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Survey of actinosporean types (Myxozoa) belonging to seven collective groups found in a freshwater salmon farm in Northern Scotland

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Abstract. A study of the actinosporean fauna of oligochaetes from a freshwater salmon farm in Northern Scotland was carried out from October 1996 to August 1998. Following the examination of 28,387 oligochaete worms belonging to the families Tubificidae, Lumbriculidae, Naididae and Enchytraeidae, five types of echinactinomyxon (four previously described), six types of raabeia (five previously described), three types of synactinomyxon (all previously described), four types of aurantiactinomyxon (three previously undescribed), one type of triactinomyxon (previously described), one type of neoactinomyxum (previously undescribed) and one type of siedleckiella (previously undescribed) were identified. The triactinomyxon type was released from unidentified immature oligochaetes. Of the twenty-one types of actinosporeans found, thirteen types were released from *Tubifex tubifex* (Müller), three types were released from *Lumbriculus variegatus* (Müller), three types from both *L. variegatus* and *T. tubifex* and two types from immature oligochaetes.

Actinosporeans have been known as parasites of aquatic oligochaetes since the discovery of *Synactinomyxon tubificis*, *Triactinomyxon ignotum* and *Hexactinomyxon psammoryctis* by Stolc (1899). However, knowledge of actinosporeans has been relatively limited, possibly because they have been thought to have little direct economic significance (McGeorge et al. 1997).

The taxonomy of actinosporeans has been revised several times by several authors (Ikeda 1912, Janiszewska 1957, Levine et al. 1980, Sprague 1982, Lom 1990) and recently Kent et al. (1994) redefined the phylum Myxozoa Grassé, 1970 to solve the taxonomic and nomenclatural problems arising from the two-host life cycle of myxozoans as first described by Wolf and Markiw (1984). The distinction between the two previously recognised classes Actinosporea and Myxosporea disappeared and the class Actinosporea was suppressed, becoming a synonym of the class Myxosporea Bütschli, 1881. The generic names of actinosporeans were retained as collective-group names, and it was proposed that they were used to characterise different morphological types of actinosporeans. Actinosporeans for which the myxosporean stage is not known are to be retained as *species inquirendae* until their specific identity is established. Lester et al. (1998) proposed that the International Code of Zoological Nomenclature should be applied to newly described actinosporeans, so that genera and species of actinosporeans should be named even when no myxosporean stage is known. However, in this study we describe actinosporeans as "types" with numbers according to Kent et al. (1994) to prevent future confusion in life-cycle studies and for uniformity with other recently published descriptions of actinosporeans. So far, more than 100 different species and types of actinosporeans have been identified, but there have as yet been relatively few studies on the actinosporean fauna in fish farms (Hamilton and Canning 1987, Yokoyama et al. 1991, Styer et al. 1992, McGeorge et al. 1997, El-Mansy et al. 1998a) and natural waters (El-Mansy et al. 1998b, Xiao and Desser 1998a,b, Negredo and Mulcahy 2001).

This study describes twenty-one types of the actinosporean collective groups echinactinomyxon, raabeia, synactinomyxon, aurantiactinomyxon, triactinomyxon, neoactinomyxum and siedleckiella released from oligochaetes in a freshwater Atlantic salmon (*Salmo salar* L.) farm in Northern Scotland.

MATERIALS AND METHODS

Sampling site. Samples of oligochaetes were collected from a freshwater Atlantic salmon fish farm sited on the extreme NW coast of Scotland (58º30'N, 4º40'W). A small river supplies the farm and the temperature varies between 1ºC in December-January to 18ºC in July-August. The river feeding the farm contains several fish species including three-spined sticklebacks *Gasterosteus aculeatus* L., eels *Anguilla anguilla* (L.), brown and sea trout *Salmo trutta* L., rainbow trout *Oncorhynchus mykiss* (Walbaum), Atlantic salmon *Salmo salar* L., pike *Esox lucius* L., perch *Perca fluviatilis*

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(L.) and loach *Noemacheilus barbatulus* (L.). At the downstream end of the farm there is a settlement pond, which serves to sediment out wastes and uneaten food from the tank effluent and thus removes suspended pollutants prior to discharge into the river. The settlement pond measures 13 × 4 m and is 40 cm in depth. It comprises three different microhabitats; gravels accumulate in the centre of the pond with mud sediment at the edges. Fine particulates are found in parts of the settlement pond in areas where the flow is slower allowing them to settle out.

Sampling period. Oligochaetes were collected from the settlement pond of the farm at intervals of six weeks during autumn and winter and 4 weeks during the spring and summer from 15th October 1996 to 14th August 1998.

Sampling procedure for oligochaetes. Oligochaetes were collected from as many microhabitats as possible in the settlement pond on each sampling occasion. Gravel and particulate sediments were sieved through 1.5 mm, 1 mm and 500 µm mesh to separate oligochaetes, which were then placed in plastic bags. However, mud samples were not sieved and all the mud collected was put directly into another plastic bag. All oligochaete samples were transferred to the laboratory in aerated river water and sorted to species the next day.

Oligochaetes were separated from mud substrate by passing the sediment through graded sieves of 1.5 mm, 1 mm and 500 µm mesh size. Oligochaetes subjected to previous sieving at the settlement pond were re-sieved to separate them from plant debris. The contents of the sieves were then emptied into shallow basins containing dechlorinated tap water and observed under bright light to detect oligochaetes. Oligochaetes of one species were separated into a container containing aerated dechlorinated tap water. At least 1,000 worms were obtained at each sampling time.

Another method used, especially for mud samples, was to place the sediment samples onto a large-sized mesh sieve (1.5 mm) immersed in dechlorinated tap water up to the level of mesh of the sieve for at least one hour. Oligochaetes were found to make their way in large numbers into the water in the container through the mesh of the sieves. Oligochaetes were identified according to the key of Brinkhurst (1963).

Examination of worms for infection. Worms were transferred into 24-cell well plates according to the method of Yokoyama et al. (1991). Five worms of one species were placed in each individual cell well containing 2 ml of dechlorinated tap water. Plates were then kept at natural temperature and light conditions outdoors overnight. Each well was scanned using a Zeiss Treval 3 inverted microscope for released actinosporeans. When actinosporeans were observed in a well, the five worms were separated and placed individually into wells and examined daily over a four-week period to determine which of the oligochaetes were infected.

Identification of actinosporean types released. Released actinosporeans were drawn and photographed under both phase contrast and bright field. Measurements were taken from at least 20 randomly selected spores from one infected oligochaete where possible, using a micrometer calibrated eyepiece graticule. Dead, senescent or immature spores were not used for measurement. Spores were identified using the keys and diagrams of Janiszewska (1955, 1957), Marques (1984), Lom et al. (1997) and by comparison with other published reports. Spore measurements of actinosporean types were made according to the guidelines of Lom et al. (1997). The number of turns in the polar filament, usually determined by transmission electron microscopy (TEM), is given for certain actinospores where the number could be confidently determined by light microscopy. The number of secondary cells for each actinospore was determined by removing the excess water from under the coverslip and allowing the increased pressure to release and disrupt the sporoplasm. The number of cells was then counted and the findings later confirmed from TEM studies.

RESULTS

During the two-year survey, five types of echinactinomyxon, six types of raabeia, three types of synactinomyxon, four types of aurantiactinomyxon, one type of triactinomyxon, one type of neoactinomyxum and one type of siedleckiella were identified.

COLLECTIVE GROUP ECHINACTINOMYXON JANISZEWSKA (1957)

Spores with three elongated, equal sized caudal processes originating just below the spore body. The type species *Echinactinomyxon radiatum* Janiszewska, 1957 of the collective group has three equal, straight, rigid and pointed caudal processes. Four species including *Echinactinomyxon radiatum* Janiszewska, 1957, *E. astilum* Janiszewska, 1964, *E. major* Styer, Harrison et Burtle, 1992 and *E. minor* Styer, Harrison et Burtle, 1992 and seven types of echinactinomyxon (Xiao and Desser 1998a, Negredo and Mulcahy 2001) have so far been described (Table 1).

Echinactinomyxon type 1 — Figs. 1a, 2A, Table 1

Individual spores with goblet-shaped spore body, sub-spherical polar capsules and three caudal processes equal in length. Released from the oligochaete *Lumbriculus variegatus.* Spore body 22.4 µm (20.8-23.4) long and 18.3 µm (18.2-19.7) wide. Secondary cells, 64. Polar capsules elongated 7.8 µm by 5.8 µm. Caudal processes 114.9 µm (103.9-124.7) long by 6.2 µm wide.

Remarks. Echinactinomyxon type 1 has a much more rounded spore body, much shorter caudal processes than *E. major* and *E. radiatum* and much longer caudal processes than other previously described echinactinomyxon types except for the echinactinomyxon 1 of Negredo and Mulcahy (2001). These two types are also very similar in the dimensions of the spore body and polar capsules and have the same oligochaete host (Table 1). Four other echinactinomyxon types found in this study have much shorter caudal processes, although echinactinomyxon type 4 has caudal processes of similar length with that of echinactinomyxon type l. It is suggested that echinactinomyxon type l is identical with echinactinomyxon 1 of Negredo and Mulcahy (2001).

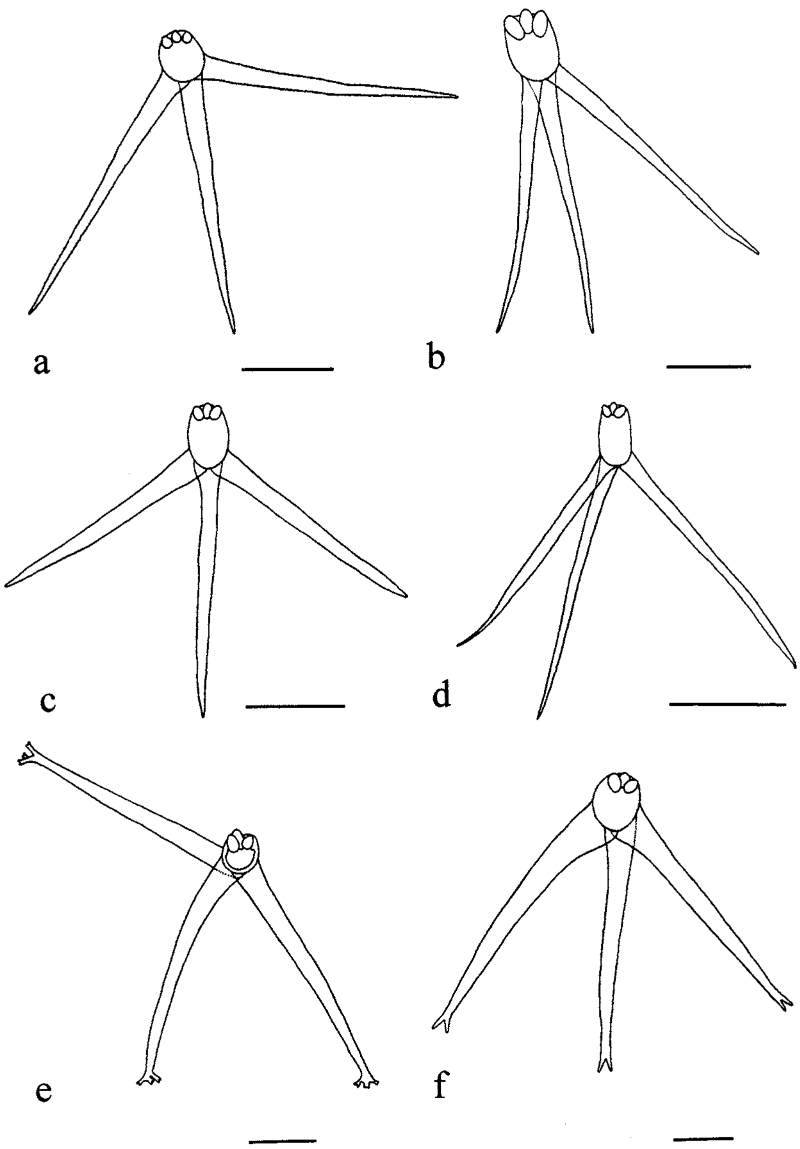

Fig. 1. **a** – echinactinomyxon type 1; **b** – echinactinomyxon type 2; **c** – echinactinomyxon type 3; **d** – echinactinomyxon type 4; **e** – raabeia type 1; **f** – raabeia type 2. Scale bars: Fig. a = 50 µm; Figs. b, e, f = 20 µm; Figs. c, d = 30 µm.

