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Silica–scaled chrysophytes of Ireland
With an appendix: Geographic variation of scale shape
of *Mallomonas caudata*

by

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with 42 figures and 4 tables

Abstract: Silica-scaled chrysophytes were studied by means of electron microscopy for the second time from Ireland. Samples were collected from 17 different localities in western and eastern Ireland during summer. Twenty-four taxa of the genera *Chrysosphaerella* (2), *Paraphysomonas* (3), *Spiniferomonas* (2) *Mallomonas* (12) and *Synura* (5) were identified, 13 of which are new records for Ireland. The species composition is typical for northern temperate areas. Comments about their ecological preferences and geographical distributions are given. *Mallomonas caudata* was the most numerous and common taxon. Therefore, as a second part of this study, the idea of using Elliptic Fourier analysis for evaluation of shape of scales was realised. As a result of this analysis, the populations of *M. caudata* from two areas (Connemara in western part and Killarney in southwestern part of Ireland) were significantly distinguished on the base of shape of their scales.

Key words: Chrysophyceae, Synurophyceae, siliceous scales, scale shape, autecology.

Introduction

The freshwater algal flora of Ireland, especially some groups such as desmids, diatoms and charophytes, is well known. The oldest publications, including descriptions of desmids new to science, were by the Irish botanist, William Archer, between 1858–1885. Later, William West, and his son George S. West carried out long-term research of desmids, and also other groups of algae from all of the British Isles (John et al. 2002). The great achievement of the West's was to prepare a series of monographs in which all known British desmids were described and illustrated (West & West 1904, 1905, 1908, 1912). Epipelic diatoms and other algae of lakes and ponds have been investigated by Round & Brook (1959), and overall detailed research of freshwater diatoms from Ireland has been performed by Foged (1977). The distribution of charophytes is known mainly through the handbook of Moore (1986). There are also

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several recent surveys of the total phytoplankton and zooplankton composition in lakes and rivers from some parts of Ireland (e. g. Pybus et al. 2003).

However, silica-scaled bearing species of chrysophytes in Ireland are still overlooked, except one unpublished survey that was carried out by Kristiansen in 1998. Thus, the main aim of this study is to contribute information about the distribution and ecology of silica-scaled chrysophytes of this island.

Material and methods

Samples were collected in three areas of Ireland during summer 2003. All samples were obtained by dragging a 40 μm mesh plankton net from the shore. Afterwards, samples were investigated by light microscopy for the presence or absence of silica-scaled chrysophytes. In the case of confirmation of the presence of silica-scale chysophytes (in 17 samples from total of 30 samples), samples were fixed with acidic Lugol`s iodine solution. They were subsequently left undisturbed for 24 hours to allow sedimentation before pipetting off the excess water. Preparations for TEM included rinsing with distilled water, centrifugation, drying on Formvar coated copper grids, and shadowcasting with chromium. The grids were examined with a transmission electron microscope Jeol 1010.

Water temperature, pH and conductivity were measured in the field using a WTW Multiline set with field probes.

Fig. 1. Positions of the sampling areas: 1 – Connemara, 2 – Killarney, 3 – Wicklow

The sampling localities

The island of Ireland is situated in the extreme north-west of Europe between 51.5° and 55.5 °N and between 5.5° and 10.5 °W. The sampling localities are located in the three areas (Fig. 1) described below.

1. Six investigated lakes (loc. 2, 3, 6, 8, 10, 11) are situated in west Ireland, near the small town Clifden and Connemara National Park. Gneiss and granite underlay the lowlands of Connemara. Western blanket bog and heathland are the main vegetation types of the whole area. Dominant flora included *Sphagnum, Carex, Drosera, Eriophorum, Erica* and *Calluna*. The peaty bogs were, and are still, used as fuel sources, these areas are easily recognized by the old cultivation ridges and hollows. Most of the land is used for agriculture, mainly as grazing for sheep and cattle. The mild oceanic climate permits a luxuriant growth of some plants, which otherwise are found in southern and southwestern Europe.

2. In the south-western part of Ireland, close to or in Killarney National Park, silica-scaled chrysophytes were found at ten localities (loc. 14, 18, 21, 24, 25, 26, 27, 28, 29, 30). Within the National Park, the most extensive areas of natural woodland remaining in the whole country are found. The three world-famous Lakes of Killarney make up almost a quarter of the Park's area. They are known as the Upper Lake (loc. 27), Muckross Lake (Middle Lake, loc. 25) and Lough Leane (Lower Lake, loc. 14, 26), and are joined at the 'meeting of the waters'. From the meeting of the waters a narrow channel known as the Long Range leads to the Upper

Table 1. List of localities including sampling dates and basic environmental parameters.

No.	Locality	Geographical position		Sampling date	Water t, °C	pH	Conductivity µS/cm
2	Shanakeever Lough	53° 27′ 09.3″N	10° 0′ 14.1″W	25. 7. 2003	16.8	6.8	84
3	Lough na mBreac Caoch	53° 26′ 53.9″N	10° 0′ 18.1″W	25. 7. 2003	18.2	6.5	110
6	unnamed lake	53° 25′ 09.2″N	9° 58′ 48.2″W	27. 7. 2003	17.4	6.6	120
8	unnamed lake	53° 25′ 15.7″N	9° 59′ 13.8″W	27. 7. 2003	18.8	7.1	116
10	Lake Fada	53° 24′ 53.8″N	10° 0′ 56.8″W	27. 7. 2003	20.2	6.5	136
11	unnamed lake	53° 25′ 10.8″N	10° 0′ 55.7″W	27. 7. 2003	19.7	5.8	123
14	Lough Leane by Ross Castle	52° 02′ 28.2″N	9° 31′ 52.8″W	31. 7. 2003	18.2	7.7	215
18	Devil's Punch Bowl	51° 58′ 39.0″N	9° 29′ 12.0″W	1. 8. 2003	11.9	6.6	39
21	Garagarry Loch	51° 59′ 36.6″N	9° 27′ 13.2″W	1. 8. 2003	16.4	6.4	42
24	Loch Doo	52° 01′ 01.2″N	9° 31′ 33.6″W	2. 8. 2003	19.5	7.2	180
25	Muckross Lake	52° 00′ 53.9″N	9° 31′ 33.6″W	2. 8. 2003	18.6	6.6	59
26	Lough Leane	52° 01′ 19.8″N	9° 30′ 26.4″W	2. 8. 2003	18.8	6.9	97
27	Upper Lake	51° 58′ 25.2″N	9° 36′ 14.4″W	3. 8. 2003	18.2	5.1	35
28	unnamed pool near Loch Beg	51° 58′ 23.4″N	9° 36′ 31.8″W	3. 8. 2003	21.3	6.9	151
29	Loch Beg	51° 58′ 21.0″N	9° 36′ 33.0″W	3. 8. 2003	20.2	6.1	41
30	Looscaungh Lough	51° 57′ 33.0″N	9° 36′ 57.6″W	3. 8. 2003	17.3	6.4	55
32	Lower Lake	53° 00′ 24.7″N	6° 20′ 08.1″W	8. 8. 2003	21.8	5.2	38

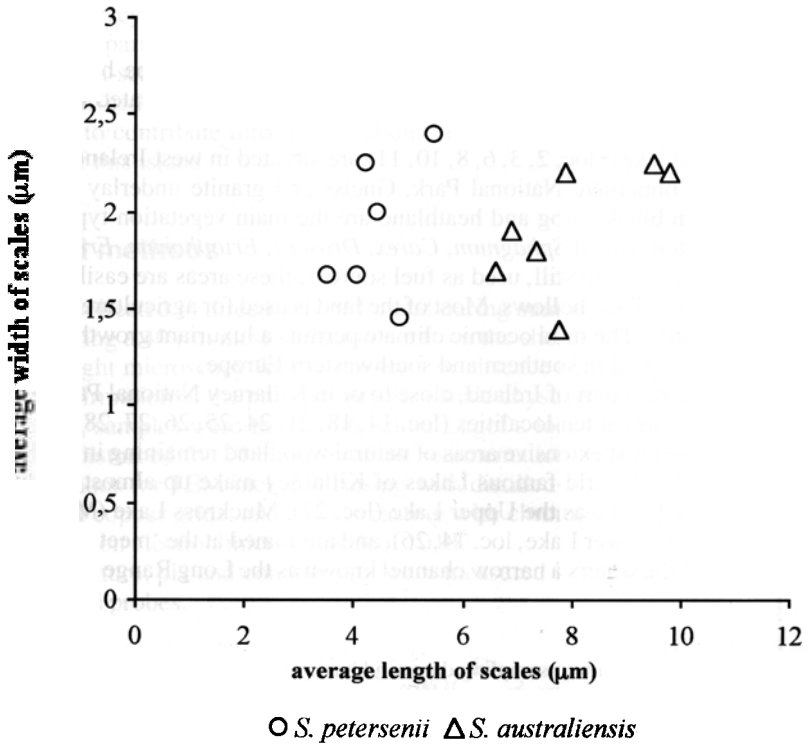○ *S. petersenii*   △ *S. australiensis*

Fig. 2. Comparison of average length and average width of body scales (in μm) of species *S. petersenii* and *S. australiensis* on the base of the dimensions as they are given in Tab. 2 on page 114.

