.1	20.0	3.1	15.3	14.0	29.0	31
	12.8	13.0	1.8	14.1	9.0	17.0	30
Anterior macronuclear nodule, width	10.4	10.0	1.5	14.3	8.0 E.0	15.0	20
Postoriar magranuclear podula longth	19.0	10.0	2.8	1/ 0	14.0	26.0	31
	13.0	13.0	2.0	17.1	9.0	17.5	30
Posterior macronuclear nodule width	9.8	9.5	1.6	16.3	8.0	14.0	31
	7.0	7.0	1.0	14.5	5.0	9.0	30
Micronucleus, length	3.2	3.0	0.5	14.3	2.5	4.5	31
	3.8	4.0	0.4	11.1	2.5	4.5	30
Micronucleus, width	2.7	2.5	0.3	12.5	2.0	3.5	30
	3.6	3.5	0.5	14.9	2.5	4.5	29
Adoral zone, length	37.4	37.0	3.5	9.4	31.0	45.0	31
	22.5	22.0	1.5	6.7	20.0	26.0	31
Paroral membrane, length	20.7	21.0	1.8	8.7	17.0	25.0	31
Fundamentary and some the	9.7	10.0	1.0	10.0	7.0	12.0	32
Endoral membrane, length	19.6	20.0	2.1	10.7	14.0	23.0	31
Dorsal cilia, Jongth (O)	9.4	9.5	13	130	8.0	12.0	22
Apex to buccal cirrus, distance (Ω)	9.5	10.0	1.3	11 1	8.0	12.0	31
Apex to paroral membrane distance (O)	8.3	8.0	0.9	11.1	6.5	10.5	31
Pharyngeal fibres, length	20.3	20.0	3.5	17.2	14.0	29.0	27
······	19.4	20.0	2.8	14.5	12.0	23.0	22
Macronuclear nodules, number	2.0	2.0	-	-	2.0	2.0	31
	2.0	2.0	-	-	2.0	3.0	31
Micronuclei, number	1.8	2.0	-	-	1.0	2.0	31
	1.0	1.0	-	-	1.0	2.0	32
Adoral membranelles, number	27.9	28.0	1.1	4.0	26.0	31.0	31
	20.3	20.0	0.9	4.5	18.0	22.0	33
Left marginal cirri, number	18.1	18.0	1.3	7.1	15.0	21.0	31
Pight morginal cirri number	13.1	13.0	1.0	7.6	19.0	15.0	23
night marginal cim, humber	20.5	21.0 12.0	1.1	0.0	11.0	16.0	26
Frontal cirri, number	3.0	3.0	-	- 0.5	3.0	3.0	31
	3.0	3.0	-	_	3.0	3.0	30
Buccal cirri, number	1.0	1.0	_		1.0	1.0	31
	1.0	1.0	-	_	1.0	1.0	30
Frontoventral cirri, number	4.0	4.0	-		4.0	4.0	31
	4.1	4.0		-	4.0	5.0	29
Postoral ventral cirri, number	3.0	3.0	0.3	8.6	2.0	4.0	31
	3.3	3.0	0.7	22.5	2.0	5.0	31
Pretransverse ventral cirri, number	2.0	2.0			2.0	2.0	31
Transverse similar work of	2.0	2.0	-	-	2.0	2.0	31
i ransverse cirri, number	5.0	5.0	-	-	5.0	5.0	31
Caudal cirri number	5.1	2.0		_	3.0	0.0	21
	3.0	3.0	_	_	3.0	3.0	26
Dorsal kineties, number	5.8	6.0	_	_	5.0	6.0	31
	6.0	6.0	_		6.0	6.0	25
Resting cyst, diameter in vivo (S)	38.9	38.0	2.9	7.4	33.0	44.0	11

near left margin in or slightly behind mid-body, with inconspicuous collecting canals. No cortical granules. Cytoplasm colourless but specimens rather dark at low magnification due to bright fat globules 1–3 μ m across, numerous elongate, irregular crystals 3–4 μ m long, and food vacuoles up to 10 μ m across containing bright and dark green algae and heterotrophic flagellates. Crawls moderately fast in straight line interrupted by short backward jerks; rotates about main body axis when swimming.