Echinactinomyxon type 2 Figs. 1b, 2B, Table 1

Individual spores with elongated spore body, subspherical polar capsules and three caudal processes equal in length. Released from the oligochaete *Tubifex tubifex*. Spore body 21.4 µm (20.7-23.3) long and 14.4 µm (12.2-16.3) wide. Secondary cells, 64. Polar capsules slightly elongated, 6.3 µm by 4.3 µm. Caudal processes equal in length 78.5 µm (70.1-88.2) long by 3.9 µm (3.6-4.4) wide.

Remarks. Echinactinomyxon type 2 differs from most of the echinactinomyxon types described here and elsewhere by its dimensions. The type species *E. radiatum* and *E. major* have a more elongated spore body and caudal processes, whilst *E. minor* and *E. astilum* have much shorter caudal processes (Table 1). Echinactinomyxon type 2 also differs from the types of Xiao and Desser (1998a) in respect of its much longer spore body or polar capsule dimensions (Table 1). Echinactinomyxon type 2 is similar in general dimensions and shape to echinactinomyxon 3 of Negredo and Mulcahy (2001) but the polar capsules are larger. Of the echinactinomyxon types described here echinactinomyxon type 3 is the closest in overall dimensions but differs from type 2 by the shape of the spores, the straight elongated spore body and much thinner caudal processes. Thus, it is concluded that echinactinomyxon type 2 is a new member of the collective group echinactinomyxon.

Table 1. Descriptive data of the echinactinomyxon types previously described and those found in this study (measurements in µm).

Species and types	Host	Dimensions of spore body	Dimensions of caudal processes	Dimensions of polar capsules	Number of secondary cells	Reference
E. radiatum Janiszewska,1952	*T. tubifex*	25-30	100-125	5	32	Janiszewska (1957)
E. astilum Janiszewska, 1964	*T. tubifex*	25-35	6-10 × 45-60	5 × 7	16	Marques (1984)
E. major Styer, Harrison et Burtle, 1992	*D. digitata*	13 × 24	5 × 138	2.5 × 5	–	Styer et al. (1992)
E. minor Styer, Harrison et Burtle, 1992	*D. digitata*	19 × 23	10 × 76	2.5 × 5	–	Styer et al. (1992)
E. "A" of Xiao and Desser 1998a	*L. hoffmeisteri*	9.5 (8.5-11)	75 (65-85)	5 × 3.5	16	Xiao and Desser (1998a)
E. "B" of Xiao and Desser 1998a	*L. hoffmeisteri*	9.5 (8.5-10.5)	50 (45-55)	3.8 × 2.7	16	Xiao and Desser (1998a)
E. "C" of Xiao and Desser 1998a	*L. hoffmeisteri*	10 (8.5-12)	83 (70-95)	3.8 × 2.2	16	Xiao and Desser (1998a)
E. "D" of Xiao and Desser 1998a	*L. hoffmeisteri*	11.5 (11-12.5)	100 (85-105)	3.9 × 2.4	32	Xiao and Desser (1998a)
E. "E" of Xiao and Desser 1998a	*L. hoffmeisteri*	9 (8-10)	90 (85-95)	3.8 × 2.7	16	Xiao and Desser (1998a)
E. type 1 of Negredo and Mulcahy 2001	*L. variegatus*	22.4 (18.2-23.4) × 19.9 (14.7-20.8)	126 (117-143) × 13.3 (13.0-15.6)	7.3 (5.7-7.8) × 5.8 (5.2-6.5)	16	Negredo and Mulcahy (2001)
E. type 2 of Negredo and Mulcahy 2001	*L. variegatus*	19.6 (18.2-20.8) × 13.0 (13.0-13.0)	82.2 (74.1-91.0) × 8.4 (7.8-10.4)	6.6 (5.2-7.3) × 4.7 (4.7-4.7)	25	Negredo and Mulcahy (2001)
E. type 3 of Negredo and Mulcahy 2001	*L. variegatus*	21.7 (16.9-26.0) × 17.7 (15.6-18.2)	91.0 (91.0-91.0) × 10.4 (10.4-10.4)	5.2 (5.2-5.2) × 5.2 (5.2-5.2)	13	Negredo and Mulcahy (2001)
E. type 1	*L. variegatus*	22.4 (20.8-23.4) × 18.3 (18.2-19.7)	114.9 (103.9-124.7)	7.8 × 5	64	this study
E. type 2	*T. tubifex*	21.4 (20.7-23.3) × 14.1 (12-15)	96.2 (85-114)	8 × 5	64	this study
E. type 3	*T. tubifex*	25.9 (24.9-28) × 14.5 (14-15.6)	93.3 (82.7-99.8)	7 × 3.6	16	this study
E. type 4	*T. tubifex*	27.3 (24.9-28.4) × 15.5 (14-16.8)	122.2 (106.8-135.7)	6.5 × 4.5	128	this study
E. type 5	*L. variegatus* *T. tubifex*	11.2 (10-12) × 8.1 (7-9)	58 (38-75) × 3 (2.9-3.1)	5 × 2	8	this study

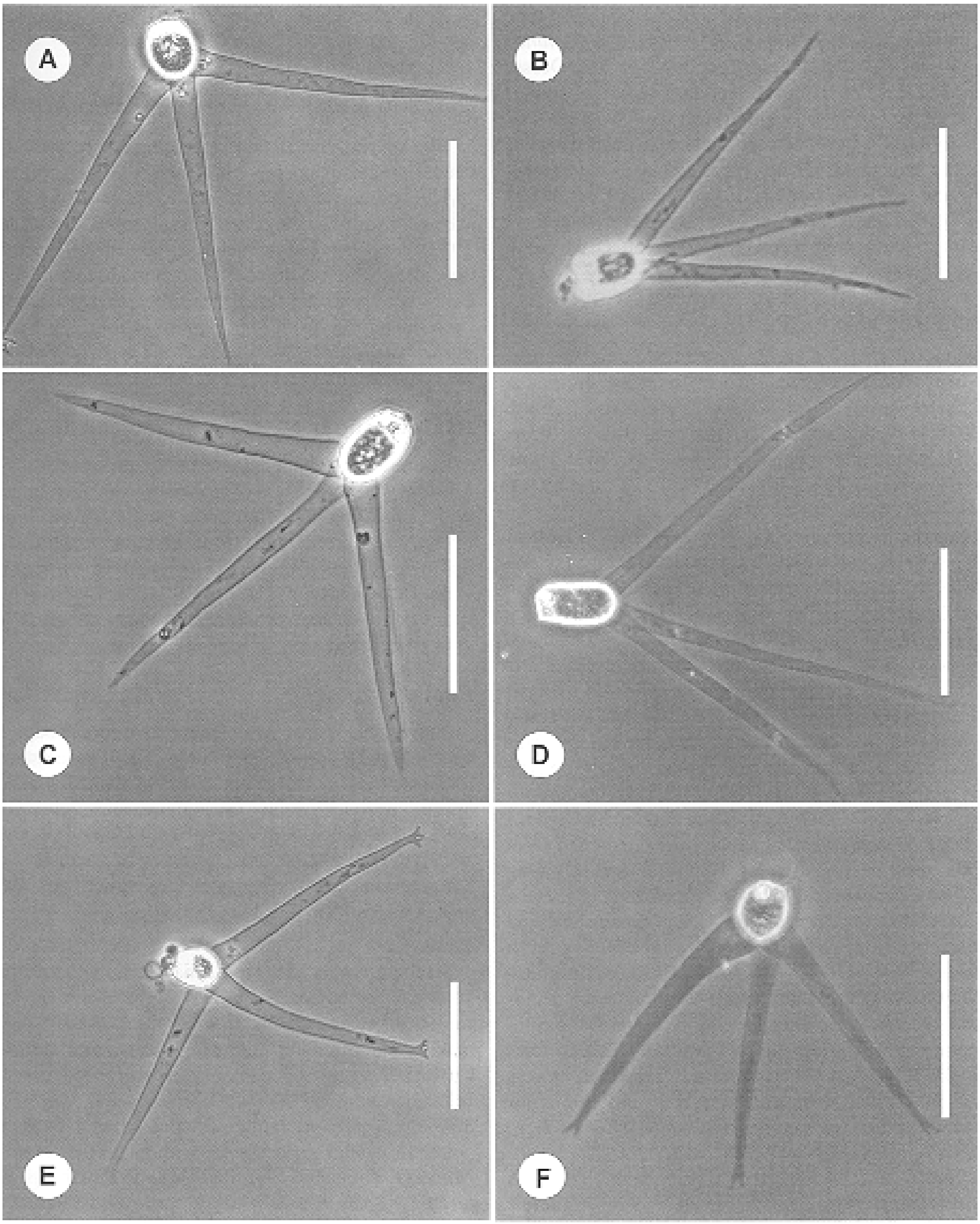

Fig. 2. **A** – echinactinomyxon type 1; **B** – echinactinomyxon type 2; **C** – echinactinomyxon type 3; **D** – echinactinomyxon type 4; **E** – raabeia type 1; **F** – raabeia type 2. Scale bars: Figs. A-E = 50 µm; Fig. F = 20 µm.

Echinactinomyxon type 3 Figs. 1c, 2C, Table 1

Individual spores with elongated but slightly rounded spore body and sub-spherical polar capsules. Caudal processes much widened at the proximal end but tapered distally. Spores released from the oligochaete *Tubifex tubifex*. Spore body 25.9 µm (24.9-28.0) long and 14.5 µm (14.0-15.6) wide. Secondary cells, 16. Polar capsules 7 µm by 3.6 µm. Caudal processes equal, 93.3 µm (82.7-99.8) long by 6.7 µm (6.5-7.0) wide.

Remarks. The spore body of echinactinomyxon type 3 is broader than *E. radiatum*, *E. astilum* and *E. minor* as well as those types described by Xiao and Desser (1998a) (Table 1). Echinactinomyxon type 3 is similar in overall size to echinactinomyxon 3 of Negredo and Mulcahy (2001) but the spore body and polar capsules are more elongated. Of the types found in the present study echinactinomyxon type 2 is the closest but differs from type 3 as detailed above. Therefore, this form appears to be a new member of the collective group echinactinomyxon.

Echinactinomyxon type 4 Figs. 1d, 2D, Table 1

Individual spores with elongated and straight caudal processes equal in size. Spores released from the oligochaete host *Tubifex tubifex.* Spore body 27.3 µm (24.9-28.4) long and 15.5 µm (14.0-16.8) wide. Secondary cells, 128. Polar capsules 7 µm by 3.5 µm. Caudal processes 122.2 µm (106.8-135.7) long by 4.6 µm (4.2-4.8) wide.

