TAXONOMIC INVESTIGATION OF SELECTED SPECIES OF STAURASTRUM MEYEN AND STAURODESMUS TEILING FROM LAKES OF THE LOWER FRASER VALLEY, BRITISH COLUMBIA

by

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Abstract

An investigation of selected taxa of _Staurastrum_ and _Staurodesmus_ (Desmidiaceae, Desmidiales, Chlorophyta) was undertaken to help clarify their taxonomy. The study was conducted on samples collected in the lower Fraser Valley (British Columbia). Sampling was done over a 2 1/2 year period in four main lakes (Jacobs, Munday, Lost and Como Lakes) with physico-chemical analyses (pH, temperature, irradiation, alkalinity, dissolved oxygen, calcium, nitrate, phosphate) used to characterize the habitats.

Observations of field material revealed nine new records and 56 new distribution records of _Staurastrum_ for British Columbia. One hundred and thirty-six clones comprising 18 taxa of _Staurastrum_ and two taxa of _Staurodesmus_ out of 310 clones of desmids successfully isolated in culture were studied.

Morphological variation of the clonal isolates was studied with the light microscope and the scanning electron microscope (SEM). Cell dimensions and cell radiation were measured in each of the 136 clones studied and the length:width ratio (L/l), standard deviation and coefficient of variation were calculated for each. For the 199 taxa studied, more than 350 publications were consulted. These included original descriptions, records of distribution of taxa studied as well as infraspecific and related taxa. Comparison of variations observed in culture and field material were made with the literature and 33 synonyms were proposed.

Growth and morphological studies in different environmental conditions (medium, irradiation, temperature, pH) were carried out with a triradiate clone of _Staurastrum_ _inflexum_ Brébisson (clone HC 18). Growth rate varied in the different environmental conditions tested but morphological variation was usually not affected. An analysis of variance showed no significant difference between cell size or cell radiation in different conditions, although higher pH (6.20 compared to 4.62) produced more tetraradiate cells. Attempts to induce sexual reproduction in different environmental conditions were unsuccessful. Control clones of _St._ _gladiosum_ Turner and _Cosmarium_ _botrytis_ Meyen ex Ralfs from culture collections did show conjugation in similar conditions.

Table of Contents

Abstract ii
List of Tables vii
List of Figures ix
List of Plates x
Acknowledgement xi
Chapter I
INTRODUCTION 1

A. CLASSIFICATION OF DESMIDS 1

B. REPRODUCTION 12

C. MORPHOLOGICAL VARIATION 17

D. GOALS OF THE PRESENT STUDY 21

Chapter II
STUDY AREAS 22

A. JACOBS LAKE 22

B. MUNDAY LAKE 24

C. LOST LAKE 26

D. COMO LAKE 26

E. OTHER SITES 27

Chapter III
MATERIALS AND METHODS 32

A. FIELD PROCEDURES 32
1. PHYSICO-CHEMICAL FACTORS 32
a. PH 33
b. Temperature 33
c. Light 33
d. Dissolved Oxygen 34
e. Alkalinity 34
f. Calcium 35
g. Nitrate And Phosphate 35
2. ALGAL COLLECTION TECHNIQUES 37
a. Plankton Samples 37
b. Periphyton Samples 37
c. Sediment Samples 38
d. Preservation Of Specimens 38

B. LABORATORY PROCEDURES 38
1. ALGAL CULTURING 38
2. ALGAL ISOLATION 39
3. SEXUALITY EXPERIMENTS 40

4. GROWTH EXPERIMENTS 42
5. ICONOTHEQUE 44
6. MORPHOLOGICAL VARIATION 45

Chapter IV
RESULTS AND DISCUSSION 50

A. PHYSICO-CHEMICAL FACTORS 50

B. DISTRIBUTION OF ALGAL GENERA IN LAKES STUDIED 60
1. JACOBS LAKE 60
2. MUNDAY LAKE 61
3. LOST LAKE 63
4. COMO LAKE 64
5. OTHER SITES 65

C. DISTRIBUTION OF *STAURASTRUM* SPP. AND *STAURODESMUS* SPP. IN LAKES STUDIED 70

D. SEXUALITY EXPERIMENTS 76
1. CLONES ISOLATED 76
2. CLONES FROM CULTURE COLLECTIONS 77

E. GROWTH PATTERN OF *STAURASTRUM INFLEXUM* (CLONE HC 18) IN DIFFERENT ENVIRONMENTAL CONDITIONS 83

F. MORPHOLOGICAL VARIATION OF *STAURASTRUM INFLEXUM* (CLONE HC 18) IN DIFFERENT ENVIRONMENTAL CONDITIONS 89
1. CULTURE MEDIA 89
2. IRRADIATION 92
3. TEMPERATURE 92
4. PH 93

G. SUMMARY OF RESULTS AND DISCUSSION 100

Chapter V
DESCRIPTION AND VARIATION OF SELECTED STAURASTRUM AND STAURODESMUS TAXA 102

A. INTRODUCTION TO TAXONOMIC TREATMENT AND KEY 102

B. *STAURASTRUM BREBISSONII* VAR. *BREBISSONII* 107

C. *STAURASTRUM GLADIOSUM* VAR. *GLADIOSUM* 120

D. *STAURASTRUM ALTERNANS* VAR. *ALTERNANS* 139

E. *STAURASTRUM MURICATUM* VAR. *MURICATUM* 156

F. *STAURASTRUM AVICULA* VAR. *AVICULA* 170

G. *STAURASTRUM PROBOSCIDEUM* FORMA *MINOR* INCLUDING *ST. PROBOSCIDEUM* VAR. *PROBOSCIDEUM* 193

H. STAURASTRUM SEXCOSTATUM VAR. PRODUCTUM INCLUDING ST. SEXCOSTATUM VAR. SEXCOSTATUM 212

I. STAURASTRUM CRENULATUM VAR. CRENULATUM 221

J. STAURASTRUM MANFELDTII VAR. PARVUM INCLUDING ST. MANFELDTII VAR. MANFELDTII 230

K. STAURASTRUM VESTITUM VAR. VESTITUM 244

L. STAURASTRUM INFLEXUM VAR. INFLEXUM 260

M. STAURASTRUM TETRACERUM VAR. TETRACERUM 271

N. STAURASTRUM FURCIGERUM VAR. FURCIGERUM AND STAURASTRUM FURCIGERUM FORMA EUSTEPHANUM 286

O. STAURASTRUM SENARIUM VAR. SENARIUM 301

P. STAURASTRUM ARACHNE VAR. ARACHNE 315

Q. STAURASTRUM OPHIURA VAR. OPHIURA AND ST. PENTACERUM VAR. PENTACERUM 326

R. STAURASTRUM GRALLATORIUM VAR. FORCIPIGERUM INCLUDING ST. GRALLATORIUM VAR. GRALLATORIUM 348

S. STAURODESMUS MUCRONATUS VAR. DELICATULUS INCLUDING STD. MUCRONATUS VAR. MUCRONATUS 353

T. STAURODESMUS DEJECTUS VAR. DEJECTUS 366

Chapter VI
SUMMARY AND CONCLUSION 381

A. SUMMARY 381

B. CONCLUSION 392

LITERATURE CITED 397

APPENDIX A - SAMPLING DATES FOR THE MAIN SITES 409

APPENDIX B - REFERENCES USED IN ICONOTHEQUE 411

APPENDIX C - NUMERICAL LIST OF CLONES STUDIED 435

APPENDIX D - DRAWINGS, INCLUDING PUBLISHED ILLUSTRATIONS OF TAXA STUDIED 438

List of Tables

1. Classification of Zygnematales 10

2. Supplementary collecting sites and physico-chemical data 30

3. Nutrient content of media used for growth experiments 49

4. Irradiation measurements 59

5. Species of Staurastrum (St.) and Staurodesmus (Std.) from lakes of the Lower Fraser Valley 71

6. Clones and environmental conditions used for sexual experiments 79

7. Summary of techniques used for desmid conjugation by different workers 81

8. Average cell dimensions of Staurastrum inflexum (clone Hc 18) in different environmental conditions 95

9. Cell radiation of Staurastrum inflexum (clone Hc 18) in different environmental conditions 97

10. Cell radiation of Staurastrum inflexum (clone HC 18) in different media and in the field 99

11. Cell dimensions and radiation of St. brebissonii ..118

12. Cell dimensions and radiation of St. gladiosum 137

13. Cell dimensions and radiation of St. alternans 154

14. Cell dimensions and radiation of St. muricatum 167

15. Cell dimensions and radiation of St. avicula 189

16. Cell dimensions and radiation of St. proboscideum var. minor 207

17. Cell dimensions and radiation of St. sexcostatum var. productum 219

18. Cell dimensions and radiation of St. crenulatum ...228

19. Cell dimensions and radiation of St. manfeldtii var. parvum 242

20. Cell dimensions and radiation of St. vestitum 258

21. Cell dimensions and radiation of St. inflexum 267

22. Cell dimensions and radiation of St. tetracerum ...283

23. Cell dimensions and radiation of St. furcigerum ...299

24. Cell dimensions and radiation of St. senarium 313

25. Cell dimensions and radiation of St. arachne 324

26. Cell dimensions and radiation of St. ophiura 342

27. Cell dimensions and radiation of St. pentacerum ...343

28. Cell dimensions and radiation of St. grallatorium var. forcipigerum 352

29. Cell dimensions and radiation of Std. mucronatus var. delicatulus 362

30. Cell dimensions and radiation of Std. dejectus 378

List of Figures

1. Illustrations of terms used in text 11

2. Location of sampling sites in the Lower Fraser Valley 29

3. Physico-chemical data for Jacobs Lake 55

4. Physico-chemical data for Munday Lake 56

5. Physico-chemical data for Lost Lake 57

6. Physico-chemical data for Como Lake 58

7. Growth rate of _Staurastrum_ _inflexum_ (clone HC 18) in different media 87

8. Growth rate of _Staurastrum_ _inflexum_ (clone HC 18) in different media and at different irradiations 88

List of Plates

1. *Staurastrum brebissonii* var. *brebissonii*........................119A

2. *Staurastrum gladiosum* var. *gladiosum*...........................138A

3. *Staurastrum alternans* var. *alternans*...........................155A

4. *Staurastrum muricatum* var. *muricatum*...........................169A

5. *Staurastrum avicula* var. *avicula*...............................192A

6. *Staurastrum proboscideum* f. *minor*..............................211A

7. *Staurastrum sexcostatum* var. *productum*.........................220A

8. *Staurastrum crenulatum* var. *crenulatum*.........................229A

9. *Staurastrum manfeldtii* var. *parvum*.............................243A

10. *Staurastrum vestitum* var. *vestitum*............................259A

11. *Staurastrum inflexum* var. *inflexum*............................270A

12. *Staurastrum tetracerum* var. *tetracerum*........................285A

13. *Staurastrum furcigerum* var. *furcigerum* and *Staurastrum furcigerum* forma *eustephanum*.....................................300A

14. *Staurastrum senarium* var. *senarium*............................314A

15. *Staurastrum arachne* var. *arachne*..............................325A

16. *Staurastrum ophiura* var. *ophiura* and *Staurastrum pentacerum* var. *pentacerum*...347A

17. *Staurodesmus mucronatus* var. *delicatulus*......................365A

18. *Staurodesmus dejectus* var. *dejectus* and *Staurodesmus grallatorium* var. *forcipigerum*.....................................380A

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I. INTRODUCTION

A. CLASSIFICATION OF DESMIDS

The Zygnematales (Chlorophyta) form a fairly homogenous order of the Chlorophyceae (Smith 1950, Bold and Wynne 1978) or Conjugatophyceae (Fott 1971, Mix 1975). They have the important characteristic of non-flagellated reproductive cells. The name Conjugales, which is sometimes used instead of Zygnematales, refers to the special mode of reproduction. The Zygnematales are either unicellular or filamentous. They have a wall composed of three layers and possess large chloroplasts and pyrenoids. Many Zygnematales secrete a mucous layer. Some authors find these characteristics to be so important that they designate the Zygnematales as a distinct class, the Conjugatophyceae (Fott 1971; Table 1B), Zygnemaphyceae (Round, 1971) or Zygophycées (Bourrelly 1966, 1972).

The Zygnematales traditionally include three families: the Mesotaeniaceae (saccoderm or false desmids), the Desmidiaceae (placoderm or true desmids) and the Zygnemataceae (Smith 1950, Bourrelly 1966, Bold and Wynne 1978; Table 1A). The Zygnemataceae are characteristically filamentous and the cells do not have any median constriction, pore or ornamentation. They are represented by such ubiquitous genera as Mougeotia, Zygnema and Spirogyra. The Mesotaeniaceae, which are unicellular, are named saccoderm desmids because their wall consists of one piece; that is the cell is not composed of two semicell joined together at the equatorial constriction, or isthmus, as in the Desmidiaceae (Fig. 1). They also lack pores in the cell wall, characteristic of the true or placoderm desmids. They differ from the Zygnemataceae by the absence of true filamentous species. The Desmidiaceae have a wall composed of two parts which forms an equatorial constriction, the isthmus. Pores are present in the cell wall (Fig. 1).

Modern ultrastructural studies reveal details of the true desmid cell that suggest modification in the classification. Different orders or families have been created to include one or two slightly different genera (e.g., the Gonatozygaceae, Table 1B). Mix (1975) proposed a classification summarizing previous findings by other investigators and her own ultrastructural research (Table 1C). This classification rests on details which could not be distinguished before the advent of electron microscopy. Although further investigations may bring more changes to her classification, it is based on solid evidence and is accepted in the present study.

Mix (1975) included the Mesotaeniaceae in the Zygnematales and recognized two sub-orders of Desmidiales, the Archidesmidiineae and the Desmidiineae.

The first sub-order includes the families Gonatozygaceae, Closteriaceae and Peniaceae. The Gonatozygaceae do not have a cell wall made of two parts, but since they possess a pore system and a sculptured wall, they are seen as placoderm desmids. The Closteriaceae and Peniaceae have a wall consisting of two or more parts and show only a slight equatorial constriction or none. Furthermore, they do not shed their primary wall.

The Desmidiaceae, which are the only family of the sub-order Desmidiinae, have a well developed system of pores and a cell wall composed of two parts forming a distinctive equatorial constriction. Members of this family shed their primary wall. The genera Staurastrum and Staurodesmus belong to this family.

The starting point for all desmid nomenclature is Ralfs' British Desmidieae (1848; see International Code of Botanical Nomenclature, ICBN 1978, Article 13.1g).

The genus Staurastrum was created by Meyen (1829) for a tetraradiate specimen (or specimens) of St. paradoxum. Ralfs' (1848, p. 119) description of the genus Staurastrum is,

> "Frond simple, constricted at the middle; end view angular, or circular with a lobato-radiate margin, or, rarely, compressed with a process at each extremity.
>
> "Frond mostly minute, simple, more or less constricted at the middle, and thus forming two segments, which are often somewhat twisted, generally broader than long, and in many species elongated laterally into a process, so that the constriction on each side is a roundish or angular sinus; in other respects the front view shows the segments quite entire.
>
> "The end view varies in form: in most of the species it is triangular or quadrangular, and the angles are either rounded or elongated into rays; in some it is circular with five or more processes forming marginal rays; in a few species it is compressed and the extremities terminate by a process..."

Ralfs' concept was modified by subsequent authors. West and West (1912, p. 119) define Staurastrum as follows:

> "...the genus Staurastrum is primarily distinguished by the radial symmetry of the cells as seen in vertical view. It embraces species of more varied character than any other genus of desmids.

> "All kinds of spine forms occur in the genus, from those in which the whole surface of the cell is covered with spines. All gradations occur from smooth to granulate species, from granulate to asperulate and minutely-spined forms, and from these to coarsely-spined forms.
>
> "...All attempts to split up this genus on natural principles have entirely failed. The relationships of the numerous species are too complex and close, so that only arbitrary lines of demarcation can be drawn..."

The concept of Staurastrum has stayed relatively unchanged since 1912. Fritsch (1930) proposed the creation of the genus Cosmostaurastrum for Cosmarium-like Staurastrum. Palamar-Mordvintseva (1976) divided Staurastrum into four genera, Cylindiastrum, Comoastrum, Raphidiastrum and Staurastrum. But the creation of the genus Staurodesmus by Teiling (1948) is the only scheme that has gained wide recognition.

According to Brook (1959a), the original description and drawing of St. paradoxum Meyen are inadequate and the material of the Jenner Herbarium in the British Museum from which the drawing was supposedly done, is of St. micron W. West. Brook suggests that St. paradoxum be considered as nominum inquirendum.

In 1939, Irénée-Marie noted that the genus Staurastrum "comporte autant d'espèces et autant d'individus que tous les autres genres ensemble, si l'on fait exception du genre Cosmarium pour le nombre des espèces, et du genre Closterium pour la quantité des individus."

Teiling (1948, 1950, 1967) suggested that radiation patterns (Fig. 1D) in desmids are not stable characteristics and cannot be considered as acceptable taxonomic criteria. Cells with angular spines which are morphologically similar are called Arthrodesmus if they are biradiate, but Staurastrum if they are tri- to pluriradiate. Dichotypical cells (Fig.1D), also termed Janus-forms (Teiling 1950), where the two semicells of the same desmid cell bear different patterns of radiation, are given as examples of the close relation between the two genera. On this basis, Teiling proposed a reorganization of the genera Arthrodesmus and Staurastrum. He placed the smooth monospinous taxa (with one spine at each angle), in the new genus Staurodesmus, whatever their pattern of radiation.

Because of the complexity of the genus, Staurastrum is often the last treated genus in floras, and sometimes is not included at all. Krieger published only two parts of his monograph on desmids in "Rabenhorst's Kryptogamen Flora" (Krieger 1937, 1939) and never published on Staurastrum. However, the genus Cosmarium was treated in subsequent publications (Krieger and Gerloff 1962, 1965, 1969). Růžička (1977, 1981) has not yet treated the genera Staurastrum and Staurodesmus in "Die Desmidiaceen Mitteleuropas".