Marginal cirral rows almost confluent posteriorly, cirri in vivo about 16 μ m long, slightly elongated in rear portion of cell, bases composed of two basal body rows each. Frontal cirri each consisting of three to four, transverse cirri of up to five, and other cirral bases of three basal body rows. Buccal cirrus near anterior end of paroral membrane (Fig. 47; Table 5). Last frontoventral cirrus usually slightly behind oral vertex; three, rarely four or five (19%, n = 31)postoral ventral cirri in mid-body and two pretransverse ventral cirri in usual position; transverse cirri distinctly enlarged, 20-28 µm long in vivo and usually motionlessly trailing behind (Table 5). Dorsal kinety pattern as in other oxytrichids (for examples see O. longigranulosa Berger and Foissner, 1989 and O. rubripuncta Berger and Foissner, 1987): kineties 1 and 2 nearly as long as body; row 3 slightly to distinctly curved posteriorly and often indistinctly separated from its offspring, the very short kinety 4, which bears the right-most caudal cirrus; row 5 extends from anterior end to mid-body; row 6 consists of two to four cilia only (Figs 48–51). Dorsal cilia 8–10 μ m long and stiffly spread in vivo, do not beat like normal cilia but become soft and flexible under cover-slip pressure. Caudal cirri fine, about 20–24 μ m long, associated with dorsal kineties 1, 2, and 4 (Fig. 48).

Adoral zone of membranelles extends over about 37% of body length; longest bases about 6–7 μ m *in vivo*, cilia 15–23 μ m long. Buccal cavity inconspicuous, narrow and flat, anterior margin curved hook-like in living cells, right margin covered by inconspicuous hyaline lip (Fig. 45). Undulating membranes almost of same length, slightly curved, double-rowed paroral optically intersects apparently single-rowed endoral (Fig. 47); paroral cilia 3–4 μ m long. Pharyngeal fibres about 22 μ m long *in vivo*.

Occurrence and ecology in Wilkes Land

Occurred together with various organisms (Table 1). Up to 152 active individuals per gram dry mass of soil were found, comprising about 9% of the ciliate community. Edaphic parameters: soil temperature 2.8–13.7°C, water content 64.9–86.8% of wet mass, loss on ignition 16.6–34.7% of dry mass, pH 5.2–5.4. Grew in the laboratory at room temperature (about 19°C) and in dried and remoistened samples at 5°C. Wet biomass of 10⁶ individuals: 18 mg.

Comparison with related species

The rather complicated nomenclature of this species (basionym: *Opisthotricha muscorum* Kahl, 1932) is detailed in Foissner and others (1991). The Antarctic population matches the brief descriptions based on living specimens given by Kahl (1932) and Foissner (1980) in size, position of buccal cirrus, shape of peristomial lip, and habitat, but the marked contractility noted by Foissner (1980) was not observed. However, individuals soon became rounded and slowed down when transferred from the refrigerator (5°C) to the microscope (beginning encystment?).

Borror (1972) proposed synonymy of the moss-dwelling O. *opisthomuscorum* and the slightly larger (90–150 μ m) fresh-water species O. *crassistilata* (Kahl, 1932) Borror, 1972. Although the infraciliary pattern of both species is virtually identical, Borror (1972) is not followed because Kahl (1932) mentioned prominent and distally frayed transverse cirri in the latter species. Since this is usually a conspicuous character, for example, in *Tachysoma pellionellum* redescribed by Foissner and Didier (1981), detailed live observations on a fresh-water population of O. *crassistilata* or O. *opisthomuscorum* are required for a final decision.

Oxytricha opisthomuscorum belongs to a group of rather similar, small-sized oxytrichids having long dorsal cilia and two macronuclear nodules with a single micronucleus in between. Of these, O. setigera Stokes, 1891, a common species in terrestrial habitats worldwide, is very much alike. However, it has only four dorsal kineties and its buccal cirrus is considerably displaced backwards (Buitkamp 1977; Foissner 1982; Song and Wilbert 1989; Foissner and others 1991). These are conspicuous characteristics identical in geographically widely separated populations. Thus, the present specimens, which have six dorsal kineties and the buccal cirrus in the usual oxytrichid position near the paroral membrane's anterior end, belong to another species, very likely O. opisthomuscorum. However, O. setigera found by Smith (1978) in sub-Antarctic and maritime Antarctic soils might be conspecific with O. opisthomuscorum because it also has an anteriorly located buccal cirrus.