Remarks. Echinactinomyxon type 4 is the largest of the types of the collective group found in this study and elsewhere (Table 1). *E. radiatum* and echinactinomyxon type 4 have very similar dimensions of both the spore body (27-30 µm compared to 27.3 µm (24.9-28.4)) and the caudal processes (125 µm compared to 122.2 µm (106.8-135.7)). On the other hand, *E. minor*, *E. astilum*, echinactinomyxon type 2, type 3 and type 5 are easily discriminated from echinactinomyxon type 4 by their much smaller spore dimensions. Echinactinomyxon type 1 has a shorter and ellipsoidal spore body and much wider caudal processes than echinactinomyxon type 4 (Table 1). *E. radiatum* has already been recorded from several sites in England by Hamilton and Canning (1987) as a parasite of *Tubifex tubifex*, which is also the host of echinactinomyxon type 4. The dimensions and the drawings of *E. radiatum* from *Tubifex tubifex* given by Janiszewska (1957) are identical to echinactinomyxon type 4 in this study suggesting that echinactinomyxon type 4 is *Echinactinomyxon radiatum.* Echinactinomyxon 2 of Negredo and Mulcahy (2001) from *Lumbriculus variegatus* was similarly identified closely with *E. radiatum*, however, the overall dimensions for this actinospore were somewhat smaller than those reported by Janiszewska (1957).

Echinactinomyxon type 5 Table 1

Echinactinomyxon type 5 has been demonstrated experimentally to be the actinosporean stage of *Sphaerospora truttae* Fischer-Scherl, El-Matbouli et Hoffman, 1986 and is also described elsewhere (Özer and Wootten 2000). Individual spores tiny, caudal processes straight but curve upwards distally. Spores released principally from the oligochaete host *Lumbriculus variegatus* (Müller), but were also obtained from *Tubifex tubifex.* Spore body elongated 11.2 µm (10.0-12.0) long and 8.1 µm (7.0-9.0) wide. Secondary cells, 8. Polar capsules 5 µm by 2 µm. Caudal processes 58 µm (38-75) long and 3 µm (2.9-3.1) wide.

COLLECTIVE GROUP RAABEIA JANISZEWSKA (1955)

The spores have three elongated, pointed and curved caudal processes arising from the spore body without a style (Janiszewska 1955). However, one of the four species *(Raabeia furciligera* Janiszewska et Krzton, 1973) described has branches at the tip of the caudal processes, which is another characteristic feature for the collective group. So far, sixteen species and types have been identified from this group (Table 2). *Raabeia gorlicensis* Janiszewska, 1955 is the type species of the collective group.

Raabeia type 1 Figs. 1e, 2E, Table 2

Spores with rounded spore body, sub-spherical polar capsules and three caudal processes with four branches at the tips. Number of secondary cells not determined. Spores were recovered from immature oligochaetes. Spore body 18.1 µm (16-19) long and 15.7 µm (14-18) wide. Polar capsules 6 µm by 4 µm lay on top of the spore body. Caudal processes 94.5 µm (85-103) long, with branches at ends, around 10 µm long.

Raabeia type 2 Figs. 1f, 2F, Table 2

Individual spores with rounded spore body, sub-spherical polar capsules and three caudal processes with four branches in two pairs at tip of caudal processes. Spores released from the oligochaete *Lumbriculus variegatus.* Spore body 18.1 µm (17.1-18.7) long and 16.1 µm (15.6-17.1) wide. Number of secondary cells not determined. Polar capsules 7 µm by 6 µm. Caudal processes 85.6 µm (82.7-99.8) long.

Remarks

Raabeia type 1 and type 2 have similar spore body, polar capsule and caudal process dimensions, as well as similar branches at the tips of the caudal processes making identification confusing. The major difference between these two types is in the form of the branches. In the literature, all the raabeia species and types, except *Raabeia furciligera* Janiszewska et Krzton, 1973, have pointed caudal processes without any branches. However, compared with raabeia type 1 and type 2, *R. furciligera* has a much larger spore body and caudal processes (Table 2) with one to five branches. Thus, it is concluded that raabeia type 1 and raabeia type 2 are two new members of the collective group raabeia. However, these two types are very close in many respects and it cannot be ruled out that they represent the same type.

Raabeia type 3 Figs. 3a, 4A, Table 2

Individual spores with very elongated spore bodies, pear-shaped polar capsules and remarkably large, elongated and curved caudal processes. Spores released

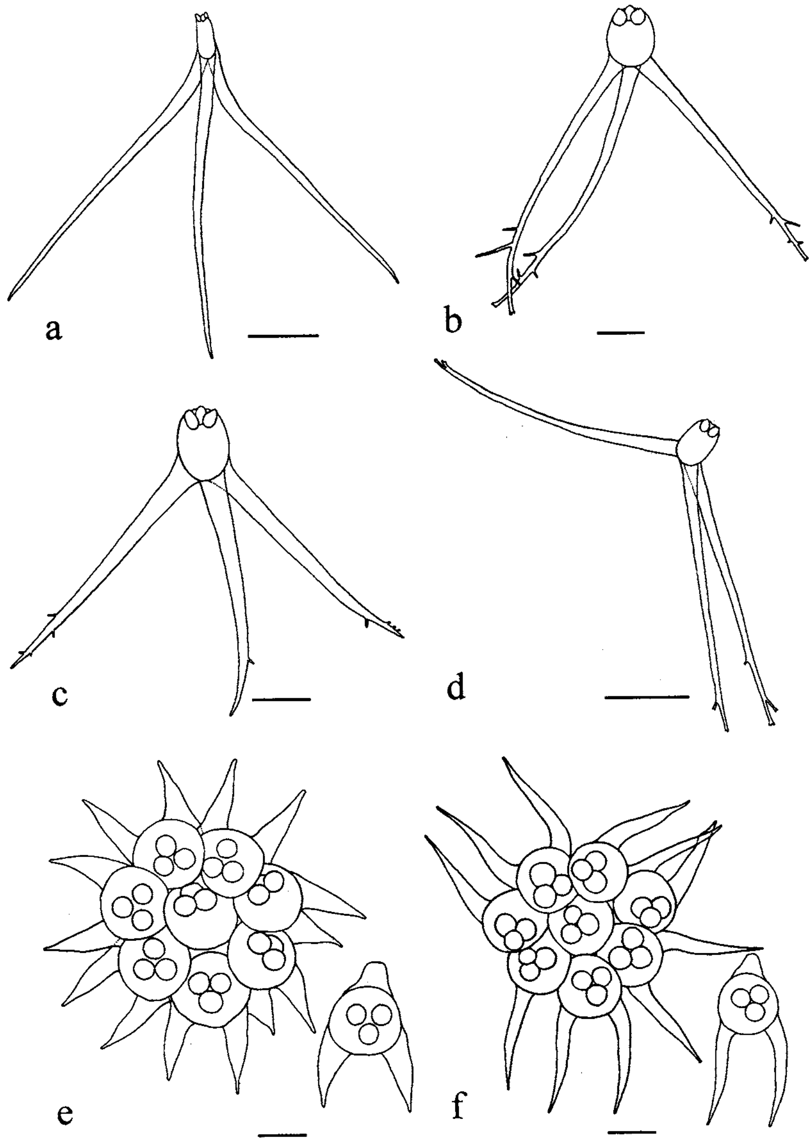

Fig. 3. **a** – raabeia type 3; **b** – raabeia type 4; **c** – raabeia type 5; **d** – raabeia type 6; **e** – synactinomyxon type 1; **f** – synactinomyxon type 2. Scale bars: Figs. a, d = 50 µm; Fig. b = 25 µm; Figs. c, e, f = 20 µm.

from *Tubifex tubifex.* Secondary cells, 16. Spore body 33.9 µm (31.3-37.5) long and 12.8 µm (12.5-14.0) wide Polar capsules 6.5 µm by 4.4 µm. Caudal processes 228.3 µm (212.5-243.8) long.

Remarks. Amongst the raabeia types described here, raabeia type 3 had the most elongated spore body and caudal processes (Table 2). The caudal processes had pointed ends and thus differed from raabeia type 1, type 2, type 4, type 5 and type 6, which had branches. *Raabeia magna* Janiszewska, 1957 and *Raabeia gorlicensis* as described by Janiszewska (1957) differ from raabeia type 3 in having a much larger spore body and much smaller caudal processes (Table 2). The other types described in the literature (El-Mansy et al. 1988a,b, Xiao and Desser 1998b) have different spore dimensions (Table 2). The *Raabeia* sp. of Yokoyama et al. (1991) has a similar caudal process length (200 µm) to that of raabeia type 3 (212.5-243.8) but its spore body is only 9 µm in diameter and the polar capsules 3.3 µm in length, similar to raabeia type 3. McGeorge et al. (1997) described a raabeia identical to raabeia type 3 from the same environment with caudal processes of similar length (219.3 µm (170-290) compared to 228.3 µm (212.5-243.8)) although spore body dimensions differ somewhat between the two types (mean 18.4 µm, range 12-25 µm in *Raabeia* sp. of McGeorge et al. [1997]; mean 33.9 µm, range 31.3-37.5 µm in raabeia type 3). McGeorge et al. (1997) noted a clear space between the base of polar capsules and the top of the spore body in their form which was also present in raabeia type 3 but not in the other raabeia types found in this study. Therefore, it is suggested that raabeia type 3 is the same as the *Raabeia* sp. of McGeorge et al. (1997).

Table 2. Descriptive data of the raabeia species and types described previously and those found in this study (measurements in µm).

Species and types	Host	Length of caudal processes	Dimensions of spore body	Dimensions of polar capsules	Number of secondary cells	Reference
R. gorlicensis Janiszewska, 1955	*T. tubifex*	170	35	4	32	Janiszewska (1955)
R. magna Janiszewska, 1957	*L. hoffmeisteri*	340	51-58	6-7	128	Janiszewska (1957)
R. furciligera Janiszewska et Krzton, 1973	*L. hoffmeisteri*	125	10.2	5	32	Janiszewska and Krzton (1973)
R. sp. of McGeorge et al. 1997	immature	219	12.8 × 18.2	6.4	–	McGeorge et al. (1997)
R. type 1 of El-Mansy et al. 1998a	*Branchiura* sp.	294	25.9 × 11.8	5.9 × 3.5	–	El-Mansy et al. (1998a)
R. type 2 of El-Mansy et al. 1998a	*Branchiura* sp.	202.8	14.1 × 12.4	5.9 × 4.7	–	El-Mansy et al. (1998a)
R. type 3 of El-Mansy et al. 1998a	*T. tubifex*	183.6	28.2 × 14.1	7.5 × 5.9	–	El-Mansy et al. (1998a)
R. type 4 of El-Mansy et al. 1998a	water	209.4	21.7 × 7.7	5.7 × 4	–	El-Mansy et al. (1998a)
R. type 1 of El-Mansy et al. 1998b	water	202.8	12.4	5.9 × 4.7	–	El-Mansy et al. (1998b)
R. type 2 of El-Mansy et al. 1998b	*T. tubifex*	209.4	7.7	5.7 × 4	–	El-Mansy et al. (1998b)
R. "A" of Xiao and Desser 1998b	*L. hoffmeisteri*	134-165	14-18	4 × 2	8	Xiao and Desser (1998b)
R. "B" of Xiao and Desser 1998b	*L. hoffmeisteri*	210-240	24-26.5	5.5 × 2.7	16	Xiao and Desser (1998b)
R. "C" of Xiao and Desser 1998b	*L. hoffmeisteri*	200-220	15.5-17.5	4.5 × 2.3	8	Xiao and Desser (1998b)
R. "D" of Xiao and Desser 1998b	*T. tubifex*	270-310	20-23	4.5 × 3	16	Xiao and Desser (1998b)
R. "E" of Xiao and Desser 1998b	*T. tubifex*	200-230	22.5-25	4.5 × 2.6	12	Xiao and Desser (1998b)
R. "F" of Xiao and Desser 1998b	*L. hoffmeisteri*	130-165	15-18	4.5 × 2.5	16	Xiao and Desser (1998b)
R. type 1	immature	94.5 (85-103)	18.1 (16-19) × 15.7 (14-18)	5 × 4	–	this study
R. type 2	*L. variegatus*	85.6 (82.7-99.8)	18.1 (17.1-18.7) × 16.1 (15.6-17.1)	7 × 6	–	this study
R. type 3	*T. tubifex*	228.3 (212.5-243.8)	33.9 (31.3-37.5) × 12.8 (12.5-14)	6.4 × 4.3	16	this study
R. type 4	*T. tubifex*	142.7 (135-164)	29.6 (28.3-31.2) × 16.5 (14.8-18.2)	6.3 × 6.4	32	this study
R. type 5	*L. variegatus*	133.3 (124-142.6)	23.7 (21.7-24.8) × 20.1 (18.6-21.7)	6 × 5	–	this study
R. type 6	*T. tubifex*	164.9 (159.1-171.6)	29.8 (28-31.2) × 17.4 (16.4-18.7)	6 × 4	–	this study