Prescott and co-workers (see Prescott et al. 1972, 1975, 1977, 1981, 1982 and Croasdale et al. 1983) just published the part on Staurastrum in the monograph on North American desmids. They opted not to recognize the genus Staurodesmus until it is proved to be a natural taxon. However, they do not specify what is meant by "natural taxon". In my opinion, the discovery of dichotypical cells where one semicell belongs to Staurastrum and the other to Arthrodesmus, prove that these genera are not natural; yet both genera are accepted by Prescott et al. (1982). The characteristics defining the genus Staurodesmus do not appear to be shared by other genera of desmids; no cells or dichotypical cells of Staurodesmus showing features used to define another genus have been reported. I thus recognize the genus Staurodesmus as valid.

Thus Staurastrum is a neglected member of the desmids. The reason for this situation seems to lie in its complexity. Many of the Staurastrum taxa are poorly described, and subsequent misinterpretation of the original species has led to much confusion. The technical means available to observe microscopic algae were very limited in the nineteenth century and at the beginning of the twentieth century, when most species of Staurastrum were described. Since a wide body of literature exists for the desmids, many taxa may have been named simply because the author ignored the existence of a previous publication of his taxon, under a different name. Other taxa probably represent only non-permanent morphological variations of known entities.

It is difficult to define what is a desmid species. Sexual reproduction in desmids is rare and is unknown in many taxa; this is thus an aspect which cannot be part of a species definition of desmids. Features used to distinguish between species or infraspecific taxa vary between taxa. Fritsch (1953) notes that "there is a widespread lack of balance, many of the newer species differing from one another to a less degree than do the so-called varieties or forms of other species." Many such examples are found in my study: a large number of infraspecific taxa have been described for Staurastrum tetracerum. For example, St. tetracerum var. maximum Messikommer (Pl. K Fig. 13) differs from the type species (Pl. K Fig. 3) by its larger size, more open sinus, and the presence of apical verrucae. On the other hand, St. denticulatum var. denticulatum (Nägeli) Archer differs from St. avicula var. avicula Brébisson ex Ralfs because it has granules only at the angles, whereas the difference between St. lunatum var. lunatum Ralfs and St. avicula var. avicula, is the presence of one spine at each angle in the former and two spines at each angle in the latter. These examples show that what appear to be minor variations can be used to distinguish between two species, whereas more numerous differences can be classified at the varietal level. Furthermore, I found that the features used to differentiate between St. avicula var. avicula, St. lunatum var. lunatum and St. denticulatum var. denticulatum are not stable; literature reports also support these findings. This instability was not observed with St. tetracerum var. tetracerum.

Because of the large number of Staurastrum taxa described, it is difficult to come up with definite criteria which could be used to differentiate the specific and infraspecific levels for all the taxa. To do so, one must have a very good grasp of the features distinguishing the numerous taxa involved, and be able to reevaluate these taxa in the light of the new criteria established. This is a major work which has not yet been attempted. As a basis for the reevaluation of the taxa I studied, I considered that a characteristic which varies in clonal (progeny from a single cell) culture and is thus not genetically determined, does not make a good taxonomic criterion. Such variations are called "modificatio", "morpha", "facies" or "monstrositas" by Grönblad and Růžička (1959). The key included in Chapter V of this thesis highlights the features used to differenciate between the taxa studied. The shape of the semicell, the presence or absence of angular or accessory processes, the direction of the processes, the type and pattern of ornamentation and the size and radiation range, are all characteristics which were used to distinguish between the taxa. These characteristics proved stable enough in clonal culture to be used as taxonomic features.

A few studies have included basic SEM (scanning electron microscope) work to complement observations of the morphology of the cell with the light microscope or TEM (transmission electron microscope) (Couté and Rino 1975, Lorch 1978, Lott et al. 1972, Naef et al. 1978, Capdevielle and Couté 1980, Couté and Tell 1981). Lyon (1969), Pickett-Heaps (1973, 1974, 1975), Gough (1978) and Gough et al. (1976), worked at developing technical methods for processing desmids for SEM observation. Although the SEM is becoming an important tool in the study of desmid taxonomy and morphology, the time and costs involved may prevent or slow down its generalized use in floristic and taxonomic studies.

TEM work with desmids generated new information useful in classification of desmids, and also to the knowledge of their life cycle. For example, Drawert and Mix (1961), Gerrath (1968), Lott *et al.* (1972), Couté and Rino (1975), Mix (1969, 1972, 1975), Mix and Manshard (1977), Chardard (1977) worked on the ultrastructure of the cell wall, pore apparatus or internal structure of desmids. Ueda (1972), Dubois-Tylski (1973a, 1973b), Abadie and Dubois-Tylski (1974), Pickett-Heaps (1975), Noguchi (1978), Vidyavati (1982) investigated ultrastructural details of cell division and different parts of the cell cycle.

TABLE 1

CLASSIFICATION OF ZYGNEMATALES

A. Smith 1950
Bold and Wynne 1978

Class	Order	Sub-order	Family
Chlorophyceae	Zygnematales	---	Zygnemataceae
			Mesotaeniaceae
			Desmidiaceae

B. Fott 1971

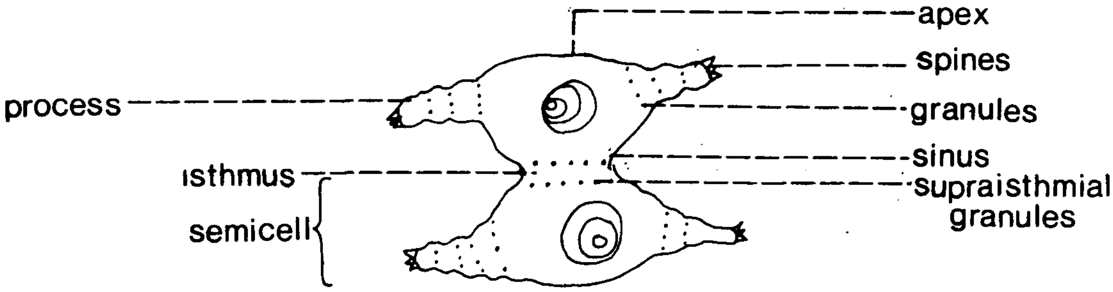
Class	Order	Sub-order	Family
Conjugatophyceae	Mesotaeniales	---	Mesotaeniaceae
	Zygnematales	---	---
	Gonatozygales	---	Gonatozygaceae
	Desmidiales	---	Desmidiaceae

C. Mix 1975

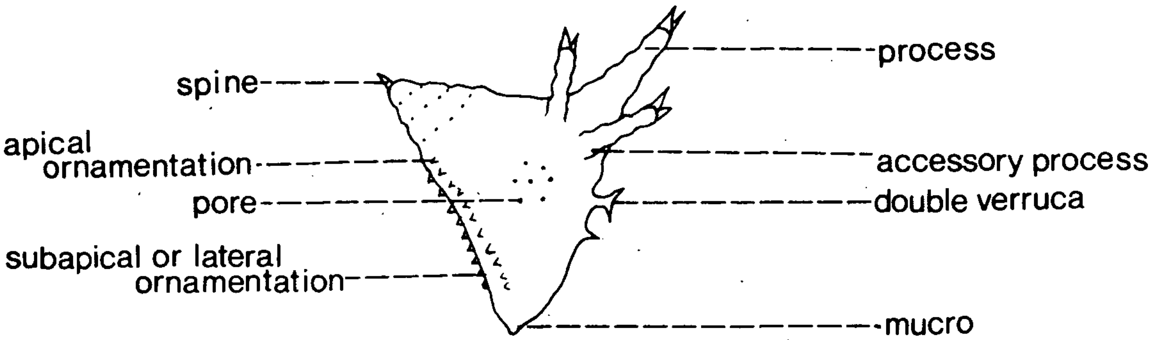
Class	Order	Sub-order	Family
Conjugatophyceae	Zygnematales (saccodermae)	---	Zygnemataceae
			Mesotaeniaceae
	Desmidiales (placodermae)	Archidesmidiineae	Gonatozygaceae
			Peniaceae
			Closteriaceae
		Desmidiineae	Desmidiaceae

Figure 1 - Illustrations of terms used in text

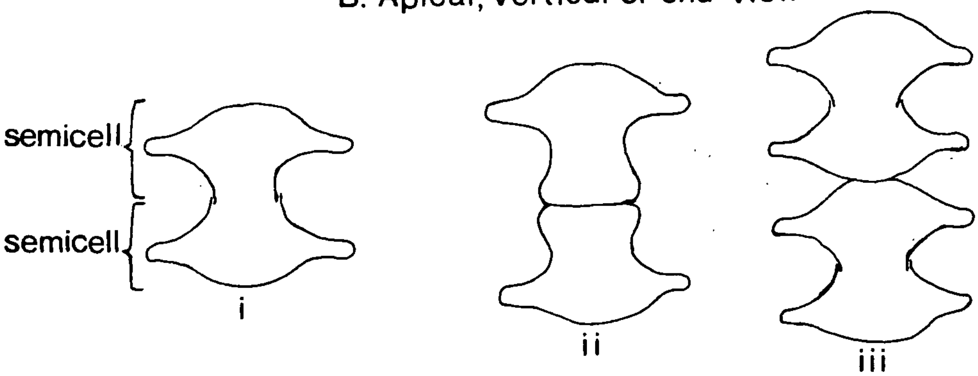
11A



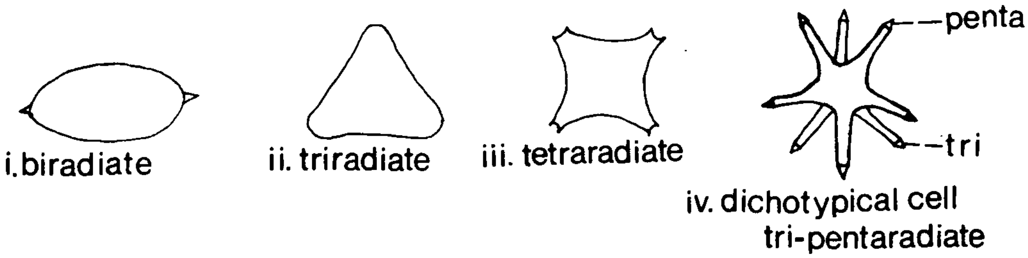
A. Front view



B. Apical, vertical or end view



C. Cell division



D. Radiation (vertical view)

B. REPRODUCTION

The life cycle of desmids is haplobiontic and haploid with a zygotic meiosis (Bold and Wynne 1978, p.13). The vegetative cells are haploid and produce haploid gametes which are amoeboid. Two gametes, each produced by a different cell, fuse to form a diploid zygote which undergoes meiosis to produce haploid vegetative cells and complete the cycle.

Cell division in the placoderm desmids is unique to algae due to the two-part structure of the cell wall and its often highly refined ornamentation. Brook (1981) recognized four types of cell division in the placoderm desmids, the *Hyalotheca*-, *Bambusina*-, *Closterium*- and *Cosmarium*-types. The last type applies to the constricted placoderm desmids and thus to *Staurastrum* and *Staurodesmus*. During the process of division of the *Cosmarium*-type, the isthmial part of the cell where the septum is formed will begin to elongate at different stages during karyokinesis or sometimes after completion of nuclear division (Fig.1Ci). The isthmial area will continue to grow and bulge eventually to form two new semicells which will later develop the normal wall ornamentation characteristic of the species (Fig.1Cii-iii). The secondary wall is deposited internally to the primary wall which will eventually be shed (Mix 1972, see her fig. 22). The secondary wall develops the pore system and the pattern of ornamentation characteristic of each taxon.

If during cell division the septum is incompletely formed, this may result in the formation of aberrant cells with two semicells at different stages of morphological development sandwiched between the two parental semicells.

Formation of asexual spores in the desmids is rare. It often results from failure of gamete fusion during conjugation, but formation of akinetes within a vegetative cell has also been observed. Brandham (1965a) gave a good account of the different types of desmid asexual spores.

Sexual reproduction in nature is rarely reported. For his "Flore desmidiale de la région de Montréal", Irénée-Marie (1939) recorded 527 taxa of desmids, but found only three occurrences of zygospores: that is, for Desmidium swartzii Agardh, Cosmarium moniliforme (Turpin) Ralfs var. punctata Lagerheim and Xanthidium antilopaeum Brébisson var. minneapoliense Wolle. West and West (1912) and West et al. (1923) reported that the zygospores of only 43 of the 169 Staurastrum known to England had been found. Of the 99 species without processes, 29 were found with zygospores, that is about 29%, while 14 zygospores of the 70 species with processes were observed, that is 20%. More elaborate Staurastrum bearing processes are more commonly found in the plankton and less likely to undergo sexual reproduction. Coesel and Texeira (1974) stated that, "It is an established fact that sexual reproduction (by means of conjugation) of the large majority of the desmids occurs only sporadically in nature or has not been observed at all."

Sexual reproduction in unialgal desmid cultures has been achieved by Starr (1955) with Cosmarium botrytis var. subtumidum Wittrock using a CO_2 enrichment method. Subsequent authors succeeded in inducing sexual reproduction with unialgal cultures of placoderm desmids: Cook (1963), Brandham (1967), Brandham and Godward (1964), Kies (1968), Lippert (1967), Pickett-Heaps and Fowke (1971), Ling and Tyler (1972) Watanabe (1979), Dubois-Tylski (1977), Blackburn and Tyler (1980, 1981). Brandham and Godward (1964) used, among others, homothallic clones of St. denticulatum (Nägeli) Archer and St. polymorphum Brébisson ex Ralfs, whereas Winter and Biebel (1967) induced sexuality in an heterothallic clone of St. gladiosum Turner.

Ichimura and Watanabe (1976) and Watanabe and Ichimura (1978a, 1978b) applied a new approach based on sexual isolation, to the species concept in desmids. They worked with the Closterium peracerosum-strigosum-littorale complex. The Charles-Stalker isolation index (Stalker 1942) developed for Drosophila was applied to determine degrees of sexual isolation between individuals or groups of individuals similar in shape and dimensions. When male and female of different species of Drosophila were mixed, the index, which is concerned with fertilized females, is defined as:

$$\frac{\%\ \text{conspecific} - \%\ \text{alien}}{\%\ \text{conspecific} + \%\ \text{alien}}$$

Watanabe and Ichimura (1978a) grouped clones of Closterium of the above named complex, from different locations in Japan on the basis of morphological variation. The isolation index showed no sexual isolation in one group (=0) and negative sexual isolation (-1) in another group. Negative sexual isolation would mean that some clones showed a higher rate of conjugation when mixed with morphologically similar clones from another location than when mixed with morphologically similar clones from the same location. Watanabe and Ichimura (1978b) mentioned a previous occurrence of negative sexual isolation in Drosophila, although the phenomenon has not been clearly explained. Isolation between morphological groups ranged from complete to partial.

Coesel and Texeira (1974) randomly selected 120 strains of 16 desmid genera, including 17 Staurastrum clones, and subjected them to Starr's technique for inducing sexual reproduction in desmids (Starr 1955). Only three clones showed conjugation, none were Staurastrum. Those conjugating were: Closterium moniliferum, C. limneticum Lemmermann var. fallax Růžička and Micrasterias papillifera Brébisson. Coesel and Texeira agreed that Starr's success was due to the fact that, "Attempts have been made to isolate sexual strains only from natural populations of desmids in which there was already some evidence of sexual reproduction" (Starr 1955).

Coesel and Texeira noted that most available sexual clones of desmids belong to the Mesotaeniaceae and to the genus Closterium. Sexuality seems to be a more restricted phenomenon in the more advanced desmid genera. Coesel and Texeira (1974) stated that, "According to Fritsch (1930) there is a general tendency in this group, particularly in the more advanced (i.e. morphologically most differentiated) genera, towards the elimination of sexual reproduction."

In his introduction to the first International Desmid Symposium, Mollenhauer (1975) stated that "in desmids, there is a marked tendency to abandon sexual processes in the course of evolution."

C. MORPHOLOGICAL VARIATION

Much morphological variation has been observed in desmids. As early as 1899, G.S. West published a paper "On variation in the Desmidieae and its bearings on their classification", in which he stresses that:

> "On the examination of a large number of specimens of one species from many widely separated localities, certain examples are sure to be found which exhibit some variation from the typical plant, and without a very careful study of the species it is difficult to determine whether this variation is merely of a transitory or accidental nature, the specimen being the direct offspring of some type-form, or whether it constitutes a true variety produced by a gradual evolution from the original type."

Present-day desmid taxonomists stress the importance of evaluating the variability of a species to avoid describing taxa based on single specimens or non-permanent morphological variation. Grönblad and Růžička (1959) noted that the definition of a desmid taxon is difficult to formulate and is the result of the subjective interpretation of the investigators. Thus they recommended naming non-permanent variabilities with non-taxonomic terms, such as : "modificatio", "morpha", "facies", "monstrositas", rather than describing new varieties and forms. The terms "morpha" and "facies" have been used commonly by such authors as Croasdale, Förster, Peterfi and Thomasson.

Variability in morphology in the field has been noted as early as 1887 with Euastrum and Micrasterias by De Wildeman. Variation in Staurastrum has been observed by different investigators. Reynolds (1940) observed the seasonal variation of radiation (see Fig. 1D) in specimens identified as Staurastrum paradoxum from the Swithland Reservoir close to Leicester in England. Grönblad and Scott (1955) described the variation of populations of St. bibrachiatum Reinsch from two Italian lakes and among material collected by A.M. Scott from Mississipi (U.S.A.), and consequently emended the definition of the species. Lind and Croasdale (1966) described the variability of St. sebaldi Reinsch var. ornatum Nordstedt from the Sasumma Reservoir in Kenya, Africa. Brook and Hine (1966) examined 200 specimens of St. freemanii W. et G.S. West from a pond in New Guinea, and on the basis of their results, proposed a revision of the species and its varieties. Peterfi (1972) worked on the variability of populations of St. monticulosum (Brébisson) Ralfs, St. subavicula (West) W. et G.S. West and St. forficulatum Lundell from Romanian bogs. Following Grönblad and Ruzicka (1959) suggestion, he described non-taxonomic modification often corresponding to taxonomic characteristics defining other species or varieties already known. Gerrath (1983) looked at the morphological variation and radiation of St. pentacerum (Wolle) Smith, its varieties tetracerum (Wolle) Smith and hexacerum Irénée-Marie, and St. sublongipes G.M. Smith. All of these taxa were found to differ only in radiation, and the presence of dichotypical cells with the two semicells of different radiations, prompted him to emend the description of St. pentacerum to include all the above named taxa. Morphological variation of other genera of desmids in the field has also been observed (Ruzicka, 1966; Tyler, 1970; Bicudo and Sormus, 1972; Gerrath, 1979a, b, 1982).