Lake, which is the smallest of the lakes. Due to the sandstone and blanket bog of the catchment area the Upper Lake is slightly acidic and oligotrophic. Both Muckross Lake and Lough Leane lie astride the sandstone/limestone boundary, and the presence of limestone means that both of these lakes are slightly richer in natural nutrients than the Upper Lake. Lough Leane is by far the largest of the three lakes, at approximately 19 km², and is also the richest in nutrients (Sandover 2003).

3. Only one locality (loc. 32) with silica-scaled chrysophytes was found from Wicklow Mountains National Park, located in east Ireland. The Wicklow Mountains themselves are comprised of a large mass of granite which, as it solidified many millions of years ago, compressed and baked the adjacent sedimentary rocks forming mica-schist (Sandover 2003).

Further descriptions of the localities, including the dates of sampling and the environmental parameters are given in Tab. 1.

Results

Chrysophyceae

Chrysosphaerella coronacircumspina Wujek & Kristiansen   Figs 3, 4
Some scales and spines of this species were obtained. It is distributed in many parts of the world. Not reported from the British Isles. It is a new record for Ireland.

Chrysosphaerella longispina Lauterborn   Figs 5, 6
Several plate scales and spine scales, both long and short, were found.
Previous British records: Brook (1955).
It is a new record for Ireland.

Paraphysomonas imperforata Lucas   Fig. 7
Only one single scale was obtained from each of both localitie:
Previous British records: Preisig & Hibberd (1982).
Not previously recorded from Ireland.

Paraphysomonas vestita (Stokes) de Saedeleer   Fig. 8
Several spine scales were found.
Previous British and Irish records: Manton & Leedale (1961), Kristiansen (1979), Kristiansen (1998, unpubl. obs.), Preisig & Hibberd (1982).
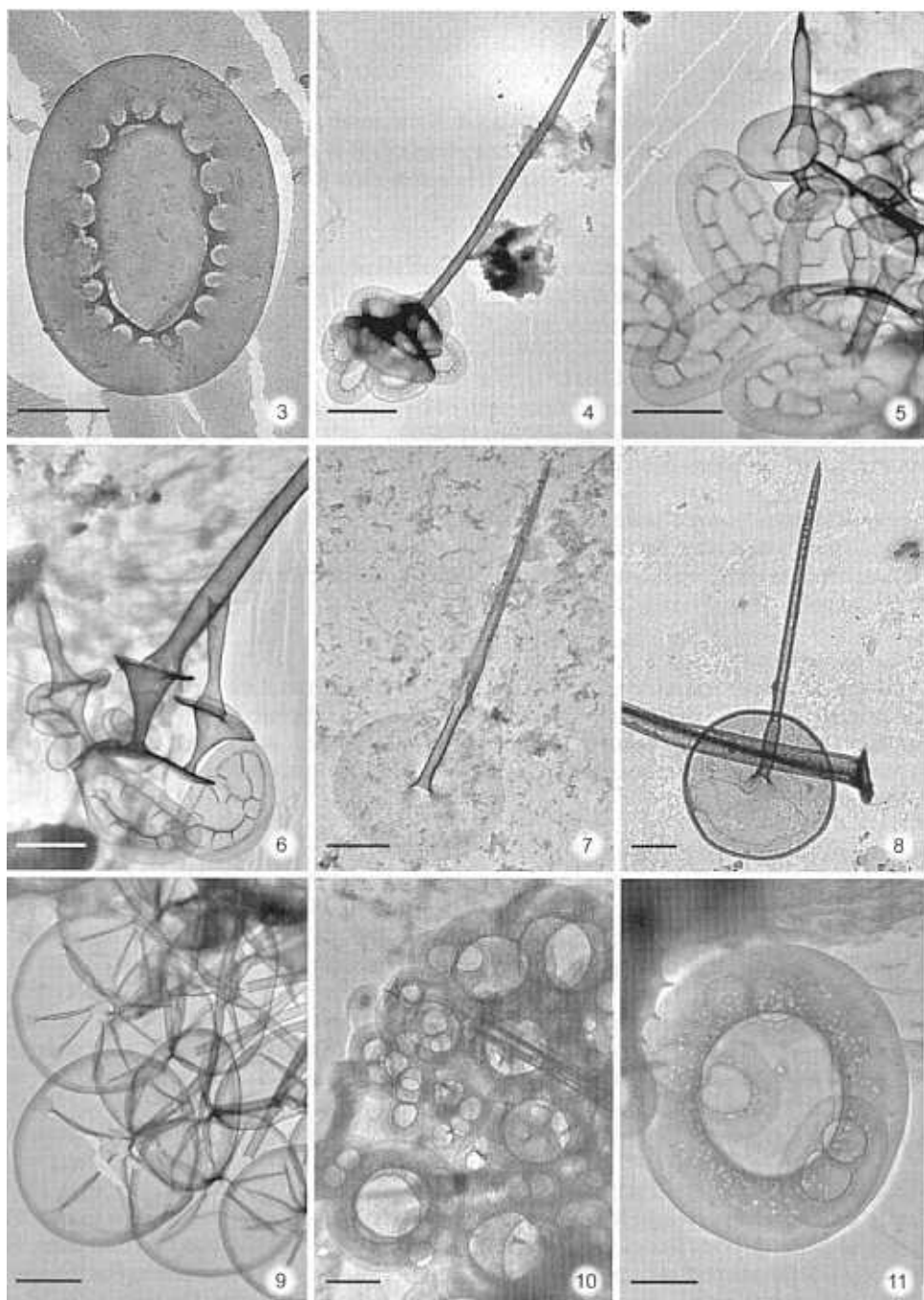
Paraphysomonas sp.   Fig. 9
Some scales closely resemble scales of *P. vestita* but differ from it by the presence of 6–7 radial ridges on the base plate. Such scales have been reported before from Japan by Takahashi (1976) as a taxon with provisional designation *P. vestita* form. no. 1, and from Madagascar by Hansen (1996) as *P. vestita* ssp. The number of radial ridges on the base plate was 5–7 in both studies.

Spiniferomonas trioralis Takahashi
Single scales and spines were observed rather rarely. At localities 6 and 28 co-occurred with *S. serrata*. It is one of the most commonly reported silica-scaled chrysophyte with world wide distribution.
Previous Irish records: Kristiansen (1998, unpubl. obs.).

Spiniferomonas serrata Nicholls   Figs 10, 11
Many scales and characteristic spines with a base plate with a serrated margin were obtained.
Not previously reported from the British Isles or Ireland.

Synurophyceae

Mallomonas cf. *acaroides* Perty em. Ivanov   Figs 12, 13
Scales different from typical *Mallomonas acaroides* var. *acaroides* scales were found. The domes of both the body scales and the apical scales are large and divided into two parts. For the body scales, one part is smooth and the other is perforated with small pores. For the apical scales, the smooth part is ornamented with parallel or branching ribs. On both sides of the dome, there are lateral extensions without ornamentation. The shield of the dome-bearing scales has several rows of pores (15–20) and well developed, delicate, irregularly-shaped reticulum. Domeless body, apical and rear scales have shields with struts radiating from the sub-

marginal ribs and from the posterior border rib of dome. A few scales with completely smooth shield were observed. Several small pores are positioned near the base of the V-rib. Posterior flanges are marked with delicate struts or may show rudimentary reticulation. Posterior scales are domeless and asymmetric. No bristles were obtained.