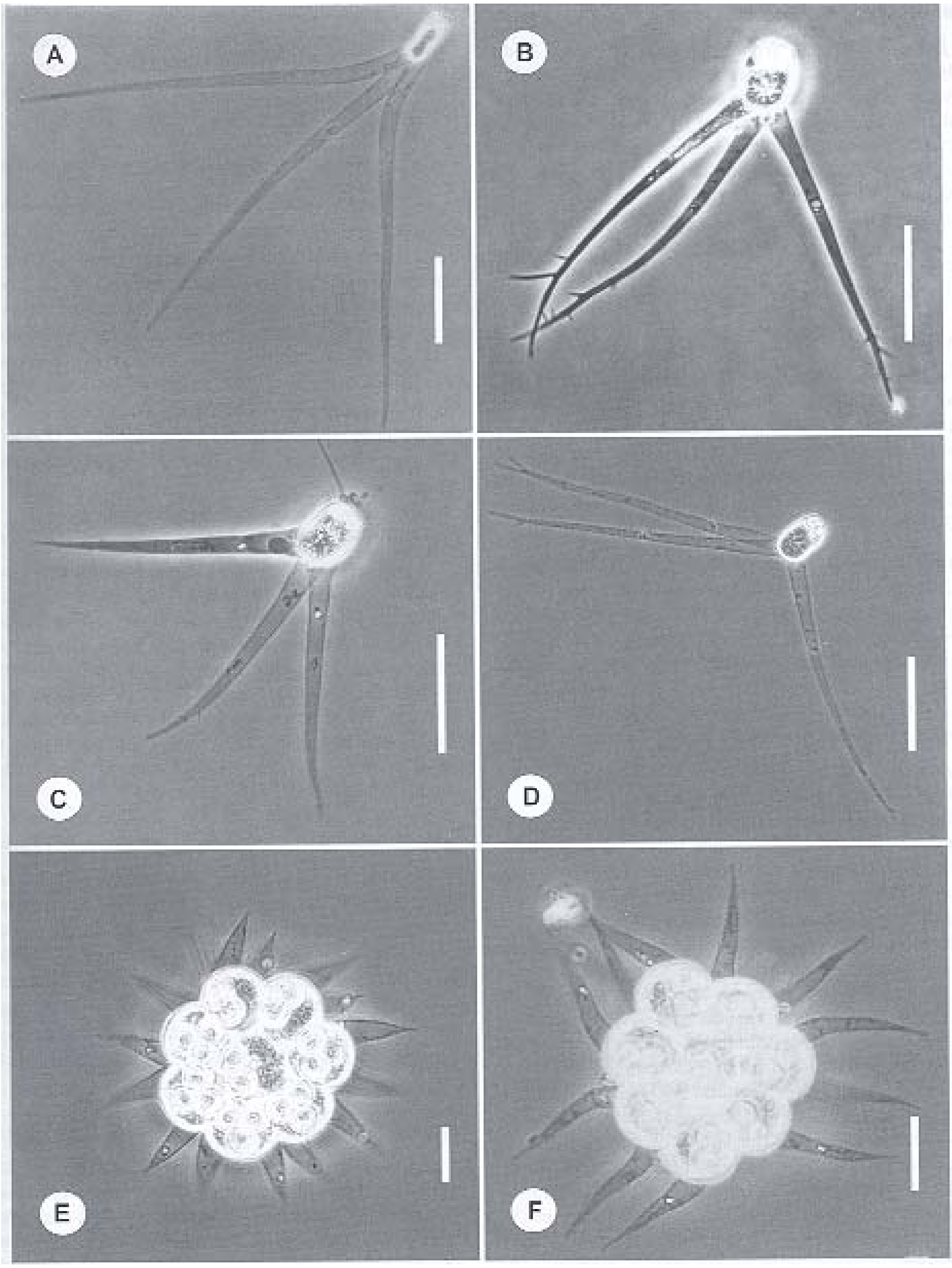

Fig. 4. **A** – raabeia type 3; **B** – raabeia type 4; **C** – raabeia type 5; **D** – raabeia type 6; **E** – synactinomyxon type 1; **F** – **s**ynactinomyxon type 2. Scale bars: Figs. A-D = 50 µm; Figs. E-F = 20 µm.

Raabeia type 4 — Figs. 3b, 4B, Table 2

Individual spores with goblet-shaped spore body, sub-spherical polar capsules and three caudal processes equal in length and bearing several branches at the distal end. The number and the size of these structures are variable. The maximum number recorded was seven on one of the three caudal processes. The size of the structures varied even on the same caudal process. Spores released from *Tubifex tubifex.* Secondary cells, 32. Spore body 29.6 µm (28.3-31.2) long and 16.5 µm (14.8-18.2) wide. Polar capsules 8 µm by 5 µm. Caudal processes 142.7 µm (125-164) long.

Raabeia type 5 — Figs. 3c, 4C, Table 2

Individual spores morphologically similar to raabeia type 4 but with more rounded spore body and shorter branches. Spores released from *Lumbriculus variegatus.* Spore body is 23.7 µm (21.7-24.8) long and 20.2 µm (18.6-21.7) wide. Number of secondary cells not determined. Polar capsules 6 µm by 5 µm. Caudal processes 133.3 µm (124-142.6) long.

Raabeia type 6 — Fig. 3d, 4D, Table 2

Individual spores with elongated spore body, sub-spherical polar capsules and three caudal processes with voluminous branches. Spores released from *Tubifex tubifex.* Number of secondary cells not determined. Spore body 29.8 µm (28.0-31.2) long and 17.4 µm (16.3-18.7) wide. Polar capsules 7.8 µm by 4.6 µm. Caudal processes 164.8 µm (159.1-171.6) long.

Remarks

Raabeia type 4, type 5 and type 6 had round to goblet-shaped spore bodies, sub-spherical polar capsules and three caudal processes equal in length, rather similar to the members of the collective group echinactinomyxon. However, the spores were always observed with branches at the distal end of caudal processes and thus differed from the other types of raabeia found which did not have these structures.

Amongst the other known species or types of the collective group raabeia, raabeia type 4, type 5 and type 6 could easily be discriminated from *R. magna*, *R. gorlicensis* and *Raabeia* sp. of Yokoyama et al. (1991), *Raabeia* sp. of McGeorge et al. (1997), the types of El-Mansy et al. (1998a,b) and Xiao and Desser (1998b) by the branches 2/3 along the length of the caudal processes rather than by their pointed ends. However, *Raabeia furciligera*, the closest species previously described, can also be distinguished from these types by the position and shape of the branches on the caudal processes.

Raabeia type 4, type 5 and type 6 also have similar branches 2/3 along the length of their caudal processes, but while the branches of raabeia type 5 are very small and sometimes difficult to see under low magnification, those of raabeia type 4 and type 6 are more elongated and, in the latter more voluminous. Raabeia type 5 had a slightly more rounded spore body than that of raabeia type 4 and type 6 and its caudal process dimensions were also different (Table 2). Thus, it is concluded that raabeia type 4, type 5 and type 6 are new members of the collective group raabeia.

COLLECTIVE GROUP SYNACTINOMYXON STOLC (1899)

Individual spores with either two long and one short elongated or conical caudal processes or three elongated equal sized processes. Eight spores bound together by the shortest of the three caudal processes of each spore or by one of the equal sized caudal processes, thus creating a circle. Four species including *Synactinomyxon tubificis* Stolc, 1899; *Synactinomyxon longicauda* Marques et Ormières, 1982; synactinomyxon "A" and "B" of McGeorge et al. (1997) and one type of Xiao and Desser (1998a) have so far been identified (Table 3). The type species of the collective group is *Synactinomyxon tubificis.*

Synactinomyxon type 1 — Figs. 3e, 4E, Table 3

Spores arranged in a star-like structure, with 8 spores bound together by short caudal processes. Seven spores form a circle in the centre of which an additional spore is positioned. Spores released from *Tubifex tubifex* and *Lumbriculus variegatus*. Spore body 17 µm (14.0-19.2) in diameter. Secondary cells, 32. Polar capsules 5 µm by 4 µm. Six to seven coils of polar filament were seen inside polar capsules. Short caudal process linking the eight spores 5.3 µm (3.2-7.4) long, long caudal processes 18 µm (15.0-21.0) long.

Synactinomyxon type 2 — Figs. 3f, 4F, Table 3

Spores arranged in a star-like structure, with 8 spores bound together by short caudal processes. Seven spores form a circle in the centre of which an additional spore is positioned. Spores released from *Tubifex tubifex*. Spore body 16.8 µm (16.4-17.2) in diameter. Secondary cells, 64. Polar capsules pear-shaped 6.2 µm by 5.2 µm. Six to seven coils of polar filament within polar capsules. Short caudal processes 5.4 µm (3.8-7.8) long, long caudal processes 33.6 µm (31.2-37.4) long.

Synactinomyxon type 3 — Figs. 5a,b, 6A, Table 3

Eight spores joined together by tip of one of their caudal processes. Connection between the eight spores very strong. Three caudal processes equal in size, much elongated and thus different from the other synactinomyxon types described here. Spores released from *Tubifex tubifex* and *Lumbriculus variegatus*. Spore body 25.6 µm (21.8-26.5) long and 21.8 µm (18.7-23.4) wide. Secondary cells, 16. Polar capsules with six coils of polar filament, sub-spherical, 5 µm by 4 µm. Caudal processes equal in size, 74 µm (71.8-78.0) long. Type 3 represents *Synactinomyxon longicauda*.