Morphological variation of desmids was observed in cultures grown under different environmental conditions (Rosenberg, 1940, 1944; Kallio, 1953; Lorch, 1978; Watanabe, 1979). Brandham and Godward (1965) showed that with a clone of Staurastrum polymorphum Brébisson, high temperature favored the triradiate specimens. Brandham and Godward (1964) examined the genetics of the occurrence of bi- and triradiate cells in Cosmarium botrytis Meneghini and C. botrytis var. tumidum Wolle and found that the triradiate state was not determined genetically. Their conclusion was strengthened by Tews' (1969) investigation of the inheritance of radiation in a clone of Cosmarium botrytis var. depressum W. et G.S. West. Lehtonen (1977) summarized the morphogenesis studies done on Micrasterias. He suggested that morphogenesis was not determined genetically, but was plasmatically controlled. Cook (1963) studied the vegetative and sexual morphology of 18 clones of Closterium of the C. venus-dianae complex and concluded that morphology of the conjugation tube and zygote was more stable than vegetative morphology.

The need for using clonal material in combination with field material was stressed by different authors. Förster (1967) studied both morphological observations of field and culture material of St. pingue Teiling. He observed that in cultured material, the processes were stouter and shorter. Naef et al. (1978) studied the variation in morphology, mostly in radiation, of Staurastrum clones from Lake Geneva cultured in the laboratory and also directly in the field, with both light and SEM microscopes. They concluded that the lake has three species of triradiate Staurastrum instead of the one species, St. gracile Ralfs previously recorded: St. cingulum (W. et G.S. West) G.M. Smith, St. sebaldi var. ornatum f. planctonicum (Lutkemüller) Teiling and St. messikommeri f. planctica Thomasson. In the same paper, Bourrelly described a new forma, St. sebaldi var. ornatum f. quadribrachiata Bourrelly for a tetraradiate form which comprised only 0.3% of the triradiate cells in culture. Their in vitro cultures have stouter and smaller cells than the cultures in the lake. Mix (1965) examined the morphological variation of Micrasterias swainei Hastings and Staurastrum leptocladum Nordstedt in field material and clonal culture. Her study of the former showed it is synonymous with M. radiosa Agardh var. extensa Prescott et Scott. Her cultures of St. leptocladum formed Cosmarium-like cells which could produce normal St. leptocladum cells by cell division. Mix stressed the importance of studying both field and clonal material.

D. GOALS OF THE PRESENT STUDY

The present study is concerned primarily with documenting and analysing morphological variation with regard to the systematics of Staurastrum and Staurodesmus. The study includes both field material and clonal cultures observed over a period of two and a half years. Comparison of published descriptions and illustrations with the material observed is used to examine the taxonomy of the species. Physico-chemical analyses and identification of dominant algae growing with Staurastrum and Staurodesmus spp. are used to characterize the habitats. Collection sites are in the lower Fraser Valley, British Columbia, to the east of Vancouver. Attempts to induce sexual reproduction are undertaken to provide further genetic and morphological information regarding variability. In addition, an in depth study of the growth rate and morphological variation of one clone is carried out using different media in different environmental conditions.

II. STUDY AREAS

Most sites visited were located in the Lower Fraser Valley of British Columbia (Fig. 2B). The main collecting sites of this study were Jacobs Lake (also known as Marion Lake, see Efford 1967) in Maple Ridge, and Munday, Lost and Como Lakes in Coquitlam (Fig. 2C and D). A mean annual temperature of 9.8°C and mean annual precipitations of approximately 150 cm (Kendrew and Kerr 1955) characterize the area which is part of the Coastal Western Hemlock Zone (Krajina 1969). Stein and Gerrath (1968) and Stein (1975) have studied the algal flora of the area. Stein and Borden (unpublished) have produced a computer print-out showing the fresh-water algae recorded in British Columbia and their collection sites. A preliminary checklist was published (Stein and Borden 1979) without however stating the actual sites of collection of each alga.

A. JACOBS LAKE

Jacobs Lake (also called Marion Lake) is located in the UBC Research Forest in Maple Ridge, British Columbia (49° 18'N, 122° 33' W), about 50 km east of Vancouver (Fig. 2C). It is situated on the southern slope of the Coast Mountains which are composed of granitic bedrock of mesozoic origin, and rests in a valley about 300 m above sea level (Efford 1967). The UBC Research Forest is accessible to the public only by foot; Jacobs Lake is located a few km from the entrance and is thus rarely visited. On 25 January 1980 as well as on 11 January 1981, Jacobs Lake was covered with a thin layer of ice which was easily broken.

The UBC Research Forest has been the site of extensive logging and reforestation. Much of the secondary growth is composed of western hemlock (Tsuga heterophylla (Raf.) Sarg.), western red cedar (Thuja plicata Donn.) (Efford 1967) and some Douglas fir (Pseudotsuga menziensii (Mirbel) Franco (Wali et al. 1972). Klinka (1976) did a synecological study of the vegetation of the UBC Research Forest. Mathewes (1973) studied the postglacial changes in vegetation from sediment cores collected in Jacobs and Surprise Lakes, both located in the UBC Research Forest. The main aquatic vascular plants were Potamogeton natans L., P. epihydrus Raf., Nuphar polysephalum Engelm., Menyanthes trifoliata and Isoetes occidentalis Henders., and the alga Chara globularis Thuill. was also reported around some springs (Efford 1967). In addition, the presence of Utricularia sp. was noted at the sampling station on the west side of the lake (Fig. 2C). Kalmia sp. and Lysichitum americanum Hulten et St. John were common on the shore. Mathewes (1976) studied the sediment of Jacobs and Surprise Lakes, both in the Research Forest.

Jacobs Lake has a drainage area of about 6.5 km^2 and flows into the North Alouette River. It is about 800 m long and 200 m wide at its largest point. At high water, the maximum depth is about 7 m but varies usually around 5.5 and 6 m, and the mean depth is 2.4 m (Efford 1967). At the sampling station, water level varied from 1.17 to 1.89 m. A morphometric map of Jacobs Lake can be found in any of the following publications (Davies 1970, Efford 1967, Dickman and Efford 1972, Wali et al. 1972).

The sampling station at Jacobs Lake was located on the western side of the lake, at the site of the International Biological Program (IBP) facilities. Sampling for the present study was performed from and around the dock. A permanent metre stick provided a record of the variation of the lake level.

Much research has been pursued on Jacobs Lake in the course of the IBP. Davies (1970) worked on the productivity of the macrophytes; Dickman (1968), Gruendling (1971) and Hargrave (1969) looked at the structure and production of the periphyton community; Duthie and Sreenivasa (1970) examined the diatoms in a sediment core from Jacobs Lake; Gerrath (1965) and Stein and Gerrath (1968) investigated the desmid populations in Jacobs Lake and other lakes in the Coast Mountain area; Dickman (1969), Dickman and Efford (1972) and Efford (1967) worked on the production of the phytoplankton; Wali *et al.* (1972) analysed the nutrient composition of the lake.

B. MUNDAY LAKE

Munday Lake is located in the municipality of Coquitlam (49° 16' N, 122° 49' W), some 20 km east of Vancouver (Fig. 2D). It lies about 150 m above sea level and is part of Munday Lake Memorial Park, a municipal park for recreational activities. Despite the fact that signs at the park refer to "Mundy Lake", this spelling is incorrect. The lake empties into one major outflow at its southern end. Munday Lake is surrounded by trails winding through a wooded area. Children from nearby schools use the lake as a ground for fishing or collecting frogs or tadpoles. Swimming is forbidden.

Around the lake, the vegetation was mostly composed of Ericaceae such as *Gaultheria shallon* Pursh., *Ledum groenlandicum* Oeder, *Vaccinium* sp., *Kalmia* sp. Closer to the lake lies a terrain of soft peat deposit which also covers the bottom of the lake. In some places, much care must be exercised as the ground will not support the weight of a person. At different locations along the shore, populations of *Sphagnum* sp. may be found. The main aquatic vascular plants were *Brasenia schreberi* Gmel. at the southern end, some *Nuphar* sp. and several patches of *Potamogeton* sp.

The lake sometimes freezes over for a few weeks during winter time. This happened in 1979-80 when the ice was ca. 2 cm thick, but in 1980-81, ice was observed only close to the shore.

At Munday Lake, water samples and other physico-chemical data were collected from the dock located on the west side of the lake. This permitted sampling in deeper areas and minimized disturbing the fine peat sediment on the bottom of the lake.

Wailes (1930, 1931) published some accounts on algae and other flora and fauna found in and around Munday Lake. Donaldson (1981) and Donaldson and Stein (1984) studied the Mallomonadaceae (Synuraceae) as well as general physico-chemical aspects of the lake.

C. LOST LAKE

Lost Lake is also located in Munday Lake Memorial Park about 0.8 km east of Munday Lake and at the same elevation (Fig. 2D). The southern end of the lake is bordered by a trail and on the west side, a wooded path runs north about half the length of the lake. Lost Lake is not as heavily frequented as Munday Lake. At its southeast end, the lake drains into a man-made outflow.

Lost Lake contains some peat but not as much as Munday Lake; the bottom is largely composed of mud and sand. Patches of *Nuphar* sp. and *Potamogeton* sp. were observed at the southern and northern ends of the lake. The lake froze over during the 1979-80 winter season forming a surface of ice ca. 2 cm thick, but not during 1980-81.

The southern tip of Lost Lake is lined by a tree trunk. Water samples were collected from the trunk or by walking into the lake to a depth of 0.5-0.6 m, ca. 1-2 m from the shore. In doing so, much care was taken not to disturb the sediment.

Very little work has been done on Lost Lake. Gerrath (1965) recorded 38 desmid species from Lost Lake; there were six species of *Staurastrum*.

D. COMO LAKE

Como Lake is located about 2 km west of Munday Lake Memorial Park. It is a recreational lake encircled by one trail and surrounded by grass and houses (Fig. 2D). It is stocked with fish for the exclusive use of senior citizens and children.

A population of ducks has established permanent residence on the lake. A major outflow located at the southern extremity of the lake often dries out at least partly during the summer. Several small inflows are dispersed around the lake. The bottom and shore of the lake are composed of mud and sand.

During the summer months, large mats of Brasenia shreberi and Nymphaea odorata Ait. covered about one third of the lake. On the north side grew a large population of Typha latifolia L. At Como Lake, a dock on the eastern side of the lake provided a sampling site.

Wailes (1929) established a list of algae found in one sample collected at Como Lake. Donaldson (1981) and Donaldson and Stein (1984) made some general physico-chemical observations in the course of their study on Mallomonadaceae (Synuraceae) in Como Lake.

E. OTHER SITES

More than 20 other sites, lakes, ponds or ditches in the Lower Fraser Valley, Okanagan Valley, Vancouver Island and the Gulf Islands (British Columbia) were sampled. All the samples collected were examined for the presence of Staurastrum species. At 17 sites, physical and occasionally chemical data were gathered (Table 2).

Two lakes were visited in the Okanagan Valley (Central British Columbia), Skaha Lake (119° 30' N, 49° 25' W) and Okanagan Lake (119° 25' N, 49° 45' W). The Coquitlam (122° 47' N, 49° 16' W) and the Pitt Rivers (122° 40' N, 49° 15' W) which both flow into the Fraser River were also sampled. Blaney, Placid, Gwendoline, Eunice and Katherine Lakes are all located in the UBC Research Forest (Fig. 2C). As previously mentioned, Gwendoline, Eunice and Katherine Lakes drain into Jacobs Lake and from there into the North Alouette River. Placid Lake also flows into the North Alouette River through Blaney Lake and Blaney Creek. Mike Lake, located in Golden Ears Provincial Park, drains into the South Alouette River (Fig. 2C). The North Alouette River was sampled where it crosses 232 nd street in Maple Ridge. Whonnock Lake, which was studied by Donaldson (1981) and Donaldson and Stein (1984) for its Chrysophyceae is located some 9 km southeast of the UBC Research Forest. Trout Lake is located on the eastern outskirt of the city of Vancouver in a recreational park and Beaver Lake is in Stanley Park. Camosun Bog is found in the southeastern part of the UBC Endowment Lands and J. K. Henry Lake is in the UBC Botanical Garden (Native Garden) on the southern side of the UBC campus.

Figure 2 - Location of sampling sites in the Lower Fraser Valley
A. British Columbia; B. Area of sampling in the lower Fraser Valley; C. Main sampling sites and other lakes occasionally visited in the UBC Research Forest and Golden Ears Provincial Park; D. Lakes in Coquitlam area. Dots in Figures C and D indicate sampling stations. Scale for C and D, 1:50,000 and B, 1:25,000.

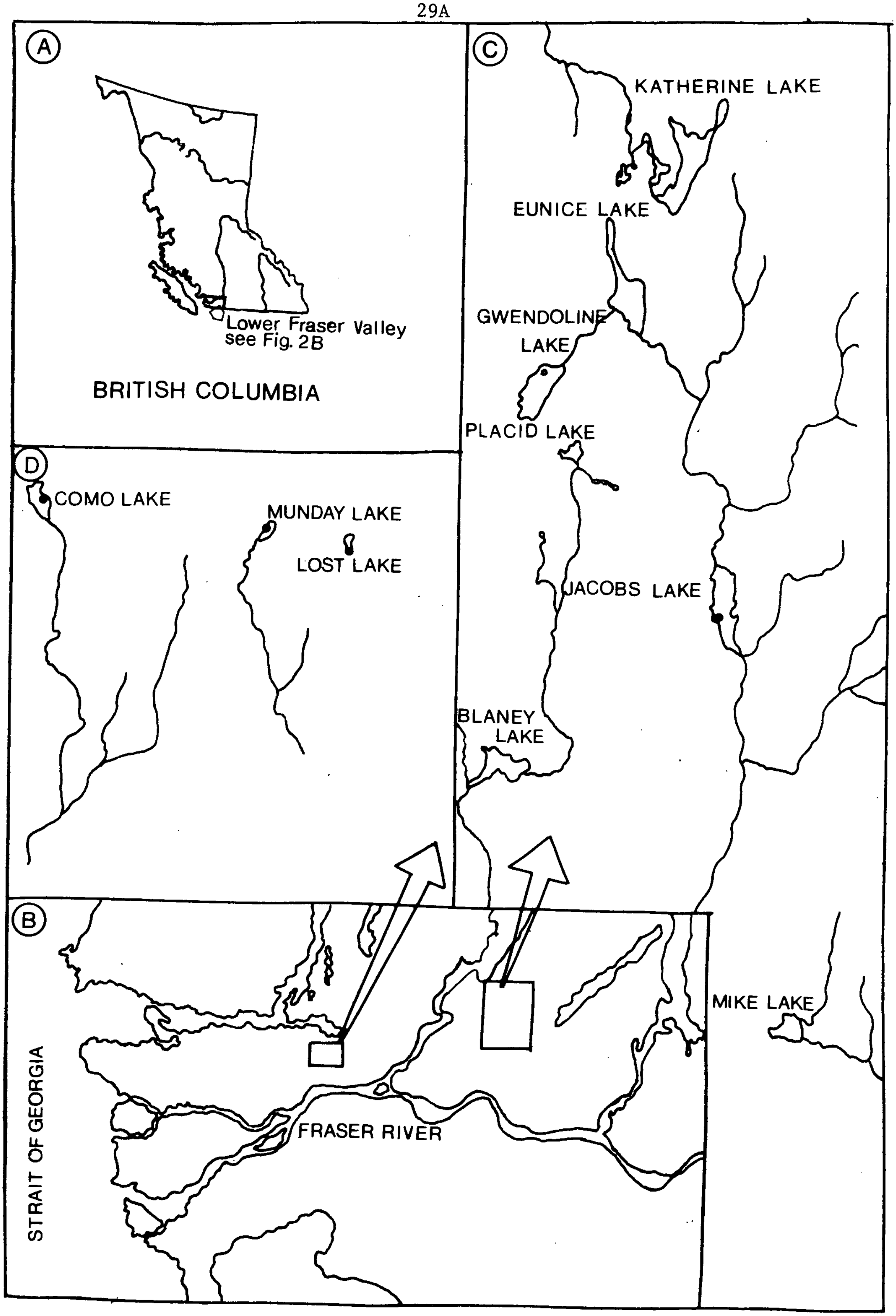

A
Lower Fraser Valley
see Fig. 2B
BRITISH COLUMBIA
C
KATHERINE LAKE
EUNICE LAKE
GWENDOLINE
LAKE
PLACID LAKE
JACOBS LAKE
BLANEY
LAKE
MIKE LAKE
D
COMO LAKE
MUNDAY LAKE
LOST LAKE
B
STRAIT OF GEORGIA
FRASER RIVER

TABLE 2

SUPPLEMENTARY COLLECTING SITES AND PHYSICO-CHEMICAL DATA (D.O.=DISSOLVED OXYGEN)

Site	Date sampled	pH	Temperature °C	Alkalinity $mg.l^{-1}$ $CaCO_3$	Calcium $mg.l^{-1}$	D.O. $mg.l^{-1}$	PO_4^{-3} $mg.l^{-1}$	NO_3^- $mg.l^{-1}$
Beaver Lake	5-IV-80	5.70	19.5	---	---	---	---	---
Blaney Lake	14-VI-79	4.40	18.8	---	---	---	---	---
	10-VIII-79	6.95	22.0	8.6	4.3	5.87	---	---
	16-V-80	6.45	12.5	3.2	2.7	10.87	---	---
	8-VIII-80	5.60	19.5	3.7	3.1	8.69	---	---
	28-VIII-81	6.30	19.0	---	---	---	---	---
Camosun bog	18-IV-81	4.15	12.0	---	---	---	---	---
Coquitlam River	7-VI-79	5.90	10.0	---	---	---	---	---
Eunice Lake	10-VIII-79	6.55	24.0	3.9	2.9	7.22	---	---
Pond beside Eunice	10-VIII-79	6.65	26.5	---	---	---	---	---
Gwendoline Lake	14-VI-79	6.35	17.5	---	---	---	---	---
	10-VIII-79		23.5	2.8	4.1	6.54	---	---
J. K. Henry Lake	18-IV-80	5.85	10.0	---	---	---	---	---
	24-VII-81	4.85	16.0	---	---	---	---	---
Katherine Lake	10-VIII-79	6.50	23.0	3.5	1.7	6.88	---	---
Mike Lake	15-VIII-79	6.20	---	---	---	---	---	---
	22-VIII-79	6.35	23.0	10.4	4.1	6.88	---	---
	12-IX-79	4.90	15.5	7.8	4.1	8.35	.05	undetectable
	30-IX-79	4.65	15.0	9.3	4.4	8.01	.06	undetectable
	28-XII-79	6.00	1.0	---	---	---	---	---
North Alouette R.	1-XI-79	6.95	7.0	---	---	---	---	---
Okanagan Lake	23-VI-79	8.10	18.0	---	---	---	---	---
Pitt River	7-VI-79	7.45	14.5	---	---	---	---	---

TABLE 2 (cont'd)

Site	Date sampled	pH	Temperature ^{o}C	Alkalinity $mg.l^{-1}$ $CaCO_3$	Calcium $mg.l^{-1}$	D.O. $mg.l^{-1}$	PO_4^{-3} $mg.l^{-1}$	NO_3^{-} $mg.l^{-1}$
Placid Lake	14-VI-79	4.40	17.5	---	---	---	---	---
	10-VIII-79	6.50	21.5	5.7	3.5	5.6	---	---
	16-V-80	6.10	12.5	1.4	2.3	10.6	---	---
	8-VIII-80	5.75	19.0	2.7	3.4	9.0	---	---
	28-VIII-81	5.70	19.5	---	---	---	---	---
Skaha Lake	23-VI-79	8.20	23.0	---	---	---	---	---
Trout Lake	1-VIII-79	7.90	22.0	20.1	8.3	5.5	---	---
	29-VIII-79	8.35	24.0	15.1	6.9	6.1	---	---
Whonnock Lake	28-VI-79	6.15	24.0	---	---	---	---	---
	29-VIII-79	6.15	22.0	1.4	2.2	4.7	---	---
	5-IX-79	5.40	18.0	---	---	---	---	---

III. MATERIALS AND METHODS

A. FIELD PROCEDURES

In 1979, from 16 May to 30 September, three main sites were sampled usually once a week: Jacobs Lake in the UBC Research Forest, Munday and Como Lakes in Coquitlam. In 1980 and 1981 the three main lakes, as well as Lost Lake in Coquitlam, were again sampled regularly. They were visited every four weeks from 25 January to 23 March, and every three weeks thereafter. Sampling ended on 28 August 1981. Actual sampling dates for each of the four major sampling sites are given in Appendix A.