Dimensions: apical scales 3.3–3.5 × 2.7–3.2 µm, dome-bearing body scales 3.9–4 × 2.5– 2.7 µm, domeless body scales 3.7 × 2.5 µm, rear scales 2.9 × 1.9 µm.

Mallomonas akrokomos Rutner in Pascher   Fig. 14

Many scales were observed at four localities. No bristles were seen in any of the samples. It has a cosmopolitan distribution.

Previous British records: Bradley (1965), Bradley (1966) Harris (1958), Lund (1937, 1942 and 1949), Williams (1965).

Not previously recorded from Ireland.

Mallomonas caudata Ivanov em. Krieger   Fig. 15

This species was found at all localities, except lake 32. Some scales had two large pores on the shield.

To get an idea of the range of the diversity of scale shape, about 240 scales of this species were analysed from four localities. Further description and results of the analysis are given as an appendix of this study.

Previous British and Irish records: Bradley (1966), Brook (1964), Canter-Lund & Lund (1995), Harris & Bradley (1957), Kristiansen (1998, unpubl. obs.), Round & Brook (1959).

Mallomonas costata Dürrschmidt   Fig. 16

Several dome-bearing scales of this species were found at two localities. *M. costata* has world wide distribution.

Not formerly recorded from Great Britain or Ireland.

Mallomonas crassisquama (Asmund) Fott var. *crassisquama*   Figs 17, 18

This was a common species in some samples. Both types of bristles (helmet and needle) were observed at the most of the localities. In some body scales, especially the thick ones, the dome was marked with papillae. Many scales (e. g. from locality 10) had no or weakly developed shield ornamentation, resembling scales of *M. acaroides*. However, the species was identified as *M. crassisquama* due to presence of spine-bearing rear scales in most of the samples. This is the most reliable distinctive character, because such scales are not present in *M. acaroides* (Kristiansen 2002). Additionally, the localities where all different types of scales were found had the range of values of pH from 5.8 to 7.2 and of conductivity from 59 to 180 µSm/cm. In contrast, *M. acaroides* is known to prefer rather more eutrophic waters with higher values of pH than were measured in this study. Not formerly recorded from Great Britain.

Previous Irish records: Kristiansen (1998, unpubl. obs).

Mallomonas hamata Asmund   Fig. 19

Only scales, but no bristles, of this species were obtained.

Previous British and Irish records: Kristiansen (1979), Kristiansen (1998, unpubl. obs.

Figs 3–11. – Figs 3, 4: *Chrysosphaerella coronacircumspina*. Fig. 3: Plate scale. Fig. 4: Plate scales and spine. – Figs 5, 6: *C. longispina*. Fig. 5: Plate scales and short spine scales. Fig. 6: Short and long spine scales. – Fig. 7: *Paraphysomonas imperforata,* spine scale. – Fig. 8: *P. vestita*, spine scale. – Fig. 9: *P.* sp., spine scales. – Figs 10, 11: *Spiniferomonas serrata*, plate scales with double and single lacuna.
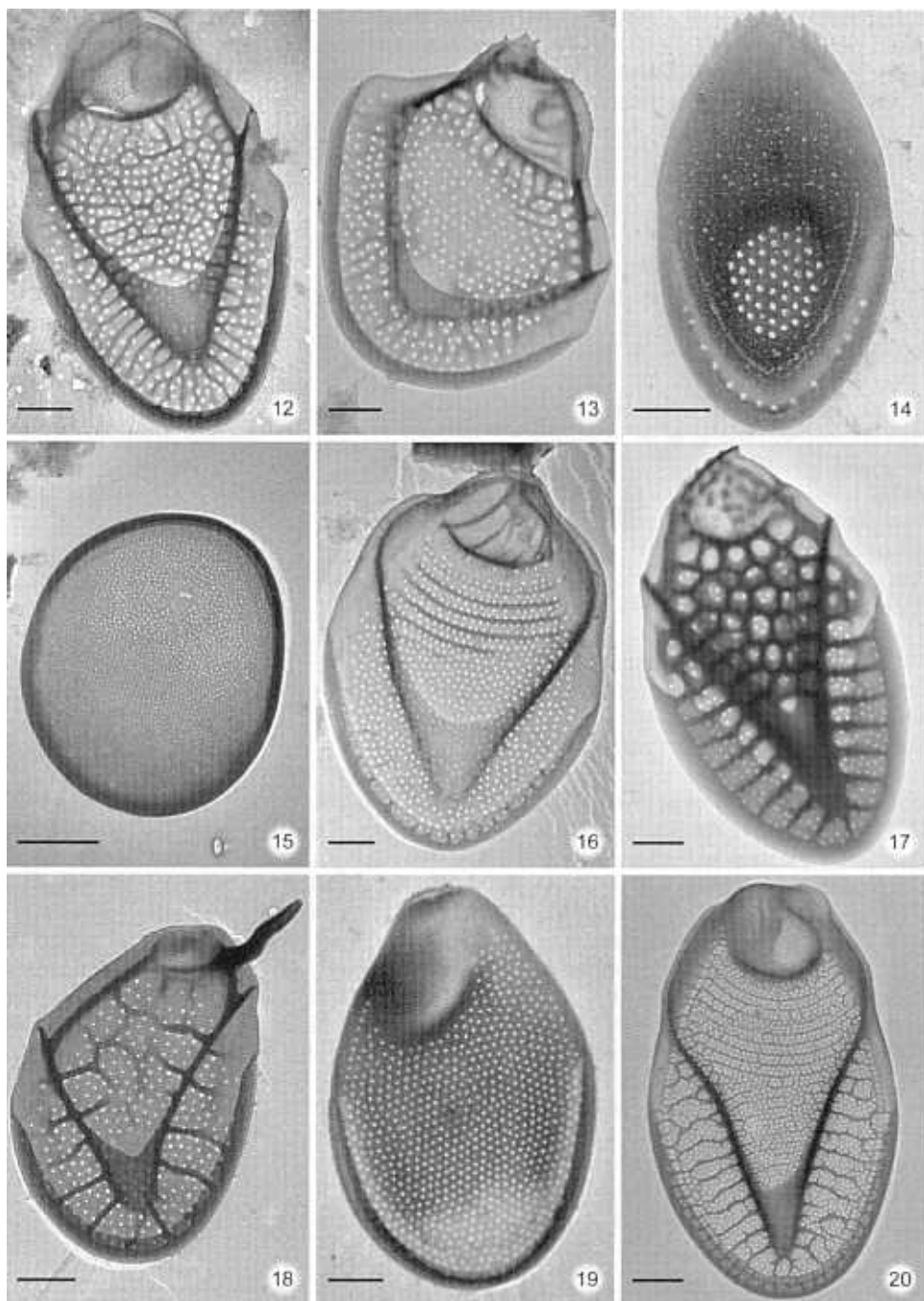
Mallomonas leboimei Bourrelly   Fig. 20
A lot of scales and bristles were found at one locality.
Previous British records: Bradley (1966), Harris (1953), Harris & Bradley (1957), Kristiansen (1979). It is a new record for Ireland.

Mallomonas papillosa Harris & Bradley var. *papillosa*   Fig. 21
Only one single scale was obtained. It has a cosmopolitan distribution.
Previous British and Irish records: Bradley (1966), Belcher (1969), Harris & Bradley (1957), Kristiansen (1998, unpubl. obs.).

Mallomonas pillula Harris f. *valdiviana* Dürrschmidt   Fig. 22
Only one scale of this species was found. It differs from f. *pillula* in that the base plate has conspicuous large pores, and in the marking of the shield and anterior flanges (Kristiansen 2002). *M. pillula* f. *valdiviana* is rather rare, with scattered records from both hemispheres. All other forms of *M. pillula* are distributed in Northern hemisphere only.
There are no findings from Ireland or from Britain.