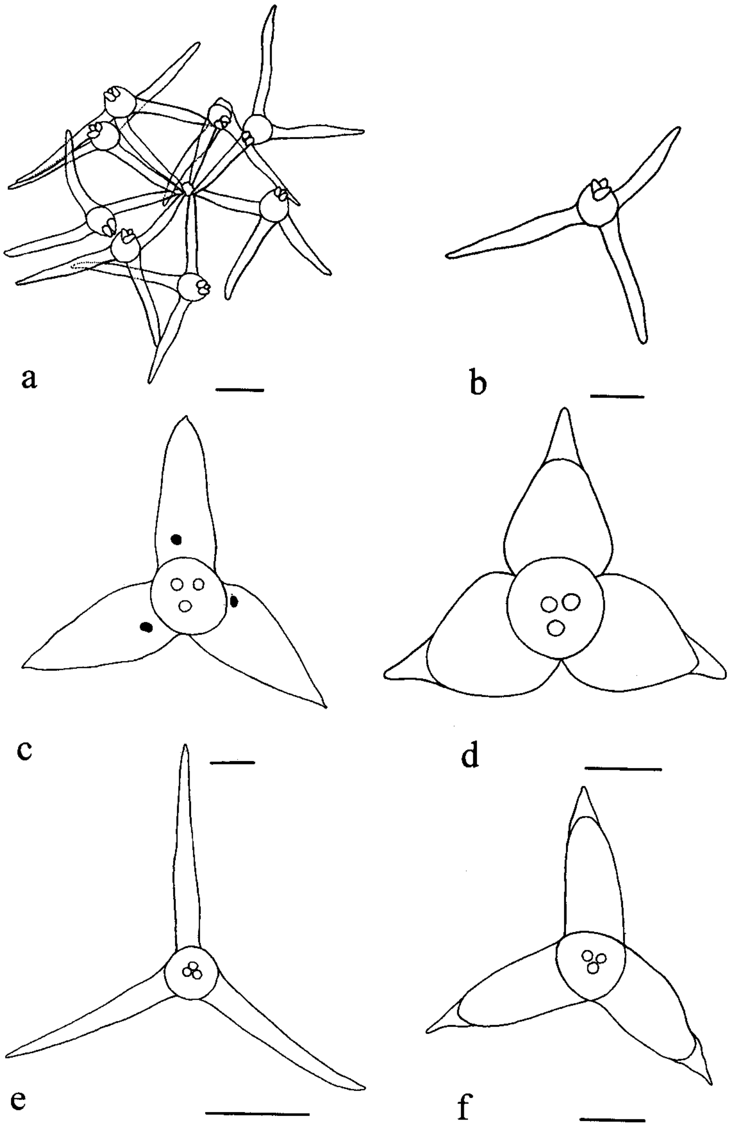

Fig. 5. **a** – synactinomyxon type 3; **b** – an individual synactinomyxon type 3 spore; **c** – aurantiactinomyxon type 1; **d** – aurantiactinomyxon type 2; **e** – aurantiactinomyxon type 3; **f** – aurantiactinomyxon type 4. Scale bars: Figs. a, b = 30 µm; Figs. c, f = 10 µm; Fig. d = 20 µm; Fig. e = 50 µm.

Remarks

Previous described synactinomyxon species have all been found in the gut epithelium of *Tubifex tubifex*. The three types of synactinomyxon described in this study were also released from *Tubifex tubifex*, although synactinomyxon type 1 and synactinomyxon type 3 were also released from *Lumbriculus variegatus*.

Of the three synactinomyxon types described in this study, synactinomyxon type 1 and synactinomyxon type 2 were very similar to synactinomyxon "A" and *Synactinomyxon tubificis*, respectively, in terms of the spore dimensions and arrangement. Synactinomyxon "A" was found in the same settlement pond used in this study and *Synactinomyxon tubificis* was also reported by Hamilton and Canning (1987) in the UK, although they did not give any measurements for the species. The measurement data given for synactinomyxon "A" by McGeorge et al. (1997) and for *Synactinomyxon tubificis* by Marques (1984) almost match the data obtained here (Table 3). Thus, it is concluded that synactinomyxon type 1 is the same as synactinomyxon "A" of McGeorge et al. (1997), whilst synactinomyxon type 2 is *Synactinomyxon tubificis* Stolc, 1899.

Of the three types of synactinomyxon found in this study, synactinomyxon type 3 had the largest caudal processes and differed from the other two types by the way the eight spores were joined together. The spore body dimensions of synactinomyxon type 3 are similar to those of synactinomyxon "B" and *Synactinomyxon longicauda* (Table 3). Synactinomyxon "B" was found by McGeorge et al. (1997) in the same settlement pond used in this study and it was considered by these authors that this type was *Synactinomyxon longicauda*.

Table 3. Descriptive data of the synactinomyxon species and types described previously and those found in this study (measurements in µm).

Species and types	Host	Length of caudal processes		Dimensions of spore body	Dimensions of polar capsules	Number of secondary cells	Reference
		short	long				
S. tubificis Stolc, 1899	*T. tubifex*	7	30	12-15	6 × 3	32	Marques (1984)
S. longicauda Marques et Ormières, 1982	*T. tubifex*	8	80	22-25	7	16	Marques (1984)
S. "A" of McGeorge et al. 1997	*T. tubifex*	5.2 (3-7)	18 (15-21)	16.5 (14-19)	5 × 4	–	McGeorge et al. (1997)
S. "B" (Syn. of *S. longicauda*)	*T. tubifex* *L. variegatus*	64.4 (55-80)		18.3 (16-20)	6 × 4	–	McGeorge et al. (1997)
S. sp. of Xiao and Desser 1998a	*T. tubifex*	138 (125-150)		17.5 (16-18.5)	7.5 × 4	32	Xiao and Desser (1998a)
S. type 1	*T. tubifex* *L. variegatus*	5.3 (3.2-7.4)	18 (15-21)	17 (14-19.2)	5 × 4	32	this study
S. type 2	*T. tubifex*	5.4 (3.8-7.8)	33.6 (31.2-37.4)	16.8 (16.4-17.2)	6.2 × 5.4	64	this study
S. type 3	*T. tubifex* *L. variegatus*	74 (71.8-78)		25.6 (21.8-26.5) × 21.8(18.7-23.4)	5 × 4	16	this study

Synactinomyxon type 3 of this study had slightly larger dimensions of both the spore body and caudal processes than synactinomyxon "B" of McGeorge et al. (1997) and was slightly smaller than *Synactinomyxon longicauda* recorded by Marques (1984), but as the spores are also joined together by the tips of one of the caudal processes, it is thus suggested that synactinomyxon type 3 is *Synactinomyxon longicauda* Marques et Ormières, 1982.

COLLECTIVE GROUP AURANTIACTINOMYXON JANISZEWSKA (1952)

Epispore is without style, with three processes of equal length, pointed and curved downwards. Bases of the processes embrace spore body almost entirely. The spores always found singly and the individual spores usually with spherical spore body. Twenty seven species and types have so far been identified (Table 4). The type species of the collective group is *Aurantiactinomyxon raabeiiuniaris* Janiszewska, 1952.

Aurantiactinomyxon type 1 Figs. 5c, 6B, Table 4

Spores always single, epispore without style with three leaf-like caudal processes of equal length. Spores collected from *Tubifex tubifex*. Individual spores with spherical spore body 14.4 µm (12-15) in diameter. Secondary cells, 64-128. Three polar capsules also spherical with a diameter of 2.7 µm (2-3). Three caudal processes equal in length, average length 32 µm (31-36) and width 14.8 µm (13-15).

Aurantiactinomyxon type 2 Figs. 5d, 6C, Table 4

Spores always single, epispore without style with three leaf-like caudal processes of equal length. Spores released from *Tubifex tubifex*. Spore body 14.9 µm (14-18.7) in diameter with three apical polar capsules 2.5 µm (1.8-2.8) in diameter. Secondary cells, 64. Three caudal processes 24.8 µm (23.4-26.5) long and 15.3 µm (14-15.6) wide.

Aurantiactinomyxon type 3 Figs. 5e, 6D, Table 4

Amongst all the aurantiactinomyxon types described here, this type was the largest. Individual spores of this type showed similarities with the characteristics of the collective group echinactinomyxon. Spores were found singly with three elongated caudal processes which were straight, rigid, pointed at the distal end and equal in length. In apical view, the spore body was spherical and the polar capsules were positioned on top of the spore body and close to each other, reminiscent of echinactinomyxon. However, there was a 120° angle between each caudal process which is typical of aurantiactinomyxon and unlike echinactinomyxon. The spores were released by *Tubifex tubifex*. Spore body 24 µm (23.4-24.9) long and 21.8 µm (20.8-23.4) wide. Secondary cells, 32. Polar capsules 4 µm by 3.2 µm. Caudal processes equal, 114.5 µm (101.4-124.8) long. Each caudal process with widened part half-way along its total length, broader and tapered to a point distally.

Aurantiactinomyxon type 4 Figs. 5f, 6E, Table 4

Spores always single, epispore without style with three leaf-like caudal processes of equal length. Spores released from *Tubifex tubifex*. Spore body 11.9 µm (11.2-14) in diameter. Secondary cells, 32. Polar capsules always spherical, 2.5 µm (2-3) in diameter. Three caudal processes 28.3 µm (23.4-31.2) long and 11.9 µm (10.9-14) wide.

Remarks

Aurantiactinomyxon type 1, type 2 and type 4 described in this study had similar dimensions of both spore body and caudal processes, but differed from aurantiactinomyxon type 3 by the much larger caudal processes of the latter (Table 4). The types found here

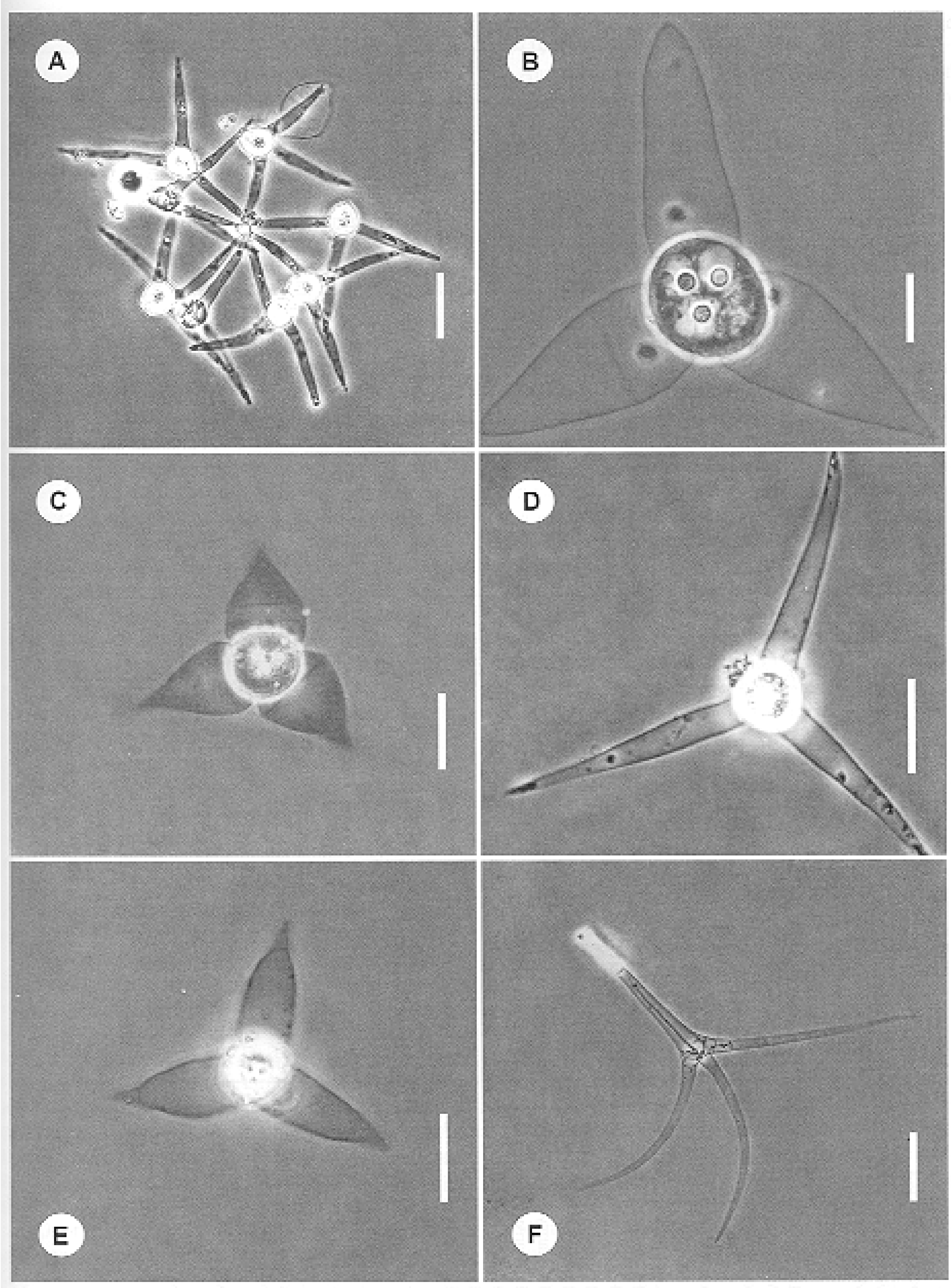

Fig. 6. **A** – synactinomyxon type 3; **B** – aurantiactinomyxon type 1; **C** – aurantiactinomyxon type 2; **D** – aurantiactinomyxon type 3; **E** – aurantiactinomyxon type 4; **F** – triactinomyxon type. Scale bars: Figs. A, D, F = 50 µm; Fig. B = 10 µm; Figs. C, E = 20 µm.