Oxytricha balladyna Song and Wilbert, 1989 resembles the Antarctic specimens in the position of the buccal cirrus, but differs distinctly in the number of dorsal kineties (four to five vs six) and in the arrangement of dorsal kinety 4, which is interrupted in mid-body, thus consisting of an anterior and a posterior fragment. However, the anterior portion is probably a fifth dorsal kinety derived from the right marginal cirral row, while the posterior portion ontogenetically very likely belongs to kinety 3, as known from typical oxytrichids, such as Oxytricha granulifera Foissner and Adam, 1983.

Oxytricha sphagni (Kahl, 1932) Borror, 1972, a poorly known species, differs from O. opisthomuscorum in the slightly larger size $(100-120 \,\mu\text{m})$, the more slender shape, and the soft, trailing dorsal cilia.

Balladyna fusiformis Kahl, 1932 is distinguished from O. opisthomuscorum by having the buccal cirrus shifted backwards and only three dorsal kineties (Kahl 1932; Hemberger 1982). Furthermore, its paroral membrane is conspicuously curved anteriorly, suggesting that it be-



Figs 55–61. Morphology and morphogenesis of *Sterkiella histriomuscorum* from life (55) and after protargol impregnation (56–61). 55: resting cyst; 56–58: early dividers showing development of oral primordium and cirral streaks. Arrows mark dissolved cirri IV/3 (57) and III/2 (58); arrowheads denote opisthe's anlagen 1–3 (57) and the disaggregating buccal cirrus II/2 (58); 59: middle divider showing development of cirral anlagen. Arrow marks dedifferentiated postoral ventral cirrus IV/2; arrowhead denotes dissolved postoral cirrus V/4; 60, 61: ventral and dorsal view of middle divider showing formation of left frontal cirrus (arrowhead), marginal anlagen, and dorsal primordia. Designation of cirri according to Berger and Foissner (1997). AZM = adoral zone of membranelles; Em = endoral membrane; Fc = frontal cirri; Fv = frontoventral cirri; Lm = left marginal cirri; Op = oral primordium; Pm = paroral membrane; Pt = posterior pretransverse cirrus; Rm = right marginal cirri; Tc = transverse cirri. Scale bar division 10 μ m.

longs to *Cyrtohymena* Foissner, 1989. Thus, it should not be synonymized with *O. setigera* as proposed by Song and Wilbert (1989).

Sterkiella histriomuscorum (Foissner and others, 1991) Foissner and others, 1991

Several populations of this species (formerly *Histriculus muscorum*) have been described from temperate and tropical latitudes (Kahl 1932; Wenzel 1953; Reuter 1961; Dragesco 1970; Foissner 1982; Berger and others 1985; Dragesco and Dragesco-Kernéis 1986; Foissner and others 1991; Augustin and Foissner 1992). Their morphometrical characteristics are within rather narrow limits and match those of the Antarctic specimens fairly well. Only a Chinese population has considerably more adoral membranelles (about 60 vs about 30), twice as many right and left marginal cirri (approximately 46 and 38 vs 16–27), and dorsal kinety 3 instead of kinety 4 associated with a caudal cirrus (error?, kineties also numbered in wrong direction; Zou and Zhang 1992).

However, the number of transverse cirri often varies between populations, that is, most have five whereas some have mainly four (Foissner 1982; Berger and others 1985). Thus, the morphology and morphogenesis of the Antarctic specimens were investigated, but only supplementary or deviating data are given.

Additional observations (Fig. 55; Table 5)

Size *in vivo* slightly smaller (70–110 x 40–60 μ m) than in other well-studied populations (100–160 x 40–70 μ m; Foissner 1982; Berger and others 1985; Augustin and Foissner 1992). Marginal cirri about 15 μ m long, frontal

cirri about 17 μ m, transverse and caudal cirri 20–24 μ m, and dorsal bristles about 3 μ m. Adoral zone of membranelles extends over about 45% of body length, longest bases 7–9 μ m; cilia 17–20 μ m long.