1. PHYSICO-CHEMICAL FACTORS

Samples and data for physico-chemical analyses were collected at one station in each lake (Fig. 2C, D). Samples and measurements were taken ca. 3 cm below the surface of the water unless indicated otherwise. All samples for chemical analyses were transported to the laboratory in an ice chest and warmed to room temperature before analysis. Before use, all containers and glassware for chemical determinations were soaked for 24 h in 50% HCl or Decon detergent followed by 24 h in distilled water and two thorough distilled water rinses. These dishes were used exclusively for chemical analyses and after each analysis, they were soaked again for 24 h in dilute Decon followed by a 24 h rinse in distilled water. All analytical chemical solutions were kept for a maximum of one year.

a. PH

A Markson model 85 field pH meter with precision to the second decimal was used. Calibration was accomplished with a commercial buffer solution at pH 4.00 and 7.00. On the few occasions when the field pH meter was out of order, pH was recorded immediately upon return to the laboratory with a Corning pH meter (model 125).

b. Temperature

A mercury thermometer graduated to the nearest degree C was held ca. 3 cm below the surface for a few minutes before taking a temperature reading. The time of recording for a given lake was fairly constant, however the different lakes were not visited at the same time of the day and this may have influenced surface temperature. Sampling time varied from early morning for Jacobs Lake, to late morning for Munday and Lost Lakes and early afternoon for Como Lake.

c. Light

Light readings were recorded occasionally with an underwater quantum sensor (model LI-185A and Li-192S, Licor Ltd.) in the air, ca. 1-2 m above the water and in the water, ca. 1 cm below the surface, at 0.5 m and at the bottom when depth permitted. A conversion factor of 1.34 was used to calculate the underwater readings as suggested by the manufacturer.

d. Dissolved Oxygen

Samples for dissolved oxygen were collected in B.O.D. bottles lowered vertically, and capped under water after all air bubbles had escaped. They were partially fixed in the field with manganese sulfate and alkali-iodide solutions. Upon return to the laboratory, sulphuric acid was added to the samples and they were either immediately analysed or stored at 5°C for a maximum of 24 h from collection time before analysis. The Winkler procedure for dissolved oxygen with azide modification was used (APHA 1975). Only one sample was analysed for each lake and sampling date.

e. Alkalinity

Alkalinity samples were collected in Pyrex or polyethylene bottles and 200 ml of each sample was analysed, when possible upon return to the laboratory, or stored at 5°C and titrated within 24 h according to the potentiometric method (APHA 1975). A Corning pH meter (model 125), with precision to the second decimal was used. Only one sample was analysed for each lake and sampling date. Because of the low alkalinity of Jacobs, Munday and Lost Lakes, end points of pH 4.50 and 4.20 were used (APHA 1975). The end point used for Como Lake was 4.80 since the alkalinity was above 10 $mg.l^{-1}$ $CaCO_3$.

f. <u>Calcium</u>

Samples for calcium were collected in polyethylene bottles and analysed by the EDTA titrimetric method (APHA 1975) with Calcon as indicator. Two determinations were taken and an average was calculated. Periodic standardization of the EDTA titrant was conducted (APHA 1975).

g. <u>Nitrate And Phosphate</u>

For nitrate and phosphate analyses, ca. 250 ml of lake water were filtered on Whatman GF/C qualitative glass fiber filters previously washed in distilled water. The filtration was done directly in the field using mouth suction or immediately upon return to the laboratory with a mechanical pump at a maximum pressure of 7 $kg.cm^{-2}$ and the samples were frozen at -10°C. During the 1979 sampling season, the samples were frozen in borosilicate Erlenmeyer flasks to avoid possible loss of nutrients, mostly phosphate, to polyethylene bottles. This practice was discontinued in the fall of 1979, because the flasks tended to break if transferred directly from -10°C to room temperature.

The samples collected in 1979 were analysed for nitrate with a Technicon AutoAnalyser. The nitrate method was that of Armstrong <u>et al.</u> (1967). It was automated for the Technicon AutoAnalyser by the method of Hager <u>et al.</u> (1968). Subsequent samples were analysed manually with a cadmium reduction column (Strickland and Parsons 1972, Stainton <u>et al.</u> 1977). A few nitrite determinations were performed following Stainton <u>et al.</u>

(1977). Phosphate was analysed by the ascorbic acid method (Stainton <u>et al</u> 1977, APHA 1975). The samples were not processed further after filtration, and the phosphate fraction analysed represents theoretically the dissolved orthophosphate present in the samples. Only one determination was usually made for nitrate and phosphate respectively, for each sampling site and date. Spectrophotometric readings were taken on an Unicam SP1800 spectrophotometer. For NO_3^-, a wavelength of 543 nm and 1 or 4 cm cells were used, depending on the concentration. The light path length recommended was 1 cm for a NO_3^- concentration of 2-20 $\mu g.l^{-1}$ and 5 cm for a concentration of 2-6 $\mu g.l^{-1}$. The nitrate precision level was 120 $\mu g.l^{-1}$ (Stainton <u>et al.</u> 1977). A wavelength of 850 nm and 4 cm cells were used for phosphate determinations. The limit of detection was 10 $\mu g.l^{-1}$ for a 5 cm spectrophotometric cell at 880 nm (APHA 1975). A curve of absorbency vs. standard concentration was established with a series of standards and further determinations always included at least one standard. Distilled water was used as a blank and absorbency values of untreated samples and of distilled water with reagents were substracted from the processed sample readings.

Phosphate is easily adsorbed by the walls of storage or analytical containers or glassware (Murphy and Riley 1956, Thayer 1970) and for this reason all dishes used for phosphate analysis were thoroughly washed in a phosphate-free detergent and kept exclusively for phosphate determination.

2. ALGAL COLLECTION TECHNIQUES

a. Plankton Samples

Plankton tows at each lake were done from the shore as described for each lake. A 64 μm mesh net was drawn ca. 10 cm underneath the surface of the water. This procedure was repeated ca. five times until about 125 ml of sample were collected in a small polyethylene bottle. The samples were carried in an ice chest to the laboratory where 15-20 ml were preserved with a solution of Lugol's iodine containing acetic acid and formaldehyde. The remaining portions of the samples were kept in glass jars under cool-white fluorescent lighting at 5 or 10°C for 1-30 days, awaiting further observation or for possible formation or germination of zygospores. Soil, peat and water (SPW) medium was sometimes added.

b. Periphyton Samples

Leaves and stems of aquatic vascular plants such as *Brasenia*, *Nuphar*, *Nymphaea*, *Potamogeton* or *Utricularia* were scraped with a clean knife or spatula. *Sphagnum* or other mosses and filamentous algae were squeezed to extract the water and algae present. The samples were stored or preserved similarly to the plankton samples.

c. Sediment Samples

Two types of sediment samples were collected in an attempt to obtain zygospores. A 1 cm diameter plastic tube was used to suck up the surface sediment and overlying water which were then transferred to a small glass vial, observed and preserved. Samples of sediment from moist or dry areas around the lakes were scooped up with a spatula and left to dry at room temperature in paper bags.

d. Preservation Of Specimens

Vials containing preserved material from field collections and dried sediment samples in paper bags are kept in the Department of Botany, University of British Columbia.

B. LABORATORY PROCEDURES

1. ALGAL CULTURING

The routine medium (SPW of Gerrath 1968) was made from ca. 25 ml of a soil obtained from the UBC Botany Department greenhouse facilities, 25 ml of dried and pulverized *Sphagnum* (collected at Jacobs and Munday Lakes) and 1 l distilled water. This mixture was autoclaved for 45 min, decanted, filtered onto 5.5 cm qualitative glass fiber filters, poured in 100 x 20 mm test tubes and reautoclaved for 15 min.

Soil-water medium (SW) was used for a few experiments and was prepared according to Nichols (1973) by steaming a mixture of 50 ml of greenhouse soil and 1 l of distilled water for three periods of 60 min. Waris medium was prepared according to Starr

(1978).

When used as a medium, lake water was first filtered on 5.5 cm GF/C glass fiber filters followed by a period of 45 min of autoclaving or three 60 min periods of steaming.

Table 3 gives the nitrate, phosphate and calcium content and the pH of the four media used. For all media except Waris, analyses were the same as for the field samples. For Waris medium, the amount of calcium, phosphate and nitrate were computed from molecular weights and the quantities given in the recipe (Starr 1978).

2. ALGAL ISOLATION

Upon return to the laboratory, 20 ml of each algal sample were transferred to the bottom of a petri dish (15 x 100 mm) and examined with a dissecting microscope at a magnification of 24-100 times. Individual cells were isolated using a capillary pipet as described in Hoshaw and Rosowski (1973). This magnification was too low to recognize the species isolated and only very striking characteristics, such as the long and slender appendages of St. pentacerum (Wolle) G.M. Smith, could be distinguished. More subtle differences were very difficult to assess and wall ornamentation completely impossible. The cells were washed by transferring them four or five times (Pringsheim 1946) in a few drops of sterile soil, peat and water medium (SPW) and placed in a well slide with 1 cm depressions resting in a petri dish. The dishes were then set up in a 20°C chamber on a 14:10 or 16:8 L:D cycle. The irradiation was about 45 $\mu E.m^{-2}.s^{-1}$ provided by two cool-white fluorescent tubes at a distance of 14 cm from the shelf. Sterile SPW was added to the depressions as necessary. After ca. two weeks, the spot plates were examined using a dissecting microscope and the cells which had divided, were picked up with a capillary pipet and transferred to a 100 x 20 mm test tube of sterile SPW. Each clone was assigned a number (HC #x; see Appendix C). A clone by definition, is a culture obtained by the division of a single cell.

Culture tubes were routinely kept suspended on metal bars in a 20°C culture chamber at an irradiation of 27 to 43 $\mu E.m^{-2}.s^{-1}$ and a 16:8 L:D cycle. Growth experiments I conducted showed these conditions to be optimal for St. inflexum Brébisson (clone HC 18). Every four to six weeks, an inoculum of each culture was tranferred to a culture tube containing fresh sterile SPW medium.

3. SEXUALITY EXPERIMENTS

Sexual reproduction was attempted on two heterothallic clones of Staurastrum gladiosum Turner from the University of Texas at Austin, culture collection (UTEX, LB1568, LB1569) and one homothallic clone of Cosmarium botrytis Meneghini from Carolina Biological Supply Co. (#2140; Burlington, North Carolina). Eighty-four clonal isolates of Staurastrum were subsequently tested in environmental conditions similar to the one used with the two sets of controls (see Table 6 in Results and Discussion). One clone of Closterium littorale Gay (HC 243) was also used. The clones were tested for homothally or heterothally. Homothally arises when cells of the same clone conjugate with each other; heterothally means that cells of one clone do not conjugate with each other but conjugate with the cells of another clone. Starr's CO_2 enrichment method, which is considered standard, was used (Starr 1955). The bottom of a deep petri dish was covered with a 5% solution of $NaHCO_3$. A watch glass was set in the petri dish, on a glass triangle which was itself resting on the bottom of a deep petri dish. This was covered with the top of the petri dish. One to two mm^3 of the strain(s) to be tested were pipetted into each watch glass. The petri dishes were covered and incubated. Variations based on successful techniques used by other workers (Table 7 in Results and Discussion) were tried. Irradiation was between 20 and 77 $\mu E.m^{-2}.s^{-1}$ provided by cool-white or gro-lux fluorescent tubes. The photoperiod was either 14:10, 16:8 or 18:6 L:D and the temperature was 16 to 25°C. Como Lake water, SPW and SW media, and Waris medium with different concentrations of nitrate were tested. The age of the cultures varied from a few days to over two months. Old cultures were sometimes diluted with fresh medium at the start of the experiment.

Samples of mud collected along the shore of the lakes and ponds containing populations of <u>Staurastrum</u> or <u>Staurodesmus</u> were dried at room temperature for at least one month. They were then wet with either sterile distilled water or SPW medium and observed every week for four to eight weeks, in an attempt to obtain zygote germination and thus isolate sexual clones.

4. GROWTH EXPERIMENTS

Experiments on the rate of growth were performed with St. inflexum (clone HC 18). Time limitation precluded using more than one clone for these experiments. Clone HC 18 was chosen because it grew well in clonal culture and the species was common in Como Lake. Culturing was carried out in 500 ml Erlenmeyer flasks. When sampled, every 1-3 days, each culture was thoroughly shaken. Factor k (divisions/day) was calculated for the exponential growth period (Guillard 1973).

One experiment tested different media: Waris, filtered Como Lake water collected on 7 June 1980, SW, SPW, enriched SPW to which vitamin B_{12} ($0.45\ \mu g.l^{-1}$) and 1 ml of a trace metal solution were added. The initial cell concentration was 513 $cells.ml^{-1}$. The irradiation was $40\ \mu E.m^{-2}.s^{-1}$ on a 14:10 L:D cycle at 16°C.

A second experiment tested the growth rate in SPW at four irradiations: 12.5, 25, 42 and 90 $\mu E.m^{-2}.s^{-1}$. The temperature was 20°C and the photoperiod 14:10 L:D cycle with an initial cell concentration of 3.7×10^3 $cells.ml^{-1}$.

The growth rate was determined from cell counts using a Sedgewick-Rafter cell. Three chi-square analyses were performed to test for randomness distribution of the Staurastrum cells throughout the Sedgewick-Rafter cell (Lund et al. 1958). Two of those accepted the randomness hypothesis (P=0.05) and one rejected it. At least 400 cells were counted in triplicate Sedgewick-Rafter cells. This minimum was determined in accordance with Woelkerling et al. (1974) and Lund et al.

(1958) to get an accuracy of ± 10%.

A third experiment used SPW medium and filtered water from Como Lake (collected 1 February 1981) with an initial concentration of 35 x 10^3 cells.ml^{-1}, to test if the larger inoculum would reduce the long lag phase previously observed in SPW but not in filtered Como Lake water. The growth rate was followed by spectrophotometric readings at 565 nm (Trainor and Schubert 1973) every two days, and cell counts ca. every 10 days. The temperature was 20° C, the irradiation 40 $\mu E.m^{-2}.s^{-1}$ and the L:D cycle 14:10.

Como Lake water, collected on 17 May 1981, was enriched with a modified Waris medium to give the nitrate, phosphate and calcium outlined in Table 3 for enriched Como Lake water (ECW). Three 500 ml Erlenmeyer flasks were set up at a temperature of 20°C, a L:D cycle of 14:10 with an irradiation of 45 $\mu E.m^{-2}.s^{-1}$. The stock culture was one month old and the initial cell concentration was 8 x 10^3 cells.ml^{-1}. After 24 days, when the cultures reached a plateau, aliquots were taken and diluted to the initial cell concentration, in Erlenmeyer flasks of enriched Como Lake water from which the phosphate portion of the enrichment solution was omitted and others from which the nitrate portion was missing. Triplicate samples were set up for each treatment. The resulting nutrient shock may have been useful for the study of sexual reproduction.

5. ICONOTHEQUE

Nordstedt (1896, 1908) has been used extensively to locate the names and original references of varieties, forms and species which were isolated in culture. For taxa published since then, however, a personal bibliographical search was necessary.

An Iconotheque containing original descriptions and illustrations as well as subsequent published figures of *Staurastrum* taxa has been compiled. Some 350 publications are included in the album, a list of which is given in Appendix B. Original publications of taxa which were only cited in other papers listed in the Iconotheque are not included. It must be noted however, that especially for long publications obtained through the interlibrary loan service of the Woodward library (UBC), often only part of the publication was ordered. This means that the Iconotheque does not include all published records of *Staurastrum* and *Staurodesmus* published in the references of Appendix B. The Iconotheque includes some 800 species, varieties and forms.

Preserved field material from samples was identified using mainly West and West (1912), West *et al.* (1923) and Irénée-Marie (1939), but also if necessary, the Iconotheque compiled.