Table 4. Descriptive data of the aurantiactinomyxon species and types described previously and those found in this study (measurements in µm).

Species and types	Host	Length of caudal processes	Dimensions of spore body	Number of secondary cells	Shape of processes	Reference
A. raabeiiuniaris Janiszewska,1952	*L. hoffmeisteri*	25-35	17	16	pointed tips	Janiszewska (1955)
A. pavinsis Marques, 1984						
short	*S. heringianus*	10-12	8	16	pointed tips	Marques (1984)
long	*S. heringianus*	15-20	12	16	pointed tips	Marques (1984)
A. stellans Marques, 1984	*Tubifex* sp.	70-90	15-20	16	pointed tips	Marques (1984)
A. trifolium Marques, 1984	*Tubifex* sp.	40-50	20-25	32	–	Marques (1984)
A. major Styer, Harrison et Burtle, 1992	*D. digitata*	11 × 36	18-22	–	rounded tips	Styer et al. (1992)
A. minor Styer, Harrison et Burtle, 1992	*D. digitata*	36	13-16	–	rounded tips	Styer et al. (1992)
A. sp. of McGeorge et al. 1997	*Tubifex* sp.	25.6 (19-31)	13.7 (12-15)	–	pointed tips	McGeorge et al. (1997)
A. type 1 of El-Mansy et al. 1998a	*T. tubifex*	17.5 × 9.9	18.3	–	pointed tips	El-Mansy et al. (1998a)
A. type 2 of El-Mansy et al. 1998a	*B. sowerbyi*	65.7 × 10.5	22.8	–	pointed tips	El-Mansy et al. (1998a)
A. type 3 of El-Mansy et al. 1998a	*B. sowerbyi*	70.3 × 8.0	22.8	–	pointed tips	El-Mansy et al. (1998a)
A. type 4 of El-Mansy et al. 1998a	*B. sowerbyi*	55.7 × 11.2	19.4	–	pointed tips	El-Mansy et al. (1998a)
A. type 5 of El-Mansy et al. 1998a	*B. sowerbyi*	17.2 × 3.9	9.9	–	rounded tips	El-Mansy et al. (1998a)
A. type 6 of El-Mansy et al. 1998a	*Limnodrilus* sp.	24.2 × 11.2	19	–	pointed tips	El-Mansy et al. (1998a)
A. type 7 of El-Mansy et al. 1998a	water	24.4 × 9.5	18.9	–	pointed tips	El-Mansy et al. (1998a)
A. type 8 of El-Mansy et al. 1998a	*Limnodrilus* sp.	12.2 × 9.0	22.6	–	pointed tips	El-Mansy et al. (1998a)
A. type 9 of El-Mansy et al. 1998a	*B. sowerbyi*	51.3 × 9.5	18.8	–	pointed tips	El-Mansy et al. (1998a)
A. type 10 of El-Mansy et al. 1998a	*B. sowerbyi*	16.7 × 8.8	15.5	–	rounded tips	El-Mansy et al. (1998a)
A. type 11 of El-Mansy et al. 1998a	*B. sowerbyi*	31.9 × 3.7	8.5	–	rounded tips	El-Mansy et al. (1998a)
A. type 12 of El-Mansy et al. 1998a	*B. sowerbyi*	26.5 × 8.7	12.1	–	rounded tips	El-Mansy et al. (1998a)
A. type 1 of El-Mansy et al. 1998b	water	51.3 × 9.5	18.8	–	rounded tips	El-Mansy et al. (1998b)
A. type 2 of El-Mansy et al. 1998b	water	22.6 × 3.9	21.1	–	rounded tips	El-Mansy et al. (1998b)
A. type 3 of El-Mansy et al. 1998b	water	17.2 × 3.9	9.9	–	rounded tips	El-Mansy et al. (1998b)
A. sp. of Xiao and Desser 1998a	*L. hoffmeisteri*	21.0 × 26.0	11 (10-12.5)	–	pointed tips	Xiao and Desser (1998a)
A. type 1 of Negredo and Mulcahy 2001	*T. ignotus*	21.1 × 16.1	14.4 (12.6-16.9)	10	pointed tips	Negredo and Mulcahy (2001)
A. type 2 of Negredo and Mulcahy 2001	*L. hoffmeisteri*	31.0 × 10.6	14.1 (13.0-15.6)	12	rounded tips	Negredo and Mulcahy (2001)
A. type 3 of Negredo and Mulcahy 2001	*T. ignotus*	20.8 × 10.4	9.1 (9.1-9.1)	10	rounded tips	Negredo and Mulcahy (2001)
A. type 1	*T. tubifex*	32 (31-36)	14.4 (12-15)	64-128	pointed tips	this study
A. type 2	*T. tubifex*	24.7 (23.4-26.5)	14.9 (14-18.7)	64	pointed tips	this study
A. type 3	*T. tubifex*	114.5 (101.4-124.8)	24 (23.4-24.9) × 21.8 (20.3-23.4)	32	pointed tips	this study
A. type 4	*T. tubifex*	28.3 (23.4-31.2)	11.9 (11.2-14)	32	pointed tips	this study

also showed some differences from aurantiactinomyxon types described by previous authors. *Aurantiactinomyxon raabeiiunioris, A. trifolium* Marques, 1984 and *A. stellans* Marques, 1984 have much larger spore body and caudal processes than aurantiactinomyxon types type 1, type 2 and type 4. The large and short types of *Aurantiactinomyxon pavinsis* Marques, 1984 from *Stylaria heringianus* Claparède, 1862 (Marques 1984) have a much shorter spore body and epispore dimensions than the four types found in this study (Table 4). Styer et al. (1992) described two aurantiactinomyxon types named *A*. "*major*" and *A*. "*minor*" released by *Dero digitata* (Müller, 1773) in ponds harbouring proliferative gill disease (PGD). Although there are some similarities in the dimensions of spore body and caudal processes measured by these authors and the types described here, their types have rounded tips to the caudal processes compared to the pointed ends of the processes of aurantiactinomyxon type 1, type 2, type 3 and type 4 (Table 4). The aurantiactinomyxon types of El-Mansy et al. (1998a,b) also have different dimensions and host species. The only type of aurantiactinomyxon released by *T. tubifex* described by these authors has much shorter caudal processes and a smaller spore body than aurantiactinomyxon type 1, type 2, type 3 and type 4. The *Aurantiactinomyxon* sp. of Xiao and Desser (1998a) also has a different host and shorter spore body dimensions (Table 4). Aurantiactinomyxon type 3 has larger caudal processes than all other aurantiactinomyxon types previously described (Table 4). Of the aurantiactinomyxon types of Negredo and Mulcahy (2001) their aurantiactinomyxon 2 is close in overall dimensions to the aurantiactinomyxon type 1 of this study but the caudal processes have rounded tips compared with the pointed and foliate processes of the latter type. The other forms described by these authors differ in dimensions from the types reported in this study.

A member of aurantiactinomyxon types have been associated with successful myxosporean transmissions (Styer et al. 1991, El-Matbouli et al. 1992, Grossheider and Körting 1992, Benajiba and Marques 1993, Yokoyama 1997, Székely et al. 1998). However, some of these authors gave no measurement data for the actinosporeans, which makes comparisons with the types described here impossible. In those types for which adequate data is provided, there are obvious differences with the types described here in shape and size, or the fish hosts are absent from the site studied here.

McGeorge et al. (1997) found an *Aurantiactinomyxon* sp. in the same settlement pond in which this study was carried out. Its spore dimensions were within the limits of the measurements of those of aurantiactinomyxon type 1, type 2 and type 4. However, the release of spores occurred at the same time as aurantiactinomyxon type 1 and the illustration given by McGeorge et al. (1997) suggests that aurantiactinomyxon type 1 is identical to the *Aurantiactinomyxon* sp. of McGeorge et al. (1997).

Aurantiactinomyxon type 2 differed from the other types and species of aurantiactinomyxon described in its dimensions and host (Table 4). Thus, it is considered that this species is a new member of the collective group aurantiactinomyxon.

Aurantiactinomyxon type 3 has larger caudal process dimensions than the other aurantiactinomyxon species and types. The closest species, *A. stellans* has caudal processes of 70-90 µm in length. The drawings given by Marques (1984) show that *A. stellans* has triangular-like caudal processes and spore body. Its polar capsules are also different in size (Table 4). The shape of individual spores is very similar to those of the actinosporean collective group echinactinomyxon and the spore was initially identified as such. However, the presence of a 120° angle between the caudal processes made the identification easier. Following the measurement comparisons with the other known aurantiactinomyxon species and types, it is concluded that aurantiactinomyxon type 3 is a new member of the collective group aurantiactinomyxon.

Aurantiactinomyxon type 4 has a smaller spore body than aurantiactinomyxon type 1 and type 2 and its caudal process dimensions are intermediate between aurantiactinomyxon type 1 and type 2, but distinct from other species or types described elsewhere (Table 4) and it thus appears to be new member of the collective group aurantiactinomyxon.

COLLECTIVE GROUP TRIACTINOMYXON STOLC (1899)

Spores with a style and three anchor-shaped caudal processes with pointed ends. Sporoplasm contains 8-256 secondary cells. The style as well as the number of secondary cells are the characteristic features and important descriptives of the collective group. *Triactinomyxon ignotum* Stolc, 1899 is the type-species. Twenty six different species and types have so far been identified (Table 5).

Triactinomyxon type Figs. 7a, 6F, Table 5

A type of triactinomyxon was released by immature oligochaetes (possibly *Tubifex tubifex*). The spores with style and three elongated caudal processes. Spore body 47.6 µm (37.5-62.5) long and 15.2 µm (14.1-16.1) wide. Secondary cells around 60. Polar capsules pear-shaped, 7 µm by 4 µm. Style 136.5 µm (115.4-156) long and widens from the spore body to the base of anchor-like projections. Caudal processes curve upwards, 161.1 µm (131.2-193.7) long.

Remarks. In the UK, MacKinnon and Adam (1924) described *Triactinomyxon ignotum*, *T. legeri* MacKinnon et Adam, 1924 and *T. mrazeki* MacKinnon et Adam, 1924 from the River Thames in London. Hamilton and Canning (1987) reported *T. ignotum* and

Table 5. Descriptive data of triactinomyxon species and types previously described and those found in this study (measurements in μm).