Several-days-old resting cysts spherical and entirely filled by cell (Table 5); wall about 2.5 μ m thick, surface smooth or slightly uneven (Fig. 55). Macronuclei fused; however, when cyst wall is ruptured two (disintegrated?) nodules sometimes stain with methyl green-pyronin. Cytoplasm contains numerous granules and some globules up to 4 μ m across.

Occurrence and ecology in Wilkes Land

First record for continental Antarctica, but previously found on Signy Island, maritime Antarctic (Foissner 1996). Occurred in raw cultures of fresh or dried and rewetted samples between 5–20°C, together with various other organisms (Table 1). Wet biomass of 10⁶ individuals: 60 mg.

Morphogenesis (Figs 56–64)

Stomatogenesis commences with a proliferation of basal bodies close above the anterior-most transverse cirrus. The anarchic field then elongates and migrates anteriad (Fig. 56). Subsequently, cirri IV/3 and V/4 dissolve and form three (proter's streaks 4–6) and two primordia (opisthe's anlagen 5 and 6), respectively (Figs 57–59). The oral primordium develops three cirral streaks at its anterior end, which form anlagen 1–3 of the opisthe (Figs 57–59). Cirri II/2, III/2, and IV/2 then reorganize to one cirral anlage each, namely proter's anlagen 2 and 3, and opisthe's anlage 4 (Figs 58, 59, 62). Some basal bodies



Figs 62–64. Morphogenesis of *Sterkiella histriomuscorum* after protargol impregnation. 62: middle divider showing formation of cirral streaks and marginal anlagen; numbers denote cirral anlagen. 63, 64: ventral and dorsal view of a late divider, showing migration of cirri and development of dorsal anlagen. Dorsal kinety 4 (arrowheads) splits from kinety 3 and is associated with the right-most caudal cirrus. Scale bar division 10 μ m.

from the opisthe's anlagen 1–3 are probably incorporated into streak 4 because these four primordia sometimes seem to be connected (Fig. 59). Then, the parental paroral membrane reorganizes at least in its anterior portion (anlage 1), forming the proter's left-most frontal cirrus (Figs 60 and 62). In all stages, the cirral streaks of proter and opisthe are distinctly separate.

Six anlagen each are recognizable in the proter and opisthe from which cirri differentiate in a posteriad direction: left frontal cirrus and undulating membranes from anlage 1; middle frontal, buccal, and one transverse cirrus, which is lacking in some populations (Berger and others 1985), from anlage 2; right frontal, left-most frontoventral, and one transverse cirrus from anlage 3; posterior frontoventral, anterior postoral ventral, and one transverse cirrus from anlage 4; two postoral ventral, one pretransverse, and one transverse cirrus from anlage 5; two anterior-most frontoventral, one pretransverse, and one transverse cirrus from anlage 6.

Marginal and dorsal kineties (Figs 60–64) develop as described by Nieto and others (1984), Berger and others (1985), and Zou and Zhang (1992).

Morphogenetic comparison

The origin of the cirral anlagen is identical to that of the Chinese population (Zou and Zhang 1992) and to that of *Stylonychia vorax* and *S. pustulata*, as described by Wirnsberger and others (1985). The Spanish population of *S. histriomuscorum* differs by developing only two (vs three) cirral streaks from the oral primordium and two (vs one) from the postoral ventral cirrus IV/2, as explicitly stated by Nieto and others (1984). However, their figures 7 and 8 indicate that the oral primordium also develops three anlagen and cirrus IV/2 only one. Thus, the morphogenesis of *S. histriomuscorum* populations having five transverse cirri is very likely identical.

The morphogenetic pattern of the population studied by Berger and others (1985) differs slightly in that at least the daughter's anlagen 2 are connected, the proter's streak 6 possibly originates de novo or from opisthe's anlagen 5 or 6, cirrus II/1 is lost, cirrus II/2 disintegrates very early, and cirrus IV/3, which probably produces one anlage less, breaks up considerably later. However, these differences should not be overemphasized since Berger and others (1985) could not unambiguously clarify the origin of proter's anlage 6. Some events, especially the temporal sequence of some processes, are undoubtedly slightly different from those observed by us, Nieto and others (1984), and Zou and Zhang (1992). Thus, S. histriomuscorum populations with four transverse cirri, like those studied by Berger and others (1985), might not be conspecific with those having five transverse cirri, as has the type population described by Kahl (1932).

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