Mallomonas punctifera Korshikov var. *punctifera*   Figs 23, 24
Several scales were found at one locality. The shield of this species is marked with a reticulum of polygonal or subcircular meshes, each including numerous pores. However, many scales with very strongly reduced reticulum were observed. Similar scales have previous been recorded from one Finnish lake by Hällfors & Hällfors (1988). It is distributed in northern temperate, arctic and subarctic areas.
Previous British records: Canter-Lund & Lund (1995), Harris & Bradley (1957), Lund (1950).
It is a new record from Ireland.

Mallomonas tonsurata Teiling em. Krieger var. *tonsurata*   Figs 25, 26
Many dome-bearing, domeless and also small spine-bearing rear scales were obtained. It is a common species with cosmopolitan distribution.
Previous British and Irish records: Harris & Bradley (1960), Kristiansen (1979), Kristiansen (1998, unpubl. obs.), West & Fritsch (1927).

Mallomonas transsylvanica Péterfi & Momeu   Fig. 27
Several body scales of this species were found. Transverse, regularly and closely spaced ribs ornamented the shield of the scales. It has a bipolar distribution.
Previous Irish records: Kristiansen (1998, unpubl. obs.).
There are no findings from Great Britain.

Synura mammillosa Takahashi   Figs 28, 29
A lot of scales of this species were observed, especially in lake 32 where it co-dominated with *S. sphagnicola*.
Previous Irish records: Kristiansen (1998, unpubl. obs.).
There are no findings from Great Britain.

Figs 12–20. – Figs 12, 13: *Mallomonas* cf. *acaroides*. Fig. 12: Dome-bearing body scale. Fig. 13: Apical scale. – Fig. 14: *M. akrokomos*, body scale. – Fig. 15: *M. caudata*, scale. – Fig. 16: *M. costata*, dome-bearing body scale. – Figs 17, 18: *M. crassisquama* var. *crassisquama*. Fig. 17: Dome-bearing body scale. Fig. 18: Spine-bearing rear scale. – Fig. 19: *M. hamata*, body scale. – Fig. 20: *M. leboimei*, body scale.
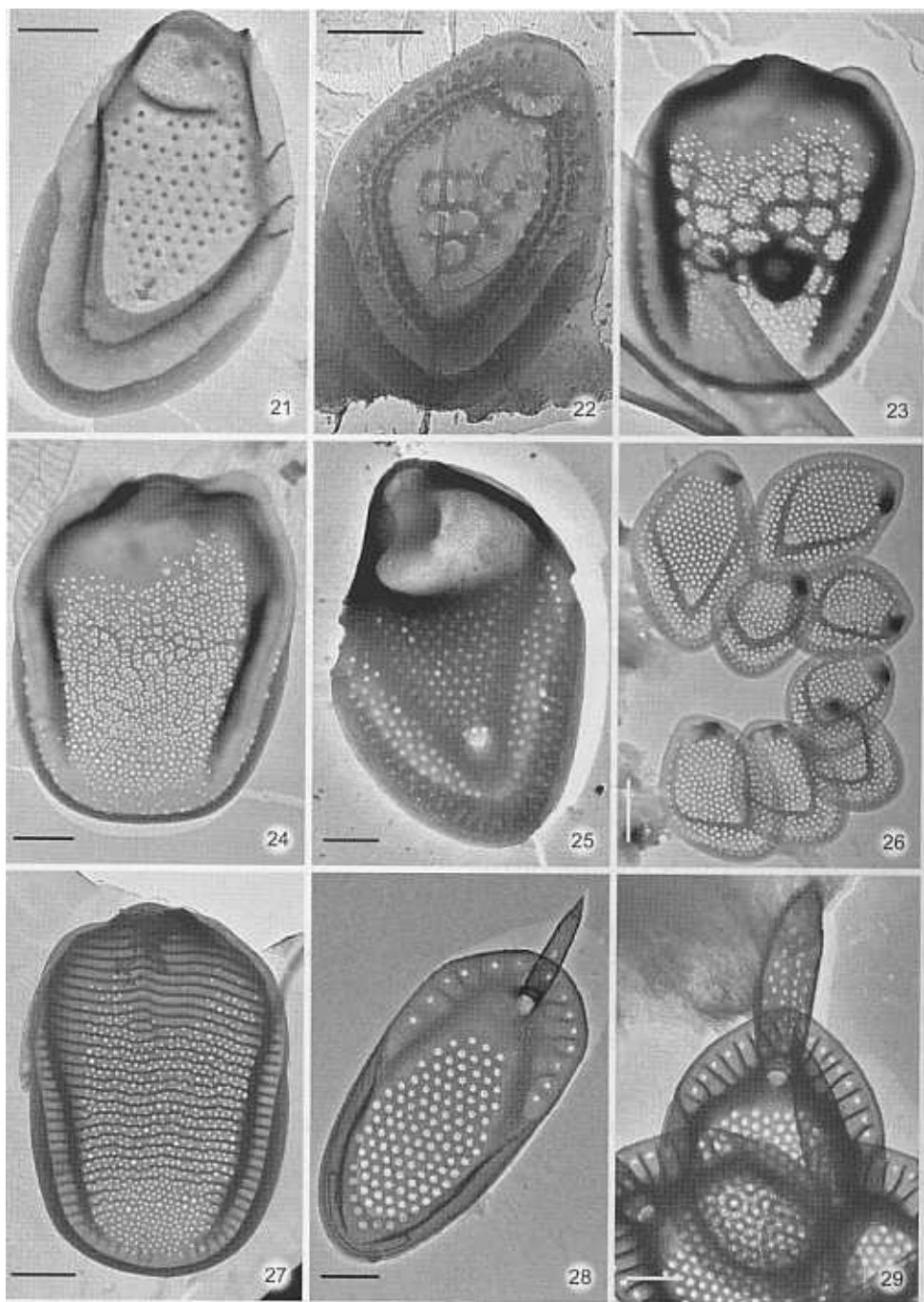
Synura petersenii Korshikov   Figs 31–34
A lot of diverse scales were obtained from two localities. Apical scales had conspicuously long and stout spines. Many body scales were narrow and very long, with numerous side ribs, markedly resembling the scales of *S. australiensis*. Such remarkably long and narrow scales were previous recorded from Alaska by Asmund (for instance photos 6/2 61. and 30/3 63. Alaska 151 – from Asmund's colletion of electron micrographs deposited in Botanical Museum, Copenhagen), and from Greenland by Kristiansen (1992), both as *S. petersenii*. Resemblance between these scales and scales of *S. australiensis* is very striking. To draw a parallel between both these taxa, many scales depicted in earlier publications were measured and the ranges of their dimensions are given in Tab. 2. The table includes dimensions of *S. petersenii* scales, especially longer scales, and scales of *S. australiensis*.

Synura petersenii Korshikov f. *praefracta* Asmund   Fig. 30
Single apical scale with long bifurcate spine was obtained. It occurs in one sample together with *S. petersenii* scales, which resemble scales of *S. australiensis*.

Synura sphagnicola Korshikov   Figs 35, 36
This was abundant in many samples, especially at localities 6 and 32 where there was a bloom of this species.
Previous British and Irish records: Bradley (1966), Kristiansen (1979), Kristiansen (1998, unpubl. obs.).

Synura spinosa Korshikov f. *spinosa*   Fig. 37
Some spine-bearing body scales and also spineless caudal scales were observed. It has a worldwide distribution.
Previous British and Irish records: Bradley (1966), Canter-Lund & Lund (1995) Kristiansen (1979), Kristiansen (1998, unpubl. obs.).

Synura uvella Stein em. Korshikov   Fig. 38
Only several scales were observed.
Previous British records: Bradley (1966), Kristiansen (1979), Reynolds & Irish (2000).
No previous record is from Ireland.

All above-mentioned species, including their abundance as estimated from EM girds (1 – only a single scale, 2 – few scales, 3 – common, 4 – very common, 5 – dominant), are summarized in Tab. 3.