6. MORPHOLOGICAL VARIATION

Morphological variation was studied by several techniques. A Leitz compound microscope with camera lucida attachment, an interference contrast Leitz microscope with photographic attachment, and Cambridge 2A and 250T SEM were used.

For SEM observations, cells were processed through critical point drying (CPD) following the method of Pickett-Heaps (1973) with minor modifications. The cells were first loaded on a prefolded polycarbonate Nucleopore filter held in a Millipore plastic filter holder using a 5 cc syringe. The filter was then removed from the holder, refolded and placed for 1.5 h at room temperature in a vial containing a 2% solution of β-glucuronidase (Pickett-Heaps 1973) made up with the growth medium; it was then rinsed in culture medium for 1.5 h and was fixed in 1% OsO_4 solution for 1 h followed by dehydration in a series of ethanol solutions of increasing concentration and in amyl acetate, placed in a small stainless steel basket and processed through CPD in a CO_2 bomb. In early preparations, each stub was coated with colloidal graphite and the cells were picked up directly by pressing the stub very gently on the opened filter pouch. However long processes or spines were often damaged or bent. The technique was thus modified as follows: the processed filter was fixed to a stub with a silver conducting paint, trimmed, and the stubs were heavily coated with gold in a vacuum evaporator and observed with the SEM. The SEM used in the first year was a Cambridge model 2A but subsequent observations were performed with a Cambridge model

250T.

EFKE KB17 120 mm films from Fotokemika (Yugoslavia) were used for SEM photography and were developed in Rodinal or occasionally in Edwal developer. Panatomic-X film (Kodak) was used for light microscope photography and processed in Edwal developer.

In the investigation of variation of clone HC 18, twenty-five cells were measured in each triplicate set-up for each environmental condition (medium, irradiation, temperature, pH). Culturing was carried out in culture tubes suspended on metal bars. The conditions tested were based on the standard culturing methods in use at UBC (see following) and literature reports. Each experiment lasted 30 days. An analysis of variance (Snedecor and Cochran 1967) was used to detect significant differences due to the conditions tested. The test for difference between variances of two independent samples (Bruning and Kintz 1977) was used to evaluate the homogeneity of the variances, since proportions were analysed (L/l ratio and percentage). No significant difference between the variances was revealed and thus the data were not transformed. Standard deviation was calculated.

SW, SPW, Como Lake water, ECW, Sand SPW and Steamed SPW media were tested for rate of growth (T= 20°C; Irradiation= 45 $\mu E.m^{-2}.s^{-1}$; 16:8 L:D cycle). The first four media were described earlier. In the Sand SPW medium, the soil fraction was cut in half by an equal amount of sand, while the Steamed SPW medium was steamed according to the method described by

Nichols (1973). Irradiations of 75, 42 and 25 $\mu E.m^{-2}.s^{-1}$ were tested on cultures in SPW medium at a temperature of 20°C, a 16:8 L:D cycle and a pH of 4.62. The effects of temperature (5, 10 and 20°C) were examined (Irradiation=45 $\mu E.m^{-2}.s^{-1}$; 16:8 L:D cycle; pH= 4.62). Cultures in SPW medium (pH= 4.62) and in SPW medium to which $CaCO_3$ was added (pH= 6.20) were tested at 20°C, an irradiation of 45 $\mu E.m^{-2}.s^{-1}$ and a 16:8 L:D cycle.

In the course of a Youth Employment Program project, Pauline Monck (unpublished) cultivated clone HC 18 in a biomonitor (Schlichting 1975) in the field and in the laboratory. For the field experiment, the biomonitor was placed at a depth of ca. 0.5 m in J.K. Henry Lake, in the UBC Botanical Garden (Native Garden). The laboratory biomonitors were placed in aquaria filled with either Munday Lake water, J.K. Henry Lake water, or SPW medium.

Thirty-five cells (based on the result of a running mean calculated on four different samples) of each isolate investigated for morphological variation were measured using the light microscope. Standard deviation and coefficient of variation were calculated for each clone. The standard conditions used were a temperature of 20°C, a L:D cycle of 16:8 and an irradiation of ca. 40 $\mu E.m^{-2}.s^{-1}$. Radiation was counted on at least 100 cells.

The basic terminology used to describe Staurastrum and Staurodesmus has been illustrated in Figure 1 (p. 8). Abbreviations chosen for dimensions are derived from Irénée-Marie (1939) who used abbreviations derived from Latin:

L = length

L(cp) = length with processes

L(sp) = length without processes

l = width

l(cp) = width with processes

l(sp) = width without processes

l(csp) = width with spines

l(ssp) = width without spines

Sp = length of spines

Pr = Length of processes

Is = width of isthmus.

The expression L/l ratio refers to the length with processes or spines (unless otherwise mentioned), divided by the width with processes or spines.

For each taxon the original description is quoted. When reference is made in the text to a Plate or Figure provided in this study, the letter P or F is always capitalised. References to illustrations by other authors are in small print. Drawing Plates are alphabetically numbered (Plates A-R) and are included in Appendix D. Photographic Plates (Plates 1-18) as well as radiation and measurement Tables (Tables 11-30) are in numerical order and are found after the corresponding taxon.

TABLE 3

NUTRIENT CONTENT OF MEDIA USED FOR GROWTH EXPERIMENTS

Medium	NO_3^- $mg.l^{-1}$	PO_4^{-3} $mg.l^{-1}$	Calcium $mg.l^{-1}$	pH
Filtered Como Lake water (7 June 1980)	0.10	0.03	11.4	6.75
Filtered Como Lake water (1 February 1981)	0.53	undetectable	10.4	6.70
Filtered Como Lake water (17 May 1981)	0.04	undetectable	10.6	5.60
Enriched Como Lake water (ECW) (17 May 1981)	0.31	0.06	62.0	--
SW (Nichols 1973, p. 22)*	0.93	1.66	--	--
SPW (Gerrath 1968)+	0.98	1.49	45.3	4.62
Waris (Starr 1978)@	18.50	4.69	14.7	6.00

* Average of values from five preparations (Coefficient of variation = 8.8%)

\+ Average of values from eight preparations (Coefficient of variation = 11.2%)

@ Calculated values

IV. RESULTS AND DISCUSSION

A. PHYSICO-CHEMICAL FACTORS

Physico-chemical factors for the main sampling sites are plotted in Figures 3-6. The scale used for each lake may vary. Irradiation measurements are given in Table 4.

pH values were lower at Munday and Lost Lakes; that is generally between 4.00 and 5.00 with values up to 6.75 during summer 1979. Values at Jacobs Lake ranged between 4.85 and 6.50, and at Como Lake, between 5.60 and 7.20. Low pH has been often associated with the presence of desmids in lakes. Moss (1973) found that desmids considered to be oligotrophic did not grow at pH over 8.6. He related his results to the unavailability of free CO_2 as a carbon source for photosynthesis at this pH. The lakes studied here are low in the nutrients analysed and are oligotrophic or dystrophic (Ruttner 1967).

The lakes froze during winter 1979-1980 but not during 1980-81. Maximum temperatures recorded in July were 26°C for Jacobs and Munday and 27°C for Lost and Como Lakes. Jacobs Lake was usually a few degrees cooler than the other lakes and the quickest to freeze during the winter due to its higher elevation and more interior location. Desmids were rare during winter and most abundant from spring to fall. Croasdale (1957, 1965, 1973) has found a rich desmid flora in the Arctic. Duthie (1964) demonstrated that if desmids are subjected to an acclimation period at 4°C, they will survive freezing well. The scarce desmid population present during the winter and at low temperature in laboratory experiments, show that the field and clonal populations in this study did not grow well at temperatures below ca. 10°C.

Alkalinity was highest at Como Lake, that is between 18 and 33 mg.l^{-1} $CaCO_3$. At Jacobs Lake, it varied between 4.85 and 6.75 mg.l^{-1} $CaCO_3$. Munday and Lost Lakes showed alkalinity from 0 to 6.3 mg.l^{-1} $CaCO_3$, which was not surprising because of their low pH. For the four lakes, alkalinity was in general highest during the summer months (Fig. 3-6). Brook (1959b) related levels of alkalinity to the occurrence of different species of desmids. The ranges of alkalinity given were usually large enough to include all four main sampling lakes in the present study. Kovask (1973) established a parallel between desmid taxa and the bicarbonate (HCO_3^-) content of lakes. He grouped the algae according to the type of lake in which they were found. Two sub-groups are of interest here: one with 0-10 mg.l^{-1} HCO_3^- and a second with 10-60 mg.l^{-1} HCO_3^-. Few species were endemic to one sub-group. Among them, St. inconspicuum belonged to the first sub-group and was found in Jacobs Lake (Table 5); St. brebissonii, St. furcigerum, St. furcigerum f. eustephanum and St. tetracerum which were in the second sub-group, were found in lakes of very low alkalinity (Jacobs, Munday and Lost Lakes; Table 5).

As expected from the higher alkalinity, calcium was two to three times higher at Como Lake than at the three other sites and varied between 8.3 and 11.8 mg.l^{-1} $CaCO_3$. At Jacobs, Munday and Lost Lakes, it ranged between 1.8 and 5.9 mg.l^{-1} $CaCO_3$. No seasonal trend could be detected. Desmids have often been characterized as calciphobic, although other related factors such as the availability of free CO_2 or the total mineral content now appear significant. Experiments by Tassigny (1971) showed that the growth of many non-oligotrophic desmids was not affected by calcium level, although oligotrophic species grew more slowly as calcium concentration increased.

Values for dissolved oxygen (D.O.) varied between 4.8 and 11.2 $mg.l^{-1}$ at Munday and Lost Lakes, with some increase during summer and a decline in the fall. Values for Como Lake varied between 3.3 and 14.7 $mg.l^{-1}$ and for Jacobs Lake, between 5.6 and 13.9 $mg.l^{-1}$. The range of variation for the four lakes was similar.

Nitrate content at Munday and Lost Lakes was much higher than at Como and Jacobs Lakes, with maximum values reaching more than 1 $mg.l^{-1}$ during winter and early spring, with a decrease during the summer and an increase in the fall. Except for a few high values in winter and spring of 1980, nitrate was generally low at Como Lake, with little seasonal variation; it ranged between a low of 8 $\mu g.l^{-1}$ and a maximum value of 820 $\mu g.l^{-1}$ on 23 February 1980. Values at Jacobs Lake were always low and varied between 8 and 80 $\mu g.l^{-1}$. Results of analyses of five sets of samples from the four main lakes showed that no nitrite was present in any of the lakes sampled.

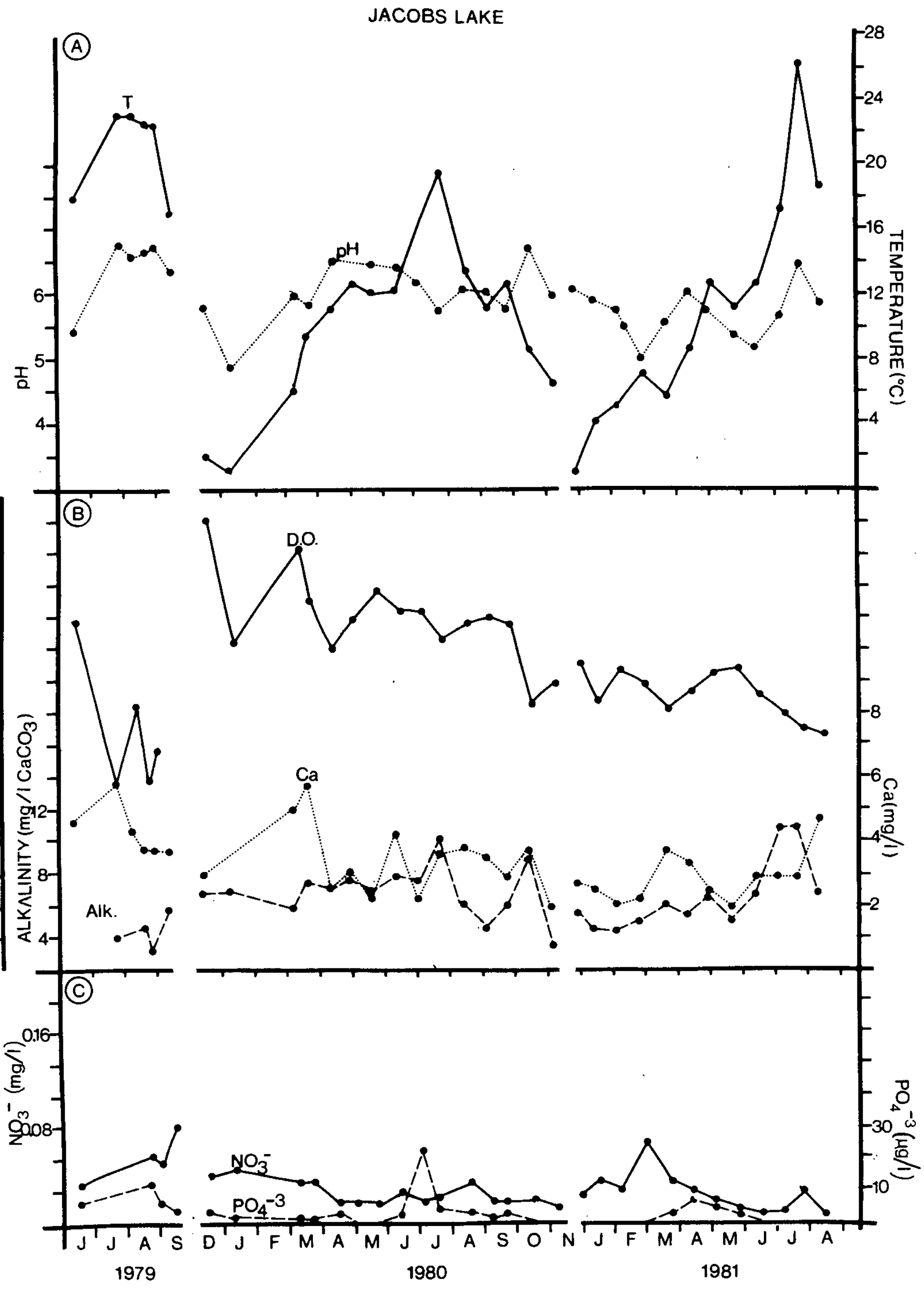
Phosphate analyses primarily showed that phosphate levels in all lakes were very low and often at the limit of detection. The highest value (50 $\mu g.l^{-1}$) recorded was at Munday Lake on 23

February 1980. All lakes showed undetectable levels of phosphate (see following) during the fall and winter of 1980-81 and at the end of the 1981 summer.

Some of these samples were analysed upon return to the laboratory before freezing, but the results were unchanged. In 1980, a series of four samples were analysed upon return to the laboratory and then after a period of 4.5 months, during which the samples were frozen at −10°C in order to measure the possible loss of phosphate to the polyethylene bottles. No loss was detected. This suggests that losses during freezing were not responsible for the low phosphate level observed.

In general, phosphate values in 1979 and the first half of 1980 were higher than in 1981. Contamination of glassware may have been partly responsible for these higher values, and repeated washings in Decon over time may have removed all the residual phosphate present on the walls of the glassware. Phosphate is easily adsorbed by the walls of glassware as previously noted in the Material and Methods. The ascorbic acid method used is relatively sensitive; its limit of detection being 10 $\mu g.l^{-1}$ for a 5 cm spectrophotometric cell at 880 nm (APHA 1975). Donaldson reported high values with erratic variations in Munday and Como lakes for 1978 (up to ca. 6 and 11 $mg.l^{-1}$ respectively), while in 1979, values were below 1×10^{3} $mg.l^{-1}$ (Donaldson 1981). Armstrong (pers. comm.) used glassware cleaned with strong acid and Wetzel and Likens' (1979) method for low phosphate concentration. He found that concentration of orthophosphate in Como Lake was in the order of 10 $\mu g.l^{-1}$ or less. Studies on the effects of nitrate and phosphate concentrations on desmids have not been reported in the literature.