Species and types	Host	Length of caudal processes	Length of style	Dimensions of spore body	Number of secondary cells	Reference
T. ignotum Stolc, 1899	*T. tubifex*	175-220	140-170	30-50	8	Marques (1984)
T. magnum Granata, 1923	L. udekemianus	500	25-30	–	16	Marques (1984)
T. legeri MacKinnon et Adam, 1924	*T. tubifex*	–	90-140	15-20	24	Marques (1984)
T. mrazeki MacKinnon et Adam, 1924	*T. tubifex*	120-130	150	25-65	50-100	Marques (1984)
T. ohridensis Georgievitch, 1940	*T. ohridensis*	–	120-140	20-30	8	Marques (1984)
T. petri Georgievitch, 1940	*Lumbriculus* sp.	–	–	–	8	Marques (1984)
T. naidanum Naidu, 1956	*N. communis*	120	100	–	12	Marques (1984)
T. robustum Marques, 1984	*E. tetraedra*	–	90-110	50	28	Marques (1984)
T. dubium Granata, 1924	*T. tubifex*	–	–	–	32	Marques (1984)
T. major Styer, Harrison et Burtle, 1992	*D. digitata*	6 × 176	no style	5-9 × 108	–	Styer et al. (1992)
T. minor Styer, Harrison et Burtle, 1992	*D. digitata*	7.5 × 158	no style	7-10 × 35	–	Styer et al. (1992)
T. type 1 of El-Mansy et al.1998a	*Stylaria*, *Tubifex*	128	102	36.6 × 10.6	27	El-Mansy et al. (1998a)
T. type 2 of El-Mansy et al.1998a	water	–	–	101.2 × 14.1	–	El-Mansy et al. (1998a)
T. type 3 of El-Mansy et al.1998a	*Nais*, *Tubifex*	127.5	150	47.1 × 10.6	8	El-Mansy et al. (1998a)
T. type 4 of El-Mansy et al.1998a	Limnodrilus	173.4	137.5	41.2 × 8.8	8	El-Mansy et al. (1998a)
T. type 1 of El-Mansy et al.1998b	*water*	230	123	50.6	–	El-Mansy et al. (1998b)
T. type 2 of El-Mansy et al.1998b	water	152.6	117.7	25.4	–	El-Mansy et al. (1998b)
T. type 3 of El-Mansy et al.1998b	water	224.6	87.7	44.7	8	El-Mansy et al. (1998b)
T. type 4 of El-Mansy et al.1998b	water	281.7	149	45	–	El-Mansy et al. (1998b)
T. type 5 of El-Mansy et al.1998b	water	249	90.6	37.7	–	El-Mansy et al. (1998b)
T. “A” of Xiao and Desser 1998b	*L. hoffmeisteri*	340-380	150-180	40-70	256	Xiao and Desser (1998b)
T. “B” of Xiao and Desser 1998b	*L. hoffmeisteri*	200-210	100-120	20-25	32	Xiao and Desser (1998b)
T. “C” of Xiao and Desser 1998b	*L. hoffmeisteri*	280-300	157-174	28-31	8	Xiao and Desser (1998b)
T. “D” of Xiao and Desser 1998b	*L. hoffmeisteri*	105-115	40-45	20-25	32	Xiao and Desser (1998b)
T. “E” of Xiao and Desser 1998b	*L. hoffmeisteri*	270-300	153-167	47-53	32	Xiao and Desser (1998b)
T. “F” of Xiao and Desser 1998b	*L. hoffmeisteri*	160-300	–	46-56	16	Xiao and Desser (1998b)
T. type	immature	161.1	136.5	47.6 × 15.2	60	this study

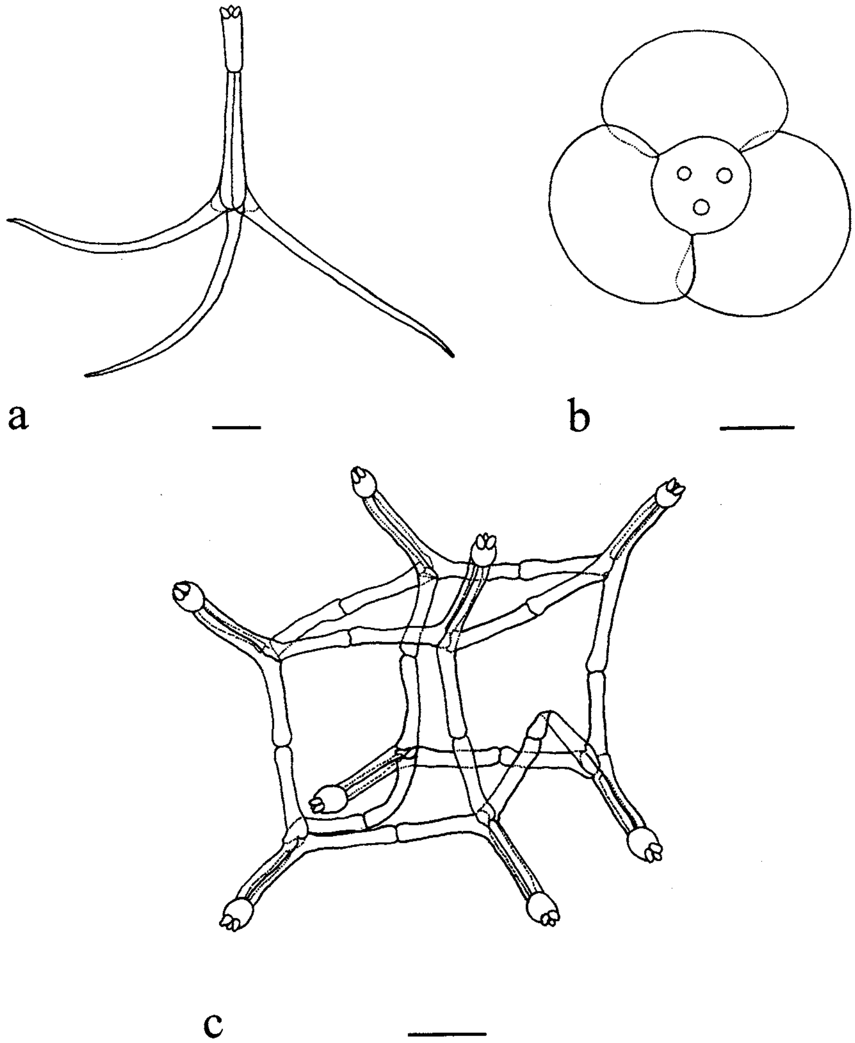

Fig. 7. **a** – triactinomyxon type; **b** – neoactinomyxum type; **c** – siedleckiella type. Scale bars: Figs. a, c = 50 µm; Fig. b = 10 µm.

T. dubium Granata, 1924 to be present in a fish farm where whirling disease occurs and they pointed out that *T.* '*gyrosalmo*' of Markiw and Wolf (1983) was probably *T. dubium*.

The number of secondary cells is of particular importance in the species identification of members of the collective group. Most of the species described so far have different numbers of secondary cells which makes comparisons simple. The style and the caudal processes are also significant but their size variability creates problems in species comparison. The triactinomyxon type under study has 60+ secondary cells, whilst *T. ignotum*, *T. ohridensis* Georgievitch, 1940, *T. naidanum* Naidu, 1956, *T. magnum* Granata, 1923, *T. legeri* and *T. dubium* have only 8, 8, 12, 16, 24 and 32 secondary cells, respectively. The triactinomyxon stage of *Myxobolus articus* Pugachev et Khokhlov, 1979 of Kent et al. (1993) has much larger caudal processes (294-360 µm) than the type described here, while the triactinomyxon stage of *Myxobolus cotti* El-Matbouli et Hoffmann, 1987 of El-Matbouli and Hoffmann (1989) has just 16 secondary cells and a total style + epispore length of only 88.64 µm. Styer et al. (1992) reported two triactinomyxon species; *T.* "*major*" and *T.* "*minor*", however neither of them possessed a style, a characteristic feature of the genus, so there must be some doubt as to whether the identification was correct. Six types of triactinomyxon were described by Xiao and Desser (1998b), and of these triactinomyxon "B" and "C" were similar to the triactinomyxon type in this study with respect to spore dimensions but differed in the number of secondary cells, whilst the rest had much longer caudal processes and different numbers of secondary cells (Table 5). In addition, nine types of triactinomyxon described by El-Mansy et al. (1998a,b) also differed from our triactinomyxon type in spore dimensions (Table 5). Amongst triactinomyxon species only *T. mrazeki* has as many as 50-100 secondary cells per spore. Its style is 150 µm in length and the spore body is 25-65 µm in length. The triactinomyxon described here was 136.5 µm (115.4-156) in length and the spore body 47.6 µm (37.5-62.5) and there were 60+ secondary cells. Very large differences in spore dimension were observed. Similarly *T. ignotum*, as described by Janiszewska (1955) has a spore body of 20-30 µm and a style of 110-165 µm in length. Marques (1984) however, gives different measurements for the equivalent dimensions of the same species with a spore body of 30-50 µm and a style of 140-170 µm. It is obvious that large variations in dimensions of the same species is likely. McGeorge et al. (1997) reported a triactinomyxon form in the same settlement pond as used here and they named it as *T. mrazeki* due to similarities in spore dimensions and number of secondary cells. The triactinomyxon type described here has a similar length of style (115.4-156 µm compared to 110-150 µm) but larger caudal processes (131.3-193.7 µm compared to 107-150 µm) than that of McGeorge et al. (1997). There was a similarity in the number of secondary cells (60+) found in both types (Table 5). Given the size variation that may exist within a single triactinomyxon type, it seems probable that the type described here is *T. mrazeki* MacKinnon et Adam, 1924.

Collective group neoactinomyxum Granata (1922)

Spores with three caudal processes, disc-like or triangular in apical view, of equal size, bases of the processes enclose the epispore body. The type species of the collective group is *Neoactinomyxum globosum* Granata, 1922. So far, three species and 9 types have been identified (Table 6).

Neoactinomyxum type — Figs. 7b, 8A, Table 6

Individual spores with rounded spore body, with three apically located polar capsules and three wide, short and equal sized caudal processes. Spores released from *Tubifex tubifex*. Spore body 17.6 µm (12-20) in diameter. Secondary cells, 32. Three polar capsules 3 µm (2.9-3.1) in diameter. Caudal processes 29.1 µm (24-31) long and 18.8 µm (15-20) wide.

Remarks. The type species *Neoactinomyxum globosum* was reported from *Limnodrilus udekemianus* Claparède, 1862 by Janiszewska (1955) with 3 globular caudal processes. *Neoactinomyxum globosum*, *Neoactinomyxum eiseniellae* (Ormièrez et Frézil, 1969) and *Neoactinomyxum minutum* Marques, 1984 have smaller spore body and caudal process dimensions than those of the neoactinomyxum type in this study (Table 6). Similarly, the caudal processes of the neoactinomyxum type are larger than those of *N. globosum*, *N. eiseniellae* and *N. minutum.* Hand drawings of these forms given by Marques (1984) also show differences from neoactinomyxum type. While *N. eiseniellae* has the polar capsules very closely located together, in *N. minutum* they are on top of the spore body occupying nearly all the available space when viewed apically. *Neoactinomyxum globosum* resembles neoactinomyxum type but has smaller dimensions. The neoactinomyxum type is larger than that described by Negredo and Mulcahy (2001) and the polar capsules appear to be more widely spaced. Yokoyama et al. (1993) reported a neoactinomyxum form from *Branchiura sowerbyi* Beddard, 1892 involved in the experimental transmission of *Hoferellus carassii* Akhmerov, 1960 from *Cyprinus carpio* L., but they did not provide any data about this form, and the photographic plate given is not adequate to make a comparison. The neoactinomyxum stage spore of *Sphaerospora renicola* Dyková et Lom, 1982 also differs from neoactinomyxum type in this study by its shape and dimensions (Molnár et al. 1999). In the light of comparisons with other known species of the collective group neoactinomyxum, it seems that this type is a new member of the group.