Discussion

The climate of the Ireland is mild and water temperatures of all localities were found in the range from 11.9 to 21.8 °C. The average air temperature on the island is about 15 °C for July and 4–5 °C for January. The number of days annually with frost is about 10 in coastal areas

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Figs 21–29. – Fig. 21: *Mallomonas papillosa* var. *papillosa*, anterior scale. – Fig. 22: *M. pillula* f. *valdiviana*, dome-bearing body scale. – Figs 23, 24: *M. punctifera* var. *punctifera*. Fig. 23: Body scale. Fig. 24: Aberrant body scale. – Figs 25, 26: *M. tonsurata*. Fig. 25: Body scale. Fig. 26: Spine bearing rear scales. – Fig. 27: *M. transsylvanica*, body scale. – Figs 28, 29: *Synura mammillosa*. Fig. 28: caudal scale. Fig. 29: body scale.
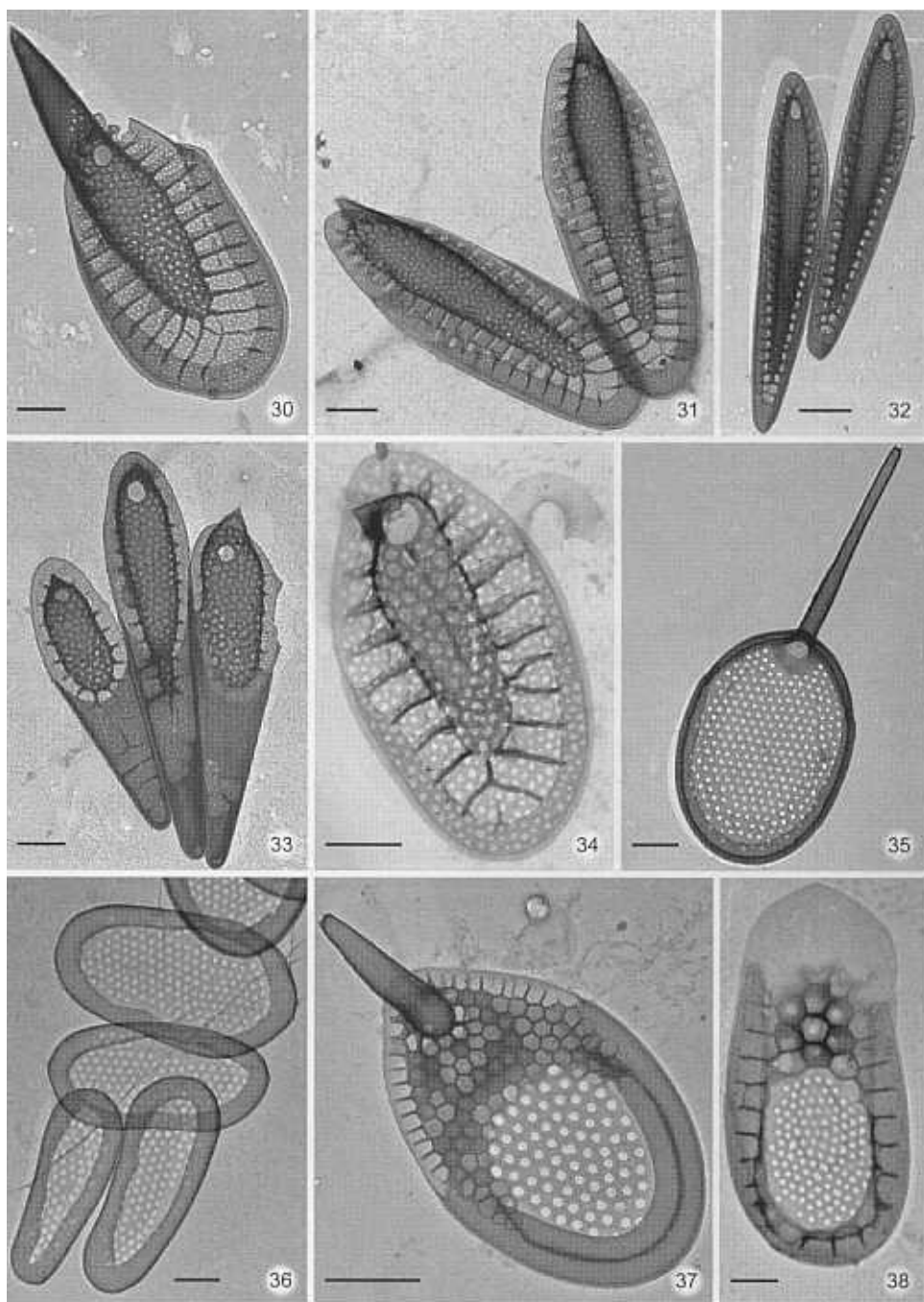
and this mild oceanic climate permits a luxuriant growth of many subtropical plants (e. g. *Fuschsia* and *Araucaria* origin from Chile). However, the composition of the chrysophyte flora on the island seems to be generally similar to those which have been reported from northern arctic and subarctic localities. In this survey, no warm-water taxa were identified from a total number of 24 taxa of silica-scaled chrysophytes. On the contrary, some species, such as *Mallomonas hamata, M. leboimei* and *M. pillula* f. *valdiviana, M. punctifera* var. *punctifera* and *Spiniferomonas serrata* are typical found in cold northern areas (Kristiansen 2002, Siver 1988).

M. leboimei is always associated with acidic localities, primarily with peaty acidic pools (Asmund 1959, Harris 1953, Fott 1962), and it seems that its restricted distribution to Europe and North or Central America may be related to a lower number of peaty bogs in the south hemisphere.

Other *Mallomonas* species have a cosmopolitan distribution (e. g. *Mallomonas akrokomos*) or are distributed very widely (e. g. *M. caudata, M. crassisquama*), and their occurrence in Ireland was not unexpected. Additionally, some scales were found which were difficult to assign to a species. These are discussed below.

M. punctifera var. *punctifera* occurred at one locality. In addition to typical *M. punctifera* scales, many isolated scales with a trace of secondary reticulum were observed. Hällfors & Hällfors (1988) recorded similar *M. punctifera* scales together with both typical *M. punctifera* scales and similarly aberrant *M. transsylvanica* scales from Finland. They hypothesize that there is exchange of genetic material between these species, producing lines of cells with more or less intermediate morphology. They state that presence of *M. transsylvanica* genes in *M. punctifera* is expressed by the secondary meshwork being reduced, frequently to traces only, and the bristles being somewhat irregularly curved (Hällfors & Hällfors 1988). The scales are also very similar to the scales of *M. nieringii* (Siver 2001). However, they possess base plate pores in the proximal region of the scales between the ends of the submarginal ribs, which is typical for scales of *M. punctifera* (Siver 2001).

Unusual scales of *Mallomonas* cf. *acaroides* were observed in samples from two localities. Within *M. acaroides*, 4 varieties are accepted: var. *acaroides*, var. *inermis* Fott, var. *muskokana* Nicholls and var. *obtusa* Ito (Kristiansen 2002). A survey of a specific Greenlandic morphotype, suggested as a form of var. *acaroides*, was carried out by Kristiansen et al. (1995).

All varieties of *M. acaroides* are distinguished (besides other features) on the basis of the type of bristle. Unfortunately, no bristles were found in this material. However, the scales found here differ from var. *acaroides*, var. *inermis* and the specific Greenlandic morphotype by having different ornamentation of the shield and also by the preference for alkalic and rather eutrophic waters. Var. *muskokana* is known to prefer soft humic waters, but in this species most scales have a shield which is smooth or has very weakly developed reticulum (Nicholls 1987). On the other hand, var. *muskokana* has posterior scales without a dome, similar to the appearance of posterior *M.* cf. *acaroides* scales. The ornamentation of the shield of var. *obtusa* resembles that of *M.* cf. *acaroides*, but scales of var. *obtusa* have very broad anterior flanges marked with struts that absent at *M.* cf. *acaroides*.

Finally the *M.* cf. *acaroides* scales seem to be very similar to scales which have been published by Momeu & Péterfi (1983), as *M. stictopteris*. Péterfi & Momeu (1976) have de-

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Figs 30–38. – Figs 30–34: *Synura petersenii*. Fig. 30: Apical scale – stout spine with acute tip. Fig. 31: Body scales. Figs 32, 33: Posterior and caudal scales with different length of upturned posterior rim. Fig. 34: Body scales typical for *S. petersenii* f. *petersenii*. – Figs 35, 36: *S. sphagnicola*. Fig. 35: Body scale. Fig. 36: Spineless caudal scales. – Fig. 37: *S. spinosa*, body scale. – Fig. 38: *S. uvella*, spineless posterior scale.