Figure 3 - Physico-chemical data for Jacobs Lake (n=see Materials and Methods). A. pH (··········) and temperature (———); B. Dissolved oxygen (———), alkalinity (-----) and calcium (··········); C. NO_3^- (———) and PO_4^{-3} (-----)



JACOBS LAKE
A
T
pH
TEMPERATURE (°C)
B
D.O.
Ca
Alk.
D.O. (mg/l)
ALKALINITY (mg/l CaCO3)
Ca (mg/l)
C
NO_3^- (mg/l)
PO_4^{-3} (µg/l)
J J A S D J F M A M J J A S O N J F M A M J J A
1979
1980
1981

Figure 4 - Physico-chemical data for Munday Lake (n=see Materials and Methods) A. pH(..........) and temperature (———); B. Dissolved oxygen (———), alkalinity (----) and calcium (..........); C. NO_3^- (———) and PO_4^{-3} (----)

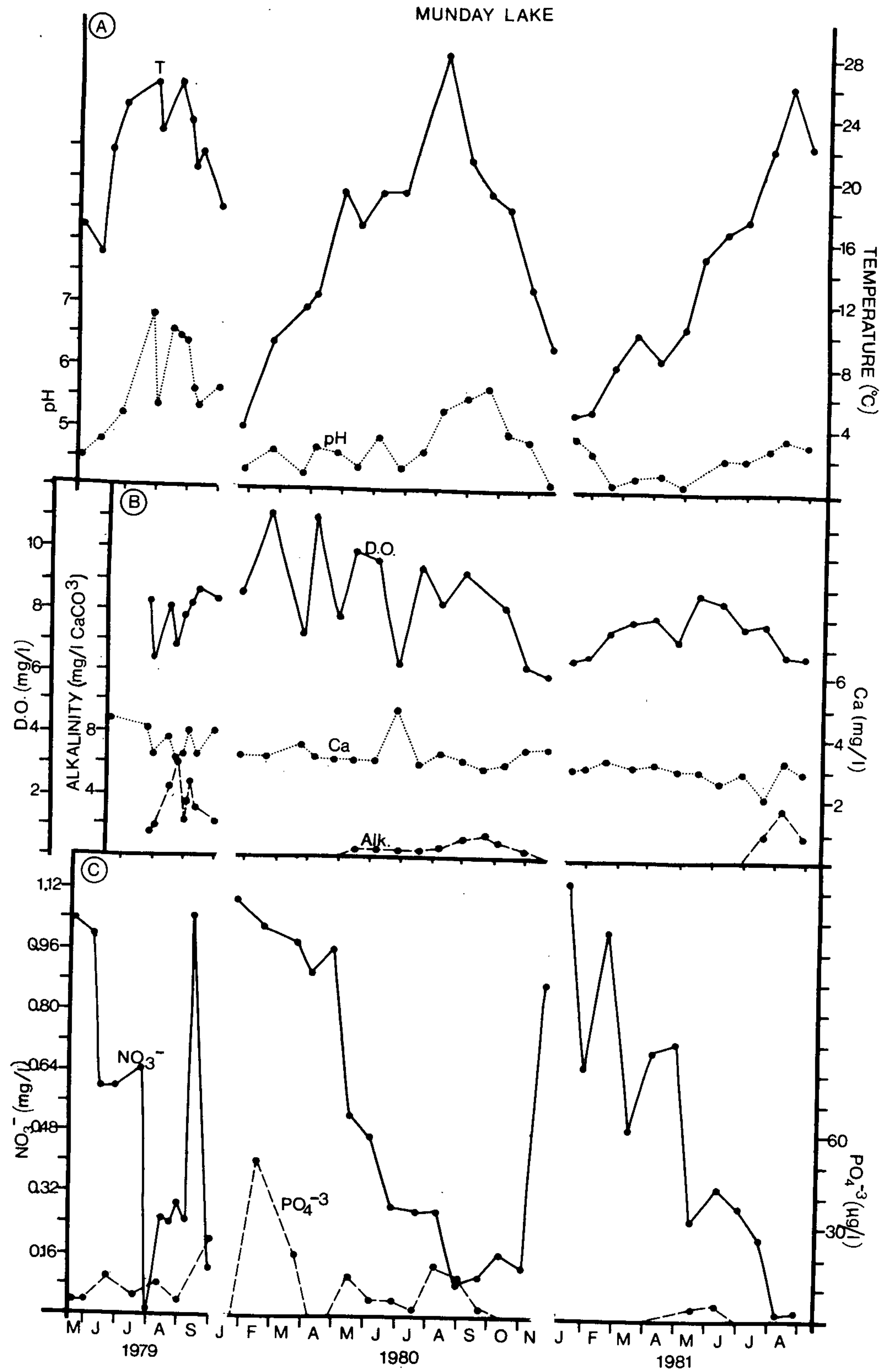
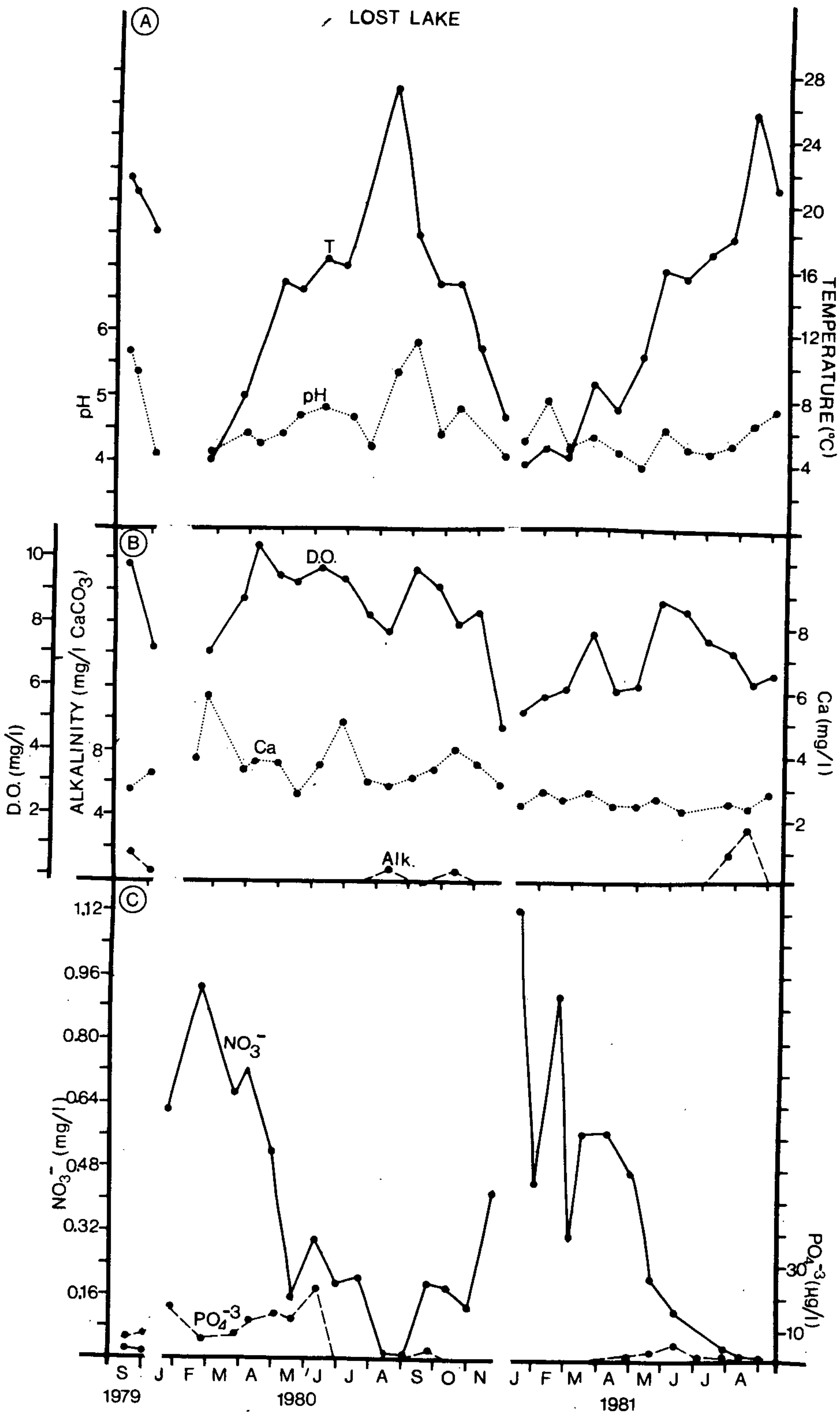

MUNDAY LAKE
A
T
pH
TEMPERATURE (°C)
B
D.O.
Ca
Alk.
D.O. (mg/l)
ALKALINITY (mg/l CaCO3)
Ca (mg/l)
C
NO3-
PO4-3
NO3- (mg/l)
PO4-3 (µg/l)
M J J A S J F M A M J J A S O N J F M A M J J A
1979
1980
1981

Figure 5 - Physico-chemical data for Lost Lake (n=see Materials and Methods) A. pH (··········) and temperature (————). B. Dissolved oxygen (————), alkalinity (– – – –) and calcium (··········); C. NO_3^- (————) and PO_4^{-3} (·– – – –)



A
LOST LAKE
T
pH
6
5
4
28
24
20
16
12
8
4
TEMPERATURE (°C)
B
D.O.
Ca
Alk.
10
8
6
4
2
D.O. (mg/l)
ALKALINITY (mg/l CaCO3)
Ca (mg/l)
C
1.12
0.96
0.80
0.64
0.48
0.32
0.16
NO3- (mg/l)
NO3-
PO4-3
30
10
PO4-3 (µg/l)
S J F M A M J J A S O N J F M A M J J A
1979
1980
1981

Figure 6 - Physico-chemical data for Como Lake (n=see Materials and Methods) A. pH (··········) and temperature (———). B. Dissolved oxygen (———), alkalinity (-----) and calcium (··········); C. NO_3^- (———) and PO_4^{-3} (-----)

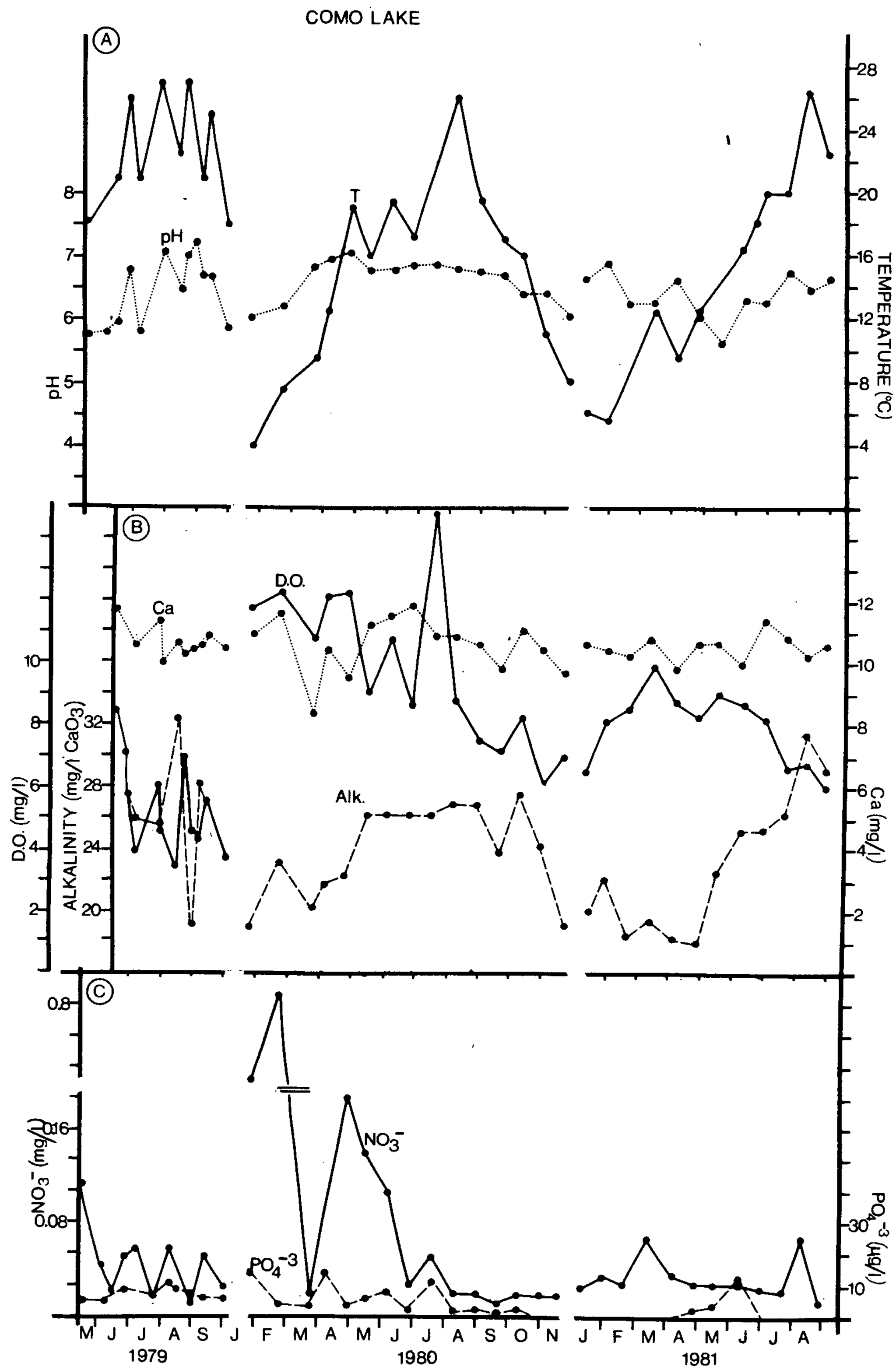

COMO LAKE
A
pH
T
TEMPERATURE (°C)
B
D.O.
Ca
Alk.
D.O. (mg/l)
ALKALINITY (mg/l CaO3)
Ca (mg/l)
C
NO3−
PO4−3
NO3− (mg/l)
PO4−3 (µg/l)
M J J A S J F M A M J J A S O N J F M A M J J A
1979
1980
1981

TABLE 4

IRRADIATION MEASUREMENTS ($\mu E.m^{-2}.s^{-1}$)

Date	Jacobs Lake			Lost Lake			Munday Lake			Como Lake		
	air	water		air	water		air	water		air	water	
		0.01 m	0.5 m		0.01 m	0.5 m		0.01 m	0.5 m		0.01 m	0.5 m
1980												
7-VI	1150	804	---	1170	1000	---	1950	1849	---	1800	1380	---
27-VI	235	174	---	235	234	---	235	187	---	215	148	---
18-VII	1110	750	---	1500	1206	---	705	603	---	1800	1809	---
30-VII	720	723	---	1725	1407	---	1650	1547	---	---	---	---
1981												
22-II	600	335*	---	---	---	---	---	---	---	---	---	---
13-III	85	27	---	---	---	---	---	---	---	---	---	---
7-IV	345	241	---	850	871	---	190	255	---	480	375	---
17-V	700	630	---	350	281	---	550	361	228	500	349	228+
9-VI	660	603	---	2000	2010	1057	1010	871	509	100	87	47
30-VI	145	125	88	150	125	52	220	168	105	120	134	67
22-VII	290	235	---	100	94	43	730	402	395	830	697	469
11-VIII	120	67	43	600	630	268	900	871	603	1500	1340	1005
28-VIII	780	871	670	1300	1333	402	900	670	416	840	670	375@

* 0.175 m = 47; 0.325 m = 23

\+ 1.0 m = 161

@ 0.75 m = 188

B. DISTRIBUTION OF ALGAL GENERA IN LAKES STUDIED

Algae other than *Staurastrum* and *Staurodesmus* were generally identified only to genera. A brief overview of the lakes according to their phycological components and their relative seasonal abundance follows.

1. JACOBS LAKE

Phytoplankton in samples from Jacobs Lake was scarce. The samples were collected from the dock in a relatively shallow area and the top part of the loose sediment was sometimes disturbed; thus desmids as well as diatoms living on the sediment were occasionally found in plankton samples. *Tetmemorus granulatus* (Brébisson) Ralfs or *Tabellaria fenestrata* (Lyngb.) Kützing which were also abundant on the sediment at some times of the year were found in the plankton. The only other taxon found in abundance was *Dinobryon*, on 10 August 1979. Although it is not usually considered as periphytic, it was also found in some amount among the periphyton collected on the same date.

Periphyton samples including epipelic and epiphytic samples were richer in algae, particularly in desmids and diatoms. Water containing microscopic algae was collected after squeezing plants of *Utricularia* or filaments of Zygnemataceae. These plants were found in early spring and supported a good desmid growth.

Desmids were abundant from early March through late September; the peak season for *Staurastrum* spp. was July and

August. *Tetmemorus granulatus* proved to be a very abundant and an often dominant periphytic alga during the summer months. *Tetmemorus*, *Penium* and *Closterium* were the only desmid genera present in any great abundance, although a large number of genera (19) were recorded. *Staurodesmus* was rare.

From late September through to the middle of March, pennate diatoms were the most abundant algae. Around the end of May and the beginning of June, *Tabellaria fenestrata* and *T. flocculosa* (Roth) Kützing were dominant.

The only member of the Cyanophyceae was *Oscillatoria* seen on 11 October 1980. On a few occasions, cells of the genera *Cryptomonas*, *Ceratium* and *Peridinium* were seen. *Synura* was observed on one occasion and *Dinobryon* was the dominant alga on 10 August 1979 as previously mentioned.

2. MUNDAY LAKE

Phytoplankton was also quite rare in samples from Munday Lake. Plankton samples were collected from a dock; periphytic species originating from the loose sediment were occasionally found in them. Among the species which can be considered as truly planktonic, *Kirchneriella contorta* (Schmidle) Bohlinand *Peridinium* were relatively abundant in June. *Tabellaria fenestrata* and *T. flocculosa* were common in September. Colonies of *Dinobryon* were particularly abundant from February to April.

Staurastrum pentacerum was found mainly in the plankton from the end of June through early August 1980; some cells persisted up to the end of October. In 1979 and 1981, only a few individuals of this species were recorded.

Periphyton samples were obtained from squeezings of Sphagnum sp. or algae growing among dead aquatic plants attached to the sediment on the shores of the lake. Desmid genera were relatively fewer than at Jacobs Lake; only 10 genera were identified. Desmids were most abundant from spring to fall. One species of Staurastrum, St. muricatum, was found in abundance among Sphagnum populations during that period. Staurodesmus was not common.

Tabellaria fenestrata and T. flocculosa were dominant during August and September and other pennate diatoms were common on the sediment.

The green algae were represented by Bulbochaete, Oedogonium and Klebsormidium and were found among decaying roots of higher plants or on the peat mats in August and September.

Peridinium was abundant in the periphyton samples in June and July and was probably mostly of planktonic origin. Cyanophyceae, Chrysophyceae and Cryptophyceae were occasionally recorded. Two species of Euglena formed a green growth on the peat mat beside the dock and were particularly noticeable during the month of August.

3. LOST LAKE

Lost Lake has an algal composition similar to that of Munday Lake, although usually with fewer individuals. The fact that aquatic vascular plants and mosses were less common may well account for this difference. The most abundant genera in the plankton were *Synura*, *Dinobryon* and to some extent, *Cryptomonas* and *Peridinium*. *Synura* was particularly abundant in samples collected in March and September 1980 and again in April 1981.

Desmid genera were similar to those in Munday Lake with the exception of one occurrence of *Spirotaenia* in Lost Lake. Species of *Staurastrum* were similar to the species found at Munday Lake. *St. pentacerum* was found only occasionally and *St. muricatum* Brébisson was less common than in Munday Lake. *Staurodesmus* was rare.

Among diatoms, the genera *Tabellaria* and *Melosira* were most common during the spring and the fall. Many genera of pennate diatoms were commonly found on the sediment or among other plants, as in the other lakes studied.

Peridinium was abundant in a sample collected on 12 September 1979. During summer time, two species of *Euglena* formed green patches on the shore of the lake, just above water level. A few other Euglenophyceae were occasionally recorded. Members of the Cyanophyceae and Cryptophyceae were very rarely observed.

4. COMO LAKE

Como Lake had the richest algal growth of the four main collecting sites, mostly in the plankton. Seasonal dominance in the plankton was assumed by different species. *Peridinium* sp. dominated the plankton in spring and fall and *Ceratium hirundinella* (O.F. Müller) Dujardin was also abundant at this time.

Dinobryon spp. were very abundant in spring and fall. *Synura* and *Mallomonas* were also well represented members of the Chrysophyceae during the cooler months of the year. *Asterionella formosa* Hass. and *Tabellaria* spp. bloomed around the same time, with *T. fenestrata* and *T. flocculosa* mainly of periphytic origin.