Collective group siedleckiella Janiszewska (1952)

Individual spores with style and three caudal processes equal in size. Spores joined by tips of the three caudal processes creating hexahedric net. Caudal processes originate just below style and project downwards without curving. Spore body barrel-shaped. The type species of the collective group is *Siedleckiella silesica* Janiszewska, 1952 and only one other type, the *Siedleckiella* sp. of Uspenskaya (1995), the actinosporean stage in the life cycle of *Zschokkella nova* Klokacheva, 1914 from *Carassius carassius* L., has been identified (Table 7).

Siedleckiella type — Fig. 7c, 8B, Table 7

Spores released by *Tubifex tubifex* showed clusters of eight spores, joined by their caudal processes, forming cube-like reticulum or net. Spores anchor-shaped with three oar-like obtuse arms that project from style. Anterior part of spore consists of three pear-shaped polar capsules. Spore body 21.8 µm (21.2-22.5) long and 17.6 µm (15.6-18.7) wide. Secondary cells, 16. Polar capsules 5 µm by 2.4 µm. Style 69 µm (62.5-71.8) long, caudal processes 60 µm (56.2-68.7) long.

Remarks. Janiszewska (1955) reported *Siedleckiella silesica* from the gut epithelium of *Tubifex* sp. The spores form a cube-shaped reticulum characteristic of the collective group. Spore body of individual spores is 30-40 µm long, which is larger than the siedleckiella type described here (Table 7). The entire length of the spore at 185-205 µm is also much larger than the mean of 150.8 µm (139.95-163) of siedleckiella type. The sporoplasm of *S. silesica* contains over 100 secondary cells compared to 16 observed in the siedleckiella type.

Table 6. Descriptive data of the neoactinomyxum species and types described previously and those found in this study (measurements in µm).

Species and types	Host	Length of caudal processes	Diameter of processes	Dimensions of spore body	Number of secondary cells	Reference
N. globosum Granata, 1922	*L. udekemianus*	20-27	12-16	9-12	16	Marques (1984)
N. eiseniellae (Ormièrez et Frézil, 1969)	*T. tubifex*	16-18	11-14	6-8	32	Ormières and Frézil (1969)
N. minutum Marques, 1984	*E. tetraedra*	21-25	12-16	12-14	32	Marques (1984)
N. type 1 of El-Mansy et al. 1998a	*B. sowerbyi*	29.3	8.5 × 16.4	21.2	–	El-Mansy et al. (1998a)
N. type 2 of El-Mansy et al. 1998a	*B. sowerbyi*	31	10.8 × 14.4	18.3	–	El-Mansy et al. (1998a)
N. type 3 of El-Mansy et al. 1998a	*B. sowerbyi*	30.2	8.5 × 16	22	–	El-Mansy et al. (1998a)
N. type 4 of El-Mansy et al. 1998a	*B. sowerbyi*	29	7 × 16	22.3	–	El-Mansy et al. (1998a)
N. type 5 of El-Mansy et al. 1998a	*B. sowerbyi*	23.1	4.4 × 13.6	21.2	–	El-Mansy et al. (1998a)
N. type 6 of El-Mansy et al. 1998a	*B. sowerbyi*	29.3	7.8 × 12.7	20.3	–	El-Mansy et al. (1998a)
N. type 7 of El-Mansy et al. 1998a	*B. sowerbyi*	31.5	8.5 × 16.4	22.6	–	El-Mansy et al. (1998a)
N. type 8 of El-Mansy et al. 1998a	*B. sowerbyi*	26.8	4.2 × 11.3	22.8	–	El-Mansy et al. (1998a)
N. sp. of Xiao and Desser 1998b	*L. hoffmeisteri*	24 (22-26)	23 (21-25)	10 (9.3-10.5)	32	Xiao and Desser (1998b)
N. type of Negredo and Mulcahy 2001	*L. variegatus*	18.1 (16.9-18.2)	25.6 (22.1-26.0)	15.6 × 12.9	16	Negredo and Mulcahy (2001)
N. type	*T. tubifex*	29.1 (24-31)	18.8 (15-20)	17.6 (12-20)	32	this study

Table 7. Descriptive data of siedleckiella species and types described previously and those found in this study (measurements in µm).

Species and types	Host	Length of caudal processes	Dimensions of spore body	Dimensions of polar capsules	Number of secondary cells	Reference
S. silesica Janiszewska, 1952	*Tubifex* sp.	150-180	30-40	–	over 100	Janiszewska (1955)
S. sp. of Uspenskaya 1995	*T. tubifex*	60-70	20-21	5 × 2.5	16-32	Uspenskaya (1995)
S. type	*T. tubifex*	60 (56.2-68.7)	21.8 (21.2-22.5) × 17.6 (15.6-18.7)	5 × 2.4	16	this study

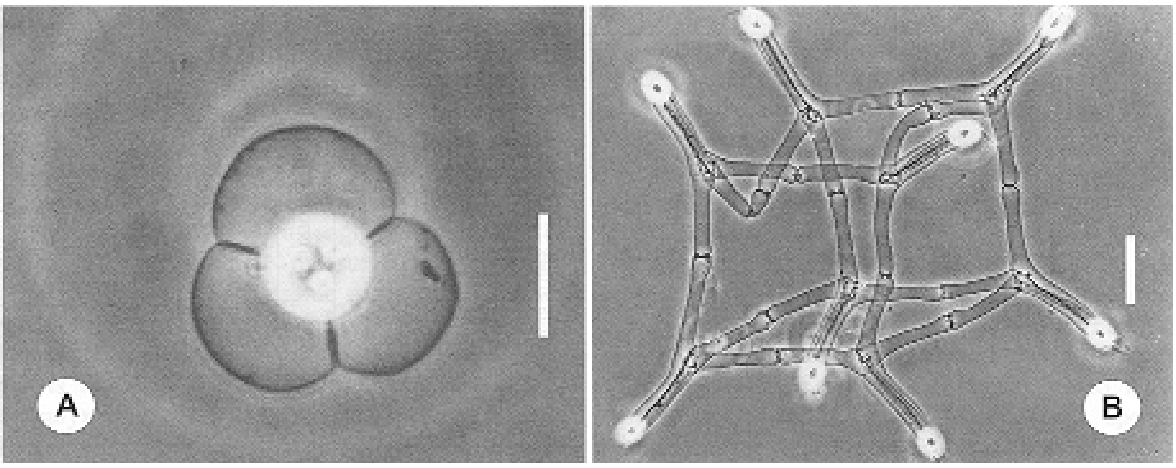

Fig. 8. A – neoactinomyxum type; **B** – siedleckiella type. Scale bars: Fig. A = 10 μm; Fig. B = 50 μm.

The morphometrics of the species of siedleckiella reported by Uspenskaya (1995) are comparable with the siedleckiella type identified here with very similar spore body and caudal process dimensions (Table 7). The number of secondary cells is also similar at 16-32 compared to 16 in the siedleckiella type. The major difference is the length of the style. While *Siedleckiella* sp. of Uspenskaya (1995) has a style with an average length of 15-17 μm, siedleckiella type has a much more elongated style. The host species for these two siedleckiella types was *Tubifex tubifex*. The length of the style, together with the absence of *Carassius auratus* L. from the river system sampled in this study, suggest that the siedleckiella type is a new member of the collective group siedleckiella.

DISCUSSION

In the present study, five types of echinactinomyxon (four previously described), six types of raabeia (five previously described), three types of synactinomyxon (all previously described), four types of aurantiactinomyxon (three previously undescribed), one type of triactinomyxon (previously described), one type of neoactinomyxum (previously undescribed) and one type of siedleckiella (previously undescribed) have been identified.

There are very few studies on actinosporeans from oligochaetes in the UK (Ikeda 1912, MacKinnon and Adam 1924, Hamilton and Canning 1987, McGeorge et al. 1997). Ikeda (1912) found four species of actinosporeans belonging to the collective groups hexactinomyxon, synactinomyxon, triactinomyxon and sphaeractinomyxon, whilst MacKinnon and Adam (1924) found three species of triactinomyxon, *Triactinomyxon ignotum*, *T. legeri* and *T. mrazeki* in natural environments in England. However, in the recent studies in fish farms Hamilton and Canning (1987) identified five actinosporean species, *Synactinomyxon tubificis*, *Echinactinomyxon radiatum*, *T. ignotum*, *T. dubium* and *Aurantiactinomyxon* sp., whilst McGeorge et al. (1997), at the same fish farm used in this study, found five different actinosporean types, *S. tubificis*, *S. longicauda*, *T. mrazeki*, *Raabeia* sp. and *Aurantiactinomyxon* sp.

El-Mansy et al. (1998a,b) in a fish farm and a lake in Hungary and Xiao and Desser (1998a,b) in a lake in Canada made comprehensive studies of the actinosporean fauna. El-Mansy et al. (1998a) found a total of twenty eight actinosporean types (four triactinomyxon types, four raabeia types, twelve aurantiactinomyxon types and eight neoactinomyxum types), which were all previously undescribed, in ponds in a carp farm. In a natural lake El-Mansy et al. (1998b) found ten actinosporeans (five triactinomyxon types, two raabeia types and three aurantiactinomyxon types) of which five were also found in the farm. Xiao and Desser (1998a,b) identified twenty five types of actinosporeans belonging to eight collective groups from a lake in Canada. Thus, although the overall numbers of actinosporean types found in the environment studied here and by these other authors are similar, there are differences in the abundance of various types. Thus, seven types of triactinomyxon were found by Xiao and Desser (1998b), four types by Mansy et al. (1998a) and five types by Mansy et al. (1998b), whilst only one type was found in this study. In contrast, the three types of synactinomyxon and four types of aurantiactinomyxon found in this study represent higher numbers than those found by Xiao and Desser (1998a).

It is interesting that no echinactinomyxon, synactinomyxon and siedleckiella types were found by El-Mansy et al. (1998a,b) despite the large total number of actinosporean types they recorded. Xiao and Desser (1998a,b) found six types each of echinactinomyxon and raabeia, comparable to the number of types found in this study, including *Echinactinomyxon radiatum* which clearly appears to be very widely distributed. Only one type of synactinomyxon was found by Xiao and Desser (1998a) compared with the three types found in this study. Siedleckiella types seem to be rather rare with only one type recorded in this study and none in the other studies. Aurantiactinomyxon types were abundant in the studies of El-Mansy et al. (1998a,b), similar to this study, but only one type was found by Xiao and Desser (1998b). Neoactinomyxum types were relatively abundant in the study of El-Mansy et al. (1998a), but only one type was found in this study and that of Xiao and Desser (1998b). Interestingly, Negredo and Mulcahy (2001) recorded only seven actinosporean types (three echinactinomyxon, three aurantiactinomyxon and one neoactinomyxum) from an Irish river, the fish fauna of which was similar to that of the present study site. The number of oligochaetes examined by these authors was considerably smaller than in the present study and may not completely reflect the actinosporean fauna. Only two actinosporean forms seem to be common to both studies. Echinactinomyxon and aurantiactinomyxon types were relatively common in the study of Negredo and Mulcahy (2001), but they did not record any synactinomyxon or raabeia types. The factors influencing the actinosporean fauna of different habitats are unknown as yet and will require detailed studies on a much wider range of habitats than have been carried out thus far.

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