Table 2. Dimensions of *Synura petersenii* and *S. australiensis* scales.

Author	Taxon	Dimensions in µm (length × width)		
		apical scales	body scales	caudal scales
Petersen & Hansen (1956) – Denmark	*S. petersenii*	3.6–4.7 × 2.2–2.5	3.5–4.6 × 1.25-2.1	1.2 × 0.6
Asmund (Asmund's collection) – Alaska	*S. petersenii*	4.3–4.6 × 1.9–2.1		6.3–7.7 × 0.9–1.1
Takahashi (1966) – Japan	*S. petersenii*	2.3–4.8 × 0.75–2.6		1.9–4.0 × 0.8–1.26
Wee (1982) – Iowa, USA	*S. petersenii* f. *petersenii*	–	2.0–6.5 × 1.0–3.5	–
Kristiansen (1992) – Greenland	*S. petersenii*	3.7–5.2 × 1.8–2.4	4.7–6.3 × 2.3–2.5	4.0–5.9 × 1.3–2.0
own observation (2003) – Ireland	*S. petersenii*	3.1–4.2 × 1.5–1.9	4.3–5.4 × 1.3–1.6	5.2–6.9 × 0.9–1.3
Croome & Tyler (1985) – Australia	*S. australiensis*	–	7.3–8.2 × 1.0–1.8	7.5 × 1.25
Cronberg (1989) – Brazil	*S. australiensis*	–	8.0–11.0 × 2.0–2.5	–
Franceschini & Couté (1991) – Brazil	*S. australiensis*	5.7–13.3 × 1.4–2.0	6.6–8.1 × 1.7–1.9	4.5–13.3 × 1.0–1.3
Kristiansen & Tong (1991) – China	*S. australiensis*	–	6.6 × 1.7	–
Vyverman & Cronberg (1993) – Papua New Guinea	*S. australiensis*	–	7.9 × 2.2	–
Wee et al. (1993) – Louisiana, USA	*S. australiensis*	–	6.9 × 1.9	–
Hansen (1996) – Madagascar	*S. australiensis*	–	8.1–11.5 × 2.0–2.4	5.6–7.3 × 1.0–1.2

scribed this species as *M. acaroides* var. *papillosa* from south-east Transsylvania (Romania). It was found again by Péterfi & Momeu (1977) in small bogs situated in the "Mestecniul de la Reci" (Romania) and reassigned to *M. strictopteris* (correct name). The taxon was found only in small meso-eutrophic bogs or swamp and within a pH range of 4.4 to 6.5 during spring (March–May). Nicholls (1982) reported similar scales which he assigned to *M. acaroides* var. *papillosa* from Ontario (Canada). The shield of these scales has weakly developed reticulation and one curved rib (similar to *M. intermedia*) that is connected to the lower edge of the dome by several short struts. Unfortunately, no information about environmental preference of this species are given.

Different levels of development of reticulation and ornamentation are known within both *M. acaroides* and *M. crassisquama* species (Siver & Skogstadt 1988). The same wide range of different mesh pattern on the shield exists obviously also within *M. strictopteris*, as is seen on scales from different localities. The appearance of *M.* cf. *acaroides* scales differs from scales of *M. strictopteris* (as reassigned by Péterfi & Momeu (1977)) in the absence of papillae on the dome and absence of a dome on posterior scales. However, we consider this taxon closely related to *M. acaroides* and have therefore identified it as *M.* cf. *acaroides*, because we do not agree with its identity as *M. acaroides* var. *papillosa* due to the absence of papillae on the scales.

Table 3. List of species with the estimated abundance.

Taxon/No. of locality	2	3	6	8	10	11	14	18	21	24	25	26	27	28	29	30	32
Chrysophyceae																	
Chrysosphaerella coronacircumspina			1											1	1		
C. longispina													1				
P. imperforata												1	1				
P. vestita													1		1		
P. sp.													1				
Spiniferomonas serrata			1						1					1			
Sp. trioralis		1	1	1										2			
Synurophyceae																	
Mallomonas cf. *acaroides*														1	1		
M. akrokomos		1			1	1											1
M. caudata	5	5	1	5	5	3	1	5	4	4	1	5	4	2	1	3	
M. costata		1											1				
M. crassisquama		1			2	1				2	4	2					
M. hamata	1			2	1												
M. leboimei													2				
M. papillosa													1				
M. pillula f. *valdiviana*														1			
M. punctifera															2		
M. tonsurata	1		1							1		2				1	
M. transsylvanica					1								1				
Synura mammillosa		3											2	2	1		5
S. petersenii						3							4				
S. petersenii f. *praefracta*													1				
S. sphagnicola			5	4	1	1							2	4	3		5
S. spinosa f. *spinosa*		2		2						3		2	2				
S. uvella	1	2		2									1				

Within the genus *Synura* 5 species were found. *Synura sphagnicola*, *S. mammillosa* and *S. spinosa* are common species, whereas *S. uvella* occurred less frequently and not as abundantly as the others. This species is known to prefer more alkaline and eutrophic waters (Hällfors & Hällfors 1988). *S. sphagnicola* was by far the most frequent *Synura* species. It is a typical member of the summer phytoplankton in acidic waters (Cronberg & Kristiansen 1980, Siver 1987). *S. mammillosa* co-occurred very often with *S. sphagnicola*. It has scattered occurrences in various parts of all continents and it is probably able to tolerate wider range of pH (both acidic and alkalic) than *S. sphagnicola*. Very variable scales of *Synura petersenii* were obtained from two localities. Scale with long spine (Fig. 30) is probably *S. petersenii* f. *praefracta* Asmund (1968). A large degree of morphological variability was found mainly in locality 27. Dimensions of the scales are included in Tab. 2. Based on EM, *Synura petersenii* f. *petersenii* was characterised by Petersen & Hansen (1956): Scales elliptical or oval, rear end scales often long and narrow. Each scale is constructed out of a hollow cavity with an api-

cal thorn, radial ribs, an upturned margin on the outer side of a perforated plane, and a pore at the base of the thorn. Playfair (1915) has described *Synura australiensis* from Australia on the base of LM only. LM and EM micrographs of morphologically identical species from other localities in Australia were published by Croome & Tyler (1985). They identified *S. australiensis* as a species closely related to *S. petersenii*, differing from it by having much more elongate scales and a higher number of cells per colony. They further emphasized that *S. australiensis* coexisted with *S. petersenii* in a few localities in Australia without any suggestion of inter-gradation in cell shape or scale morphology. However, the indication of inter-gradation in scale morphology is obvious from micrographs presented in this survey and from several other micrographs, for instance from Alaska (Asmund's collection), from Iowa (Wee 1982), and from Greenland (Kristiansen 1992). The longer and narrow scales occurring in all cases together with the shorter and broader *S. petersenii* scales indicate the ability of some populations to produce scales of very varying length. When comparing dimensions of body scales of both species in Tab. 2 we can see that the longest scales of *S. petersenii* almost reached the length of the shortest scales of *S. australiensis*. There is an approximate boundary between both taxa at the value of 6.5 µm. Lengths of caudal scales of both taxa are strongly overlapping. However, when comparing the average L/W ratio of body scales of both species (Fig. 2), there are two distinctly separated groups.

Only 5 taxa were found within the class Chrysophyceae. Two taxa belong to the genus *Spiniferomonas* and three to the genus *Paraphysomonas*, and all are among the largest members of the whole genus. The evident cause of this lower number is the use of a plankton net with the mesh size 40 µm, which does not allow for catching the smaller organisms. *Spiniferomonas serrata* is rather rare and prefers acidic oligotrophic waters, whereas *Paraphysomonas vestita* and *P. imperforata* are cosmopolitan and tolerate a wide range of environmental conditions. *Paraphysomonas* sp. with scales marked by radial ridges or ribs is considered closely related to *P. vestita*. However, it remains still uncertain, if some populations of *P. vestita* forming typical scales could not simultaneously produce scales with radial ridges or if these scales are produced by another *Paraphysomonas* species. In all surveys, typical scales for *P. vestita* and scales with radial ridges were found mixed together.