Many genera of algae were found growing among aquatic plants. Only seven genera of desmids were recorded but a few species of *Staurodesmus* and *Staurastrum* were present in high numbers from spring to the end of the summer. They occurred under the leaf blades and on the stems of *Nymphaea* and on decomposing plants of *Brasenia*, among filaments of *Spirogyra*, and were also found on the sediment.

Mougeotia was abundant mostly around February whereas *Spirogyra* was more important from April through the end of the summer. Filaments of *Oedogonium* and *Bulbochaete* were also common. *Bulbochaete* was found growing attached to the tires supporting the dock. A number of genera of Chlorococcales were found among aquatic vascular plants. Some free living coccoid Xanthophyceae were also observed.

Many pennate diatoms lived among the rooted vegetation. *Tabellaria fenestrata* and *T. flocculosa* were again the dominant diatoms during spring and fall. In a sample collected on 22 February 1981, both *Tabellaria* and *Asterionella formosa* were abundant.

Dinobryon, *Synura* and *Mallomonas* were also recorded in periphyton samples as were *Peridinium* and *Ceratium hirundinella*. These were most likely from planktonic origin. Cyanophyceae were represented by a number of genera. *Cryptomonas* and *Euglena* were relatively common.

An outflow at the south end of the lake was sampled a few times. Around the end of February, it showed a heavy growth of *Draparnaldia plumosa* (Vauch.) Ag. supporting a variety of small pennate diatoms and some Chlorococcales. *Draparnaldia* was replaced by *Spirogyra* during the spring and summer with many species of *Staurastrum* and *Staurodesmus* intermingled with the *Spirogyra* filaments. Other representatives of the most abundant algae in the lake such as *Peridinium*, *Dinobryon*, and *Tabellaria*, also occurred among the *Spirogyra* filaments.

5. OTHER SITES

Mike Lake in Golden Ears Provincial Park was visited on five occasions in 1979. Similarly to Jacobs Lake, plankton samples contained few algae. Periphyton samples yielded 14 genera and numerous species of desmids, among which were *Staurastrum* and *Staurodesmus*. Filamentous Chlorophyceae, especially *Zygnema* and *Spirogyra*, were abundant in August.

Small pennate diatoms were common as were Tabellaria fenestrata and Melosira. Euglena formed isolated green patches on the wet mud around the lake. Other algae observed included Peridinium, Ceratium, Dinobryon, Synura, Mallomonas, Oedogonium, species of Chlorococcales, filamentous and coccoid Cyanophyceae.

Beside Mike Lake lies an unnamed pond which was sampled on 15 August 1979. It was similar to Mike Lake in its algal composition. The two most abundant algae were T. fenestrata and Bambusina, which was not recorded in Mike Lake. A number of other desmid genera were also recorded including Staurastrum and Staurodesmus.

A series of lakes in the UBC Research Forest were visited on different occasions (Fig. 2C). Placid Lake was visited five times. Nine desmid genera were recorded, including Staurastrum and Staurodesmus, as well as Spirogyra, Dinobryon, Euglena, Ceratium and genera of Chlorococcales, diatoms and Cyanophyceae.

Five visits to Blaney Lake yielded ten genera of desmids, including Staurastrum and Staurodesmus. The other algae recorded were similar to Placid Lake.

Gwendoline Lake was visited on two occasions in 1979. Representatives of planktonic algae were scarce and samples collected from moss squeezings and among Drosera revealed five genera of desmids including Staurastrum, some Chlorococcales, diatoms and Cyanophyceae.

Eunice Lake was sampled on 10 August 1979 but very few algae and no Staurastrum or Staurodesmus were observed. However, a pond adjacent to the lake included five different genera of desmids including *Staurastrum*, as well as *Mougeotia*, *Scenedesmus* and *Anabaena*.

Katherine Lake, visited on the same day, showed a predominance of *Dinobryon* in its plankton. Five genera of desmids were recorded including *Staurastrum* and *Staurodesmus*, as well as filaments of *Mougeotia* and *Zygnema*, some Cyanophyceae and Dinophyceae

The South and North Alouette Rivers were sampled at their intersection with 232nd street in Maple Ridge, on 10 August and 1 September 1979, and 23 March 1980. Rock scrapings and sediment samples provided a number of species of *Cosmarium*, *Closterium* and *Cosmarium*-like *Staurastrum* living among *Spirogyra* filaments. Pennate diatoms, some of which were growing in tubes, were abundant.

Whonnock Lake was sampled on three occasions in 1979 (28 June, 29 July, 5 September). Eleven genera of desmids were recorded, however neither *Staurastrum* nor *Staurodesmus* were abundant. *Peridinium* was dominant on 28 June 1979 in the plankton. Genera of Chlorophyceae, Cryptophyceae, Euglenophyceae and Bacillariophyceae were also recorded.

A plankton tow was made in the Pitt River on 7 June 1979 just beside the Pitt River bridge. It contained mostly the species *Asterionella formosa* with some *Dinobryon*. The Coquitlam River was sampled on the same date, beside the Coquitlam bridge. The only desmid found was *Closterium*. *Dinobryon*, *Audouinella*, *Draparnaldia plumosa* and different genera of diatoms were observed.

Trout Lake was visited on four occasions (18 September, 1978, 27 May, 2, 29 August 1979). The lake supported a very rich plankton growth. Four genera of desmids were recorded, among which were Staurastrum and Staurodesmus. The dominant alga on 27 May 1979 was Anabaena; Melosira, Dinobryon and Pediastrum simplex (Meyen) Lemmermann were also quite abundant.

J. K. Henry Lake located in the UBC Botanical Garden (Native Garden) close to 16th Avenue was visited on four occasions in 1979 and 1980 (25 May 1979, 18 April, 30 May, 30 July 1980). In summer 1981, it was the site for a study conducted by Pauline Monck (unpublished) and referred to in Chapter 3 section B.6 and Chapter 4, section F.1. J.K. Henry Lake contained 16 genera of desmids and many individuals mostly of the filamentous desmids, although not many species of Staurastrum and Staurodesmus were seen. Many cells of Tabellaria and other pennate diatoms were present in the spring. Filamentous green algae, particularly the Zygnemataceae, were also abundant and species of the Chlorococcales were common. Peridinium, Cryptomonas, Dinobryon, Synura and a few genera of Cyanophyceae were also observed.

A collection trip around Stanley Park on 5 April 1980 provided a large amount of Closterium littorale Gay from a ditch not far from the Stanley Park zoo. Other lakes, ponds and ditches were sampled on Vancouver Island, the Gulf Islands, the Okanagan Valley and the lower mainland but were not of any particular interest for the study of Staurastrum or Staurodesmus.

One sample was collected on 28 July 1980 from a pond in the VanDusen Botanical Garden in Vancouver. *Spirogyra* was the main alga in that sample but *Staurastrum proboscideum* (Ralfs) Archer f. *minor* (Schmidle) Prescott, Bicudo and Vinyard was also found.

C. DISTRIBUTION OF STAURASTRUM SPP. AND STAURODESMUS SPP. IN LAKES STUDIED

Sixty-one species and varieties of *Staurastrum* (*St.*) and *Staurodesmus* (*Std.*) were identified in this study. Nine species are new records for the province, and there are 56 new distribution records for species already known in the province. These data are summarized in Table 5. The information concerning new records are based on Stein and Borden (unpublished). Since samples were sometimes screened with a dissecting microscope, or observed with a compound microscope but not identified to species level, not all the *Staurastrum* or *Staurodesmus* observed in all samples were identified. This explains the absence from Table 5 of some lakes which contained a few *Staurastrum* or *Staurodesmus* species but which were not identified. This list is not an exhaustive collation of all the species present in the lakes sampled. The taxonomic treatment of the material was very conservative. Numerous taxa of *Staurastrum* and *Staurodesmus* have been described on only minor and unstable variations and represent a major problem to taxonomists who have to decide on the validity of taxa. It was thus considered a priority to fit the specimens to known taxa, rather than describe new taxa on minor variations.

TABLE 5

SPECIES OF STAURASTRUM (St.) AND STAURODESMUS (Std.) FROM THE LOWER FRASER VALLEY

(* taxon already known to this lake; ** taxon new to this lake; *** taxon new to British Columbia)

Species	Jacobs	Munday	Lost	Como	Placid	Gwendo- line	Mike	Trout	VanDusen Garden	J.K. Henry
St. aculeatum (Ehrenberg) Meneghini	**									
St. alternans Brebisson ex Ralfs	**	*	**	**						**
St. anatinum Cooke et Wills	*		*		**					
St. anatinum var. lagerheimii (Schmidle) W. et G.S. West	**									
St. anatinum var. truncatum W. West		***								
St. arachne Ralfs	*				*					
St. arctiscon (Ehrenberg) Lundell	*				*					
St. arcuatum Nordstedt	**				*					**
St. arcuatum var. guitanense W. West										**
St. avicula Brebisson	**			*						
St. boreale W. et G.S. West	***									
St. brachiatum Ralfs	**									

TABLE 5 (cont'd)

Species	Jacobs	Munday	Lost	Como	Placid	Gwendo-line	Mike	Trout	VanDusen Garden	J.K. Henry
St. brasiliense Nordstedt var. *lundellii* W. et G.S. West					*					
St. brebissonii Archer	**		*							
St. cerastes Lundell	**									
St. coarctatum Brebisson var. *subcurtum* Nordstedt	**									
St. conspicuum W. et G.S. West	***									
St. crenulatum (Nageli) Delponte									**	
St. cornutum Archer	*									
St. furcatum (Ehrenberg) Brebisson	**									
St. furcigerum Brebisson	*									
St. furcigerum f. *eustephanum* (Ehrenberg) Nordstedt	**									
St. furcigerum f. *armigerum* (Brebisson) Nordstedt					**					
St. gladiosum Turner	*	*	*	*	**					
St. gracile Ralfs				*						
St. gracile var. *nanum* Wille	**									

TABLE 5 (cont'd)

Species	Jacobs	Munday	Lost	Como	Placid	Gwendo-line	Mike	Trout	VanDusen Garden	J.K. Henry
St. grallatorium Nordstedt var. forcipigerum Lagerheim	**									
St. inconspicuum Nordstedt	**									
St. inflexum Brebisson		**		**						
St. johnsonii W. et G.S. West	**									
St. leptacanthum Nordstedt	**				**					
St. leptocladum Nordstedt var. insigne W. et G.S. West				**						
St. longiradiatum W. et G.S. West	**				**					
St. maamense Archer	**									
St. manfeldtii Delponte var. parvum Messikommer	**			**						
St. margaritaceum (Ehrenberg) Meneghini	**	*	**							**
St. micron W. West	***									
St. muricatum Brebisson		*	*							
St. muticum Brebisson	**			**						

TABLE 5 (cont'd)

Species	Jacobs	Munday	Lost	Como	Placid	Gwendo-line	Mike	Trout	VanDusen Garden	J.K. Henry
St. ophiura Lundell	*				*					
St. orbiculare Ralfs	*				**					
St. orbiculare var. depressum Roy et Bisset	**									
St. pentacerum (Wolle) Smith		*	**	**						
St. proboscideum f. minor (Schmidle) Contant nov. comb.	***	***		***					***	
St. sebaldi Reinsch	**									
St. senarium (Ehrenberg) Ralfs		***								
St. setigerum Cleve		*	**							
St. sexcostatum Brebisson var. productum W. West	**									
St. simonyi Heimerl	**									
St. subavicula W. et G.S. West	***									***
St. subcruciatum Cooke et Wills				*						
St. subnudibrachiatum W. et G.S. West	***				***		***	***		
St. tetracerum Ralfs	*	*		*						
St. tohopekaligense Wolle	*									

TABLE 5 (cont'd)

Species	Jacobs	Munday	Lost	Como	Placid	Gwendo-line	Mike	Trout	VanDusen Garden	J.K. Henry
St. tohopekaligense var. *trifurcatum* W. et G.S. West					**					
St. vestitum Ralfs	**				**					
Std. dejectus (Brebisson) Teiling		*	**	**					**	**
Std. brevispinus (Brebisson) Croasdale				**						
Std. mamillatus var. *maximus* (W. West) Teiling				***						
Std. mucronatus var. *delicatulus* (G.S. West) Teiling		***								***
Std. mucronatus var. *subtriangularis* (W. et G.S. West) Croasdale										**

D. SEXUALITY EXPERIMENTS

1. CLONES ISOLATED

Among the 84 clones of Staurastrum spp. tested for sexual reproduction according to Starr's CO_2 enrichment method, none conjugated in the conditions described in Table 6. In a few instances there was an indication of pairing of cells. In clones HC 2, 4 and 6 (St. proboscideum f. minor) the formation of a bulge at the isthmus was observed after six days of incubation under cool-white fluorescent tubes, but conjugation never occurred. Since conjugation did not occur with Starr's method, which is considered standard, variations based on successful techniques used by others were tried without success (Table 6 and 7).

No zygotes were produced in the field samples stored in the culture chambers. Mud samples which were rehydrated did not produce any desmid cells but desmid zygotes were seen in two preserved samples from Jacobs Lake. However, since no cells were attached to the zygotes, it was impossible to determine to which species or genus they belonged.

One homothallic clone of Closterium littorale Gay (HC 243) did conjugate readily in culture without the aid of the CO_2 enrichment method. The sample from which the clone was isolated was collected on 5 April 1980 from a ditch in Stanley Park, Vancouver. Vegetative cells of Cl. littorale were abundant. The clone seemed to produce zygospores only in cultures containing mostly dead cells; bright green cultures had few or no zygospores.

2. CLONES FROM CULTURE COLLECTIONS

The following experiments were performed to determine if the experimental conditions applied to HC clones (see Appendix C) in an attempt to induce sexual reproduction would be successful with clones known to be sexual. One homothallic clone of Cosmarium botrytis (#2140) was tested under the conditions stated in Table 6. It produced zygotes after two days of incubation and, after six days, the cultures contained ca. 100% zygotes.

Heterothallic clones of Staurastrum gladiosum (LB1568, LB1569) used by Winter and Biebel (1967) and obtained from University of Texas culture collection did not show conjugation so readily. Three different sets of conditions had to be tried before obtaining zygotes (Table 6). A few zygotes were seen after 12 days in a SW medium, using Starr's CO_2 enrichment technique. Lippert (1967) mentions that after a few years in culture, clones may lose their sexual potential. That could explain partially the poor rate of success achieved with these clones.

The sites and organisms sampled in this study were not ideal for induction of sexual clones. Literature reports show that ponds or shallow areas prone to desiccation produce more sexual clones than larger bodies of water. Starr (1955) successfully isolated sexual clones from populations where there already were signs of sexual reproduction. As stressed by Coesel and Texeira (1974) and Mollenhauer (1975), success in inducing conjugation is lower with the more advanced genera of desmids and many tend to abandon the process (see section B in Introduction). The sexual stage of many species of *Staurastrum* and most taxa I studied is unknown. Although further variations and combinations of environmental conditions could be tried, the chances of inducing conjugation in HC clones are remote. Most conditions recognized as favourable in inducing sexual reproduction, as discussed in the introduction, are lacking and standard methods have failed to produce any sexuality.

TABLE 6

CLONES AND ENVIRONMENTAL CONDITIONS USED FOR SEXUAL EXPERIMENTS

Clone	Medium	Irradiation ($\mu E.m^{-2}.s^{-1}$)	L:D cycle	Temperature (^{o}C)	CO_2 enrichment	Result
HC 2, 4, 6, 12, 13, 18, 20, 22, 24, 25, 34, 39, 40, 41, 42, 43, 44, 45, 47, 49, 57, 58, 60, 62, 63, 64, 66, 67, 68, 69, 70, 71, 72, 73, 77, 79, 97, 102, 110, 115, 119, 122, 127, 133, 150, 151, 173, 205, 210, 211, 213, 223, 272, 288, 292, 295, 296, 302, 306, 312, 318, 323, 325, 340, 368, 386, 389, 414, 418, 419, 427, 433, 435, 436, 438, 468, 469, 473, 474, 479, 490, 492, 496, 497	SPW	Gro-lux 45	16:8	20	yes	No zygotes
HC 2, 4, 6, 12, 13, 18, 20, 22, 24, 25, 58, 60	SW	Gro-lux 45	16:8	20	yes	No zygotes

TABLE 6 (cont'd)

Clone	Medium	Irradiation ($\mu E.m^{-2}.s^{-1}$)	L:D cycle	Temperature (^{o}C)	CO_2 enrichment	Result
HC 2, 4, 6, 13, 18	SPW & SW	Cool-white 70	18:6	20	yes	No zygotes
HC 243 (*Cl. littorale*)	SPW	Cool-white 20-40	14:10	20	no	Zygotes
HC 2, 4, 6, 13, 18	Filtered CW(31-I-81)	Cool-white 45	16:8	20	yes	No zygotes
Co. botrytis Carolina Bio. supply Co. #2140	SPW & SW	Gro-lux 45	16:8	20	yes	Zygotes present after 2 days Ca. 100% zygotes after 6 days
	SPW & SW	Cool-white 45	14:10	20	yes	Same
St. gladiosum UTEX LB 1568 x 1569	SPW & SW	Cool-white 77	16:8	20	yes	No zygotes; some pairing
	Waris; NO_3^- = $.990 \times 10^{-3}M$ $.495 \times 10^{-3}M$ $.198 \times 10^{-3}M$ $.099 \times 10^{-3}M$	Cool-white 50	14:10	22-25	yes	No zygotes; some pairing
	SW	Cool-white 40	14:10	16	yes	Much pairing; few zygotes after 12 days

TABLE 7

SUMMARY OF TECHNIQUES USED FOR DESMID CONJUGATION BY DIFFERENT WORKERS
(Irradiation converted to $\mu E.m^{-2}.s^{-1}$)

Species	Irradiation ($\mu E.m^{-2}.s^{-1}$)	L:D cycle	Temperature (^oC)	Technique	Homo- or heterothallic	Onset of conjugation	Age of culture	Zygospore germination	Reference
Closterium venus-dianae	ca. 36	16:8	20	CO_2 enrichment or spontaneous in SW	----	----	----	----	Cook, 1963
Cl. leibleinii	ca. 54	12:12	20	CO_2 enrichment. In E.A. George medium +6% peat ext.	Homothallic	----	----	6 month old. Dried, rewet	Brandham and Godward, 1964
Cl. acerosum						----	----		
Cl. siliqua						----	----		
Cl. kutzingii						----	----		
Cl. ehrenbergii					Heterothallic	----	----		
Cosmarium botrytis						----	----		
Staurastrum polymorphum					Homothallic	----	----		
St. denticulatum						----	----		
Cl. strigosum	culture: ca. 66 conjugation: ca. 166	----	25-27	N-deficient medium. Cell concentration: 6-8 x 10^4	Heterothallic	----	1 month	----	Ichimura, 1971
Cl. littorale	4-40 W fluorescent tubes	18:6	20	SW + $CaCO_3$ 1% SW agar	Homothallic	----	3-6 wk	----	Pickett-Heaps and Fowke, 1971
Cl. moniliferum	ca. 25-41 ca. 25-41 with gro-lux tubes	18:6 14:10	14-25	Waris medium	Homothallic	5-7 days 3 days	---- ----	---- ----	Dubois-Tylski, 1973a

TABLE 7 (cont'd)

Species	Irradiation ($\mu E.m^{-2}.s^{-1}$)	L:D cycle	Temperature	Technique	Homo- or heterothallic	Onset of conjugation	Age of culture	Zygospore germination	Reference
Cl. rostratum	ca. 41 witn gro-lux tubes	18:6	22	Waris medium	Homothallic	----	----	----	Dubois-Tylski, 1973b
	ca. 17 with gro-lux tubes	24:0				8 days	----	----	
Cl. moniliferum	ca. 25 with gro-lux tubes	12:12 & 18:6	20	No N_2 or N_2 deficient Waris	Homothallic	----	----	----	Dubois-Tylski, 1977
Cl. moniliferum	conjugation: ca. 58	16:8	25	CO_2 enrichment in SW	Homothallic	Readily	3-5 wk	----	Coesel and Texeira, 1974
Cl. limneticum var. _fallax_	culture: ca. 25		culture: 20			2 days		----	
Micrasterias papillifera						----		----	
Co. botrytis v. _subtumidum_	ca. 89 with warm-white fluorescent tubes	18:6	20-23	CO_2 enrichment in SW	Heterothallic	----	----	----	Starr, 1955
Mi. mahabuleshwarensis	Gro-lux tubes	16:8	25	CO_2 enrichment of Desmid agar + soil ext.	Heterothallic	2 days	----	----	Blackburn and Tyler, 1980
St. gladiosum	ca. 36	16:8	25	CO_2 enrichment in SW	Heterothallic	2 days	----	In 2-10 wk Spontaneous after 2 months	Winter and Biebel, 1968

E. GROWTH PATTERN OF STAURASTRUM INFLEXUM (CLONE HC 18) IN DIFFERENT ENVIRONMENTAL CONDITIONS

Experiments to measure growth rate and morphological variations were not performed at the same time, although sets of conditions were often similar (see Materials and Methods). Results of the preliminary experiment on growth rate are shown in Fig. 7.

Como Lake water (7 June 1980) showed the highest factor of division per day, k=0.34 (as calculated by the computation of k for the period of exponential growth; Guillard 1973), the shortest lag phase (ca. 4 days) and the shortest period of exponential growth (ca. 9 days). However, the maximum yield after 26 days was 23 x 10^3 cells.ml^{-1}, which is 10 times lower than the yield for the SPW medium. This result was to be expected because of the low level of nitrogen and phosphorus present in Como Lake water (Table 3).

Waris medium produced an irregular exponential growth curve. After 39 days, the number of cells was equivalent to that found in Como Lake water. The growth in terms of divisions per day was 0.116 (Fig. 7).

The other media also produced a slow exponential growth period extending over ca. 1.5 month. Computation of cell numbers vs. time indicated a lag phase of about two weeks which was not apparent when log of cell numbers were used as in Figure 7. The SW medium produced a final yield of about half that for the two SPW media; that is ca. 130 x 10^3 cells.ml^{-1} in SW and

250-310 $\times 10^3$ cells.ml^{-1} in SPW. The number of divisions per day was 0.154 for the SW medium, 0.135 for the SPW medium without additions and 0.147 for the SPW medium with addition of vitamin B_{12} and trace metals.

This experiment showed SPW to be a suitable medium for the culture of clone HC 18. Although the growth rate was very slow, it followed a normal curve and gave a high number of cells for observations. For general maintenance of cultures, transferring every four to six weeks thus seems adequate, as cells are then transferred towards the end of their exponential growth phase.

Como Lake water from 1 February 1981 (Table 3) was also tested against SPW medium. After 14 days, in both media, the number of cells.ml^{-1} reached 130 $\times 10^3$ with k= 0.135 . The spectrophotometric readings showed that whereas the cultures in SPW medium continued to grow, the cultures in Como Lake water slowly levelled off after day 14.

The large inoculum used (see Materials and Methods) change the pattern of growth of clone HC 18 in SPW medium, but growth in Como Lake water from February was slower than in the preceding experiment with water from 7 June 1980. Table 3 shows differences between the chemical constituents analysed, but other chemicals which were not analysed may also have been responsible for the slower growth of clone HC 18.

The experiment on the effect of different irradiations on growth rate used only SPW medium. This choice was prompted by the routine use made of this medium during the present study, and because it yielded the highest number of cells in the preceding growth experiments. Results are given in Figure 8B.

Little difference was seen between the 90 and 42 $\mu E.m^{-2}.s^{-1}$ irradiances. At 90 $\mu E.m^{-2}.s^{-1}$ however, the lag phase was ca. three days shorter than at 42 $\mu E.m^{-2}.s^{-1}$ and although both curves followed each other very closely, the culture at 90 $\mu E.m^{-2}.s^{-1}$ was always ca. 6 $x10^3$ cells.ml^{-1} denser than the culture at 42 $\mu E.m^{-2}.s^{-1}$. The growth constant k was 0.108 in the first case, and 0.105 in the second. The culture at 25 $\mu E.m^{-2}.s^{-1}$ showed a longer lag phase and somewhat irregular exponential growth phase. The number of divisions per day was 0.105. The culture under 12.5 $\mu E.m^{-2}.s^{-1}$ showed no exponential growth phase and had a factor k of 0.065. In 63 days, it increased its cell number by a factor of 16. These observations suggest that an irradiation above 42 $\mu E.m^{-2}.s^{-1}$ up to at least 90 $\mu E.m^{-2}.s^{-1}$ is satisfactory for the growth of clone HC 18.

A third experiment used Como Lake water (17 May 1981) enriched with a modified Waris solution (Fig. 8A). In addition to the nitrate, phosphate and calcium concentrations given in Table 3, magnesium was present at a concentration of 6.82 mg.l^{-1} and 0.5 mg.l^{-1} of an iron sequestrine solution (Starr 1978) was also added.

The goal of this experiment was to test if enrichment of Como Lake water would promote the growth of clone HC 18 from Como Lake, and if the clone would grow without NO_3^- or PO_4^{-3}. The nutrient shock resulting from the omission of NO_3^- or PO_4^{-3} (see Materials and Methods) may have been useful in experiments on sexual reproduction. However, despite the enrichment of the water, the number of divisions per day (k=0.125) was not higher than in the experiment with Como Lake water collected in February and described earlier. Thus it appears that even when enriched, Como Lake water does not provide a better medium than SPW for the growth of clone HC 18 (isolated from Como Lake). When the cultures reached the end of the exponential phase after 25 days, they were diluted to their original number (day 0) with two different media composed of enriched Como Lake water: one from which the phosphate fraction had been omitted, and the other from which the nitrate fraction was missing. All three replicates of both treatments showed either no or little growth after eight days and thus these media could not be used for sexual experiments.

Figure 7 - Growth rate of <u>Staurastrum inflexum</u> (clone HC 18) in different media

A. Como Lake water, 7-VI-80 (··········) and Waris medium (– – – –)

B. SPW medium (————), SPW medium enriched with a solution of trace metals and vitamin B_{12} (SPW^{+} ··········) and SW medium (– – – –) in 40 $\mu E.m^{-2}.s^{-1}$irradiation, 14:10 L:D, 16°C

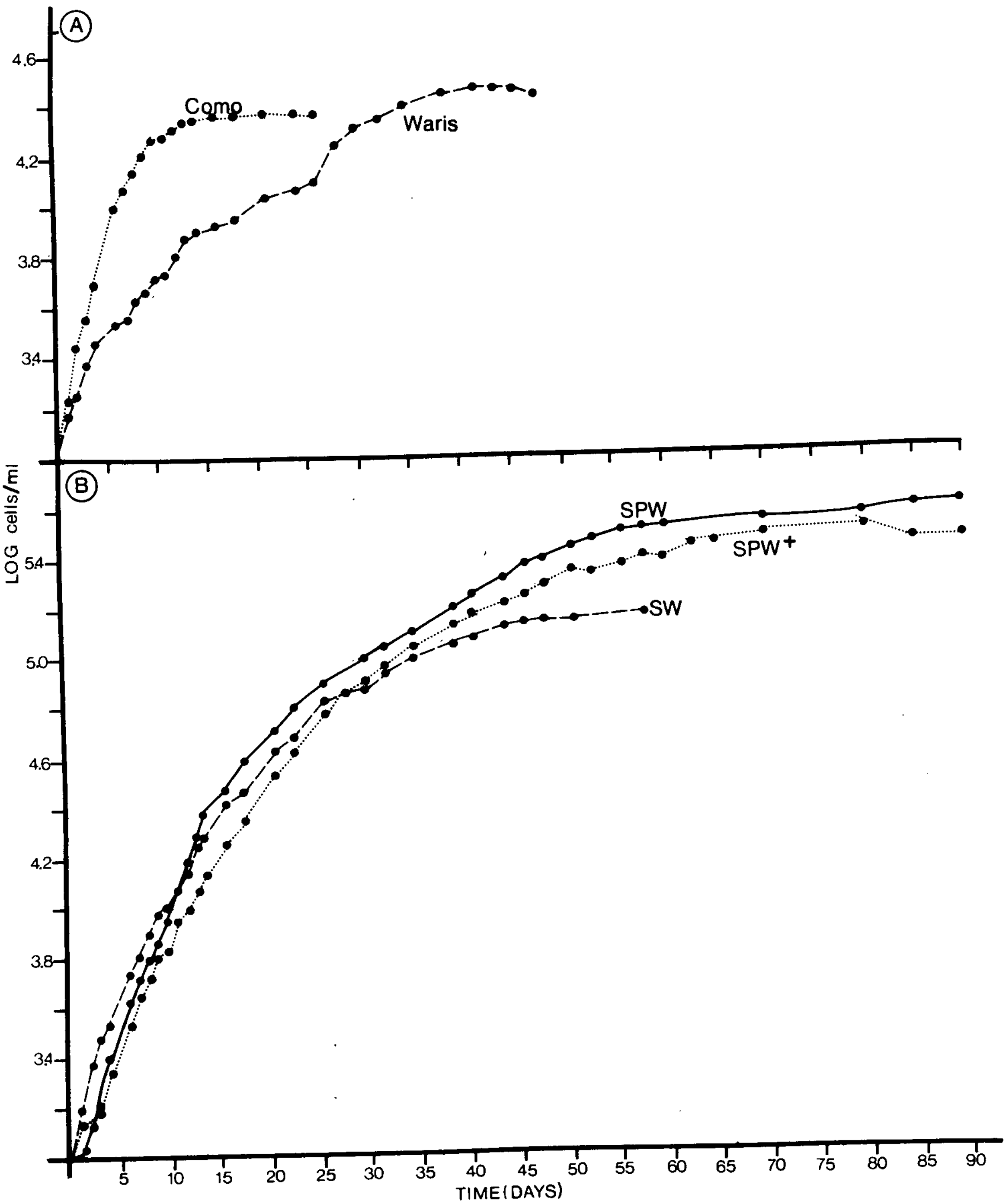
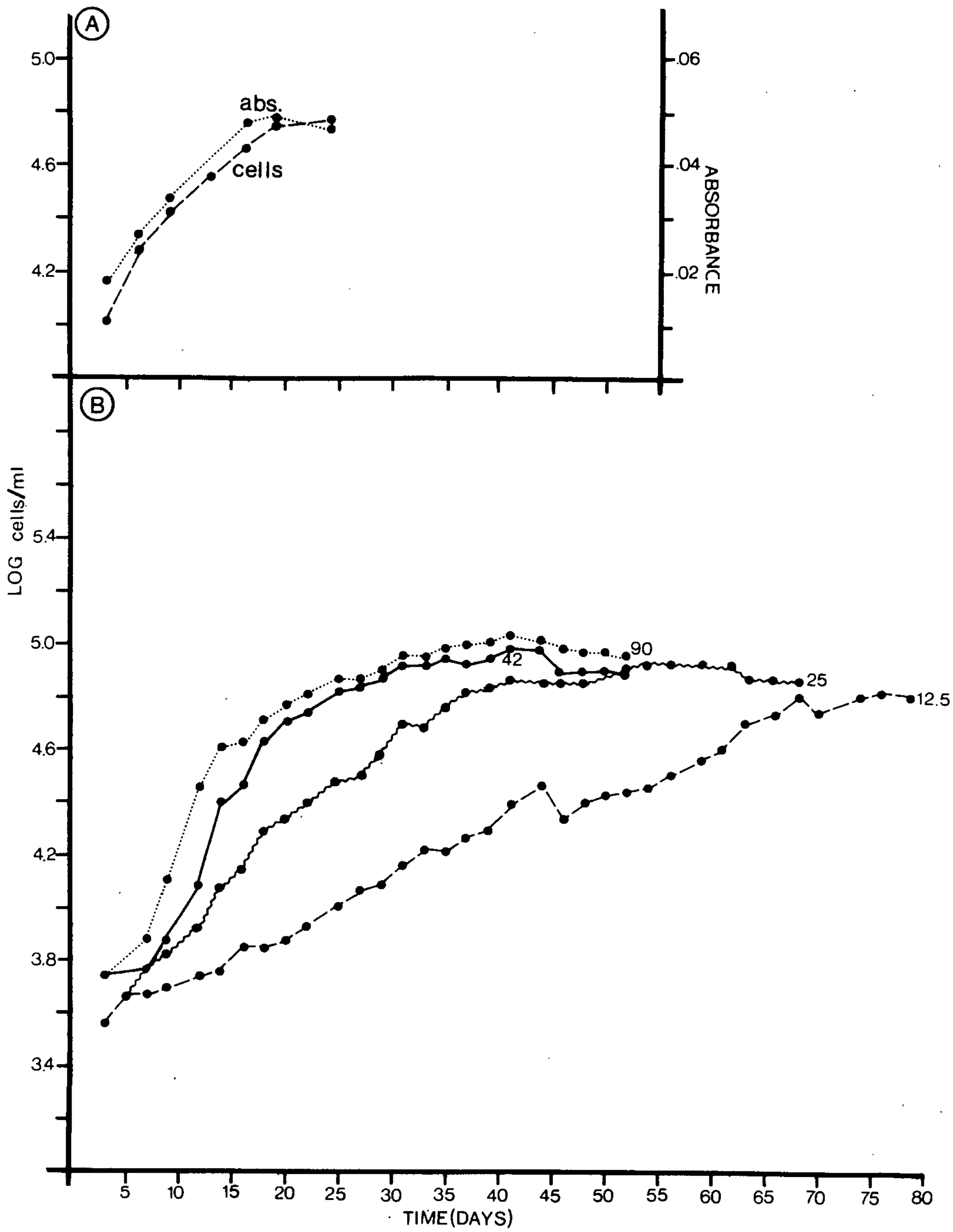

A
4.6
4.2
3.8
3.4
Como
Waris
B
LOG cells/ml
5.4
5.0
4.6
4.2
3.8
3.4
SPW
SPW+
SW
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
TIME (DAYS)

Figure 8 - Growth rate of Staurastrum inflexum (clone HC 18) in different media and at different irradiations

A. ECW 17-V-81, 45 $\mu E.m^{-1}.s^{-1}$, log cells.ml^{-1} (————), absorbance (·············)

B. SPW medium at 90 (·············), 42 (————), 25 (~~~~~~~) or 12.5 (-———-) $\mu E.m^{-2}.s^{-1}$. T=20°C, L:D=14:10



A
B
5.0
4.6
4.2
5.4
3.8
3.4
abs.
cells
.06
.04
.02
ABSORBANCE
LOG cells/ml
90
42
25
12.5
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
TIME(DAYS)

F. MORPHOLOGICAL VARIATION OF STAURASTRUM INFLEXUM (CLONE HC 18) IN DIFFERENT ENVIRONMENTAL CONDITIONS

1. CULTURE MEDIA

Clone HC 18 was cultured in different culture media for up to 30 days. Average measurements and radiation of the cells and standard deviations are given in Tables 8 and 9. An analysis of variance showed no significant difference in the L/l ratio ($F=4.61$; $P=0.05$) nor the number of triradiate cells ($F=1.41$; $P=0.05$) between the different media at 10, 20 and 30 days of culturing. The stock cultures used had 80-85% of triradiate, 10-12% of tetraradiate and 6-8% of dichotypical tri-tetraradiate cells.

The cultures in Como Lake water, ECW (Table 3), ECW without addition of nitrogen (ECW-N) or phosphate (ECW-P) contained mostly dead cells by day 30. Too few cells were present in enriched Como Lake water medium after 30 days, thus no measurements were made.

The cultures in Sand SPW medium showed a long lag phase; after 10 days, there were too few cells and measuring was begun only after 20 days.

In Pauline Monck's experiment (see Materials and Methods), all cultures showed a typical batch culture (without renewal of nutrients) growth curve, with an exponential phase tapering off to a plateau. Monck believed this result to be due to the biomonitor not allowing a free flow of nutrients through the membrane filter. If nutrients had been constantly replenished, they should have permitted a prolonged exponential growth. Measurements of 35 cells in each culture showed that the cells from the field were generally wider while their isthmus was slightly narrower. Average dimensions found by Ms. Monck were:

	L (μm)	l(cp) (μm)	Is (μm)	L/l
Field:	22	30	8	0.73
Laboratory:				
J.K.Henry Lake water	21	26	8	0.80
Munday Lake water	22	25	9	0.86
SPW medium	22	26	9	0.84

The most interesting results however, concern the variation in radiation. While the cells in field culture were almost all triradiate