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Appendix:
Geographic variation of scale shape of *Mallomonas caudata*

Introduction

Mallomonas caudata is one of the most common and the largest *Mallomonas* species. It is able to tolerate a wide range of environmental conditions and blooms are known both from eutrophic warm waters and cold oligotrophic waters, including occurrence under ice. Due to these factors, *M. caudata* belongs now among the most investigated *Mallomonas* species. It is easy recognisable with LM and therefore was already described by Ivanov in 1899. Since then, many forms and varieties of this species have been described based on the shape of cells and arrangement and shapes of scales. Klotter (1952) demonstrated a whole range of cell shapes as a circle, where he distinguished cells of *M. caudata* and another two forms called f. *ovalis* and f. *abnobensis*. F. *abnobensis* was observed in mesotrophic waters and characterised by cells having bipolar projections, whereas f. *ovalis* was characterised by the elliptical shape of the cell and its occurrence in oligotrophic waters. The scales were observed to be round to oval, although on the drawing of f. *ovalis* they are rather triangular. *M. caudata* Ivanov em. Kriger and *M. fastigata* Zacharias have been synonymized by Asmund & Kristiansen (1986). Two varieties of *M. fastigata*, var. *macrolepis* Conrad and var. *kriegeri* Bourrelly, were described (Starmach 1985). Bourrelly described the variety from France, from ditches with acidic waters and his drawings of the various scales correspond to the shape of scales found in this survey. Under the modern concept of *Mallomonas* taxonomy, none of the above mentioned forms and varieties are accepted (Kristiansen 2002). However, it is obvious that the appearance of cells and their scales among individual populations from separate localities is not the same. It seems that a very suitable, relatively easy and so far in this field unused method called elliptic Fourier analysis, can be applied to obtain new and notable information about the variability of scales.

Elliptic Fourier analysis was originally proposed for delineating any type of shape with a closed two-dimensional contour by Kuhl & Giardina (1982). Now, this method is used for the quantitative evaluation of biological shapes in many disciplines, for instance in genetics, taxonomy and ecology. It has been applied to both animals (e. g. Ferson et al. (1985)) and plants (e. g. Iwata et al. (2002)), but it has only sporadically been applied to the taxonomy and ecology of algae (e. g. Pelce & Sun (1993)).

In this study, we used the program SHAPE, a software package for evaluating contour shapes based on Elliptic Fourier descriptors (EFDs). This package, which has been developed by Iwata & Ukai (2002), provides easy analysis of shapes on a personal computer without special knowledge about the procedures involved in the method.

Material and methods

For the analysis four localities were chosen: 2 and 8 from the area of Connemara, and 26 and 27 from the area of Killarney. Localities 2 and 8 represent smaller oligotrophic lakes with neutral pH. Contrary to lake 2, lake 8 has no inflow or outflow. Localities 26 and 27 were also oligotrophic, but much larger and interconnected by a narrow channel (slightly acidic water from lake 27 flows into lake 26).

Transmission electron micrographs of suitable single scales of *M. caudata* were taken from the whole area of the electron microscopic grid to include the total variability of each population. From each locality a minimum of 60 micrographs of scales was taken for analysis. Thus, altogether over 260 micrographs of scales were obtained with a digital camera. Then, the micrographs were prepared for use in the program SHAPE. This means that they were converted to full colour bitmap format in the program Adobe Photoshop and all were oriented the same way. The elongated upper part of the scale, which is usually recognizable (for some small, symmetric and narrow scales it is less distinct), was oriented top right. Strongly asymmetric triangular scales, which occur very rarely (about 4–6 triangular scales out of circa 70 scales per locality), were not included in the analysis. Afterwards, we used the program SHAPE version 1.2 (Iwata & Ukai 2002), a software package of four programs.

The contour of scales was coded by the first program ChainCoder, which transfer the information of contour to the chain-code file. From chain code information, the second program Chc2Nef (Elliptic Fourier transformation program) calculated the normalised 20 EFDs (descriptors). The normalisation was performed manually (selected normalisation based on the longest radius) by aligning of scale position. As a starting point for rotating all contours of scales, the middle of the rim in the proximal part of the scale was chosen. Then, the third program PrinComp performed a principal component analysis (PCA) of the normalised EFDs derived by Chc2Nef. The contour shape variation accounted for each principal canonical axis was visualized by means of the fourth program PrinPrint.

The first 4 EFDs (descriptors) were further analysed in the statistical program PAST to compare morphology of scales consecutively between each two populations from all 4 localities (thus 6 comparisons altogether). Significance of the difference between each two localities (populations) was tested by means of Discriminant/Hotelling analysis.

Results and discussion

The contour images on Fig. 39 demonstrate the main trends in variability of scale morphology for each principal component axis. For each axis, the minimal, average and maximal values are figured to clearly show main changes in scale morphology. The upper row of contours is
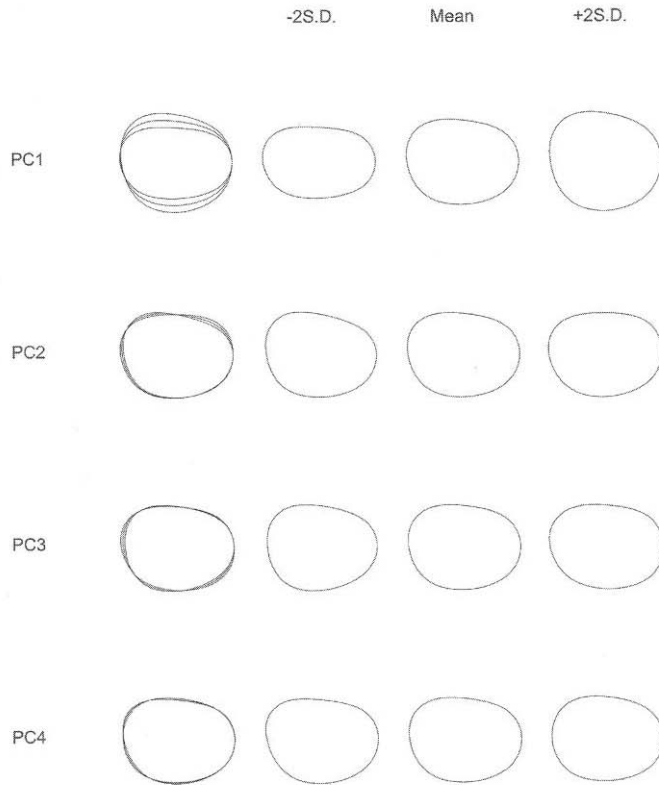
Fig. 39. Scale contours images, showed the variability of scale morphology, counted for first four principal component axes. The scales shape of the minimal (–2S.D.), average and maximal (+2S.D.) values are figured for each axis. The overlapped contours of all three shapes are shown on the left.

explained by first principal component axis, which describes 80 % of the total variability. It characterises the main change of scale morphology, clearly visible as a change of scale breadth. The scales with positive values are broad, whereas those with negative values are narrower and rather smaller. Similarly, the second row of contours describes the shape variability, explained by second ordination axis. This axis explains 9 % of the total variability and expressed the differences in shape of the right distal part of the scales. If the scale has the negative values along the second axis, its distal part is more elongated. The third and fourth axes explain only 5 and 2 % of the variation, respectively. This means that there are further slight differences in shape of both distal and proximal ends of scales.

The principal scores of PCA analysis was used to show the position of each scale in the space of first two ordination axes. As in the principal component contours, the first axis characterises the change of scale breadth and the second ones characterises mainly the changes in shape of right distal part of scales. For better clarity of differences between each two localities, separate graphs were made (Fig. 40). There is a clear difference between scales from localities 2 and 8. The separating of localities was made mainly due to differences along the first ordination axis, representing the breadth of scales. It means that the scales from lake 2 were rather broad, whereas the scales from lake 8 were predominantly narrow. In contrast, the variability of scale morphology from localities 26 and 27 from Killarney region showed similar
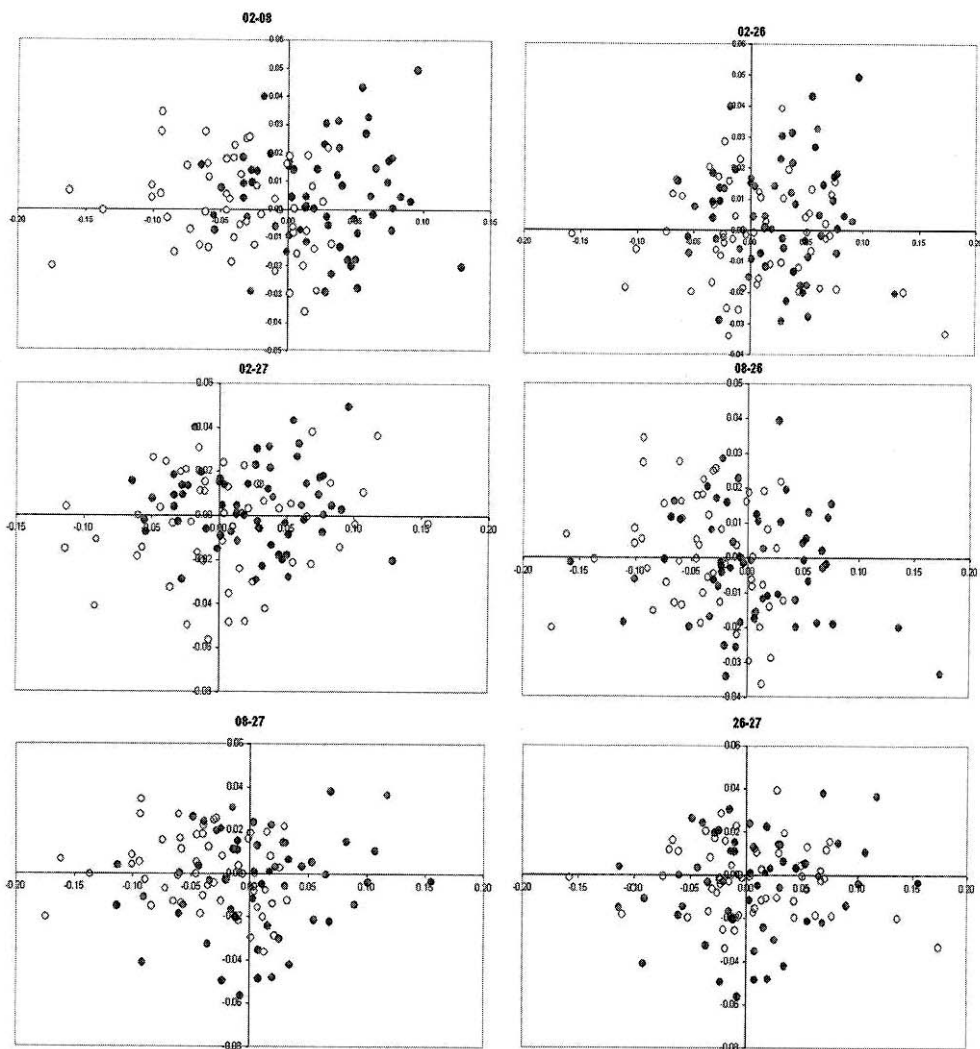
Fig. 40. Position of the scales from each two localities in the space of first two ordination axes.

patterns and separation of these localities is not obvious. Similarities between both localities are not surprising or unexpected because both lakes are interconnected and so allow separate populations to come together.

On Fig. 41 the distribution of scales on the first ordination axis is shown. Furthermore, we can see distinct difference between localities 2 and 8 in the position of the median value. The examples of scales located in extreme positive or negative position in the ordination axes are shown in Fig. 42.

The first 4 EFDs (descriptors) were further analysed to compare scale morphology consecutively between each two populations. Significance of the difference between each two localities (populations) was tested by means of Discriminant/Hotelling test. The results of the analyses are shown in Tab. 4. Again, differences between populations of lakes 26 and 27 were
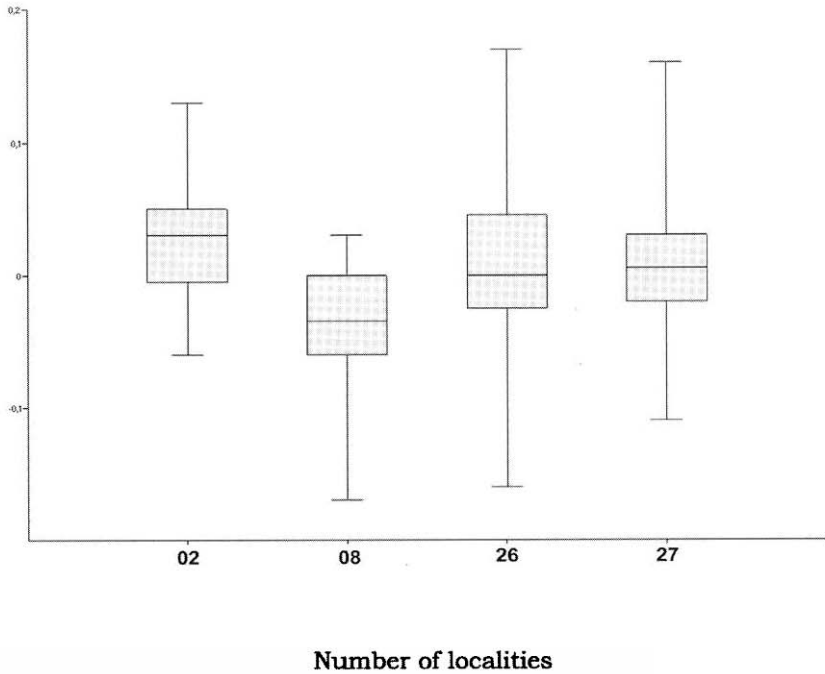
Number of localities

Fig. 41. Box plots of the distribution of scales on the first ordination axis.

not conclusive, whereas the other populations were significantly distinguished. We hypothesise that the differences in breadth of scales could be caused for example by different accessibility of silicate in the lakes or time of the investigation in relation to cell development.
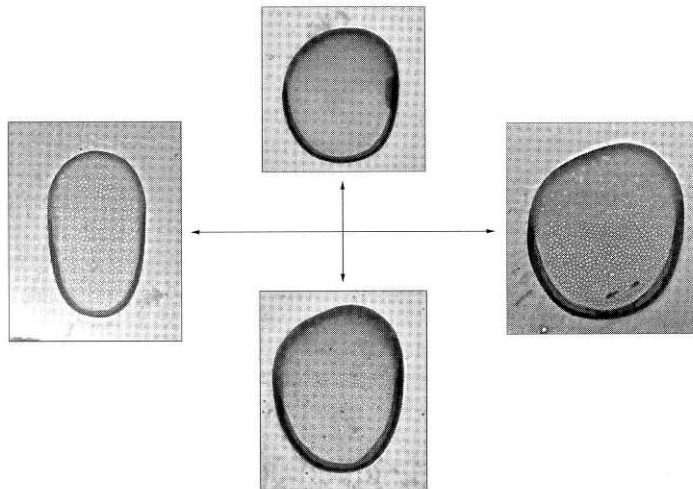

Fig. 42. The examples of the scales, located in the extreme positive and negative positions on the first and second ordination axes.

Table 4. Results of Discriminant/Hotelling test.

Localities tested	p-values
2–8	$8.31 \cdot 10^{-8}$
2–26	0.0038
2–27	0.00035
8–26	$4.59 \cdot 10^{-6}$
8–27	$2.66 \cdot 10^{-8}$
26–27	0.29

However, verification or rejection of different hypothesises requires further long-term investigation, mainly the shape variation of scales within a single cell.

Conclusions

In this regional survey of the chrysophyte flora blooms of the species *Mallomonas caudata* were found at many localities. The species was examined by means of transmission electron microscopy and altogether 260 micrographs of its scales were obtained for analysis, using a digital camera. A wide range of shape variation of the scales was observed. This variation was evaluated with an Elliptic Fourier analysis. As a result of this analysis, the populations of *M. caudata* from two areas (Connemara in western part and Killarney in southwestern part of Ireland) were significantly distinguished. The main factor separating the populations was breadth of their scales.

The method, including four above-mentioned programmes, is used so far rarely in the field of algology. However, it seems to be a very useful new method in morphology and taxonomy of some algae. The advantage of this method lies in accessibility and relative simplicity without any special knowledge about procedures for all users. Further application of this method for evaluation of shapes in algology should be welcome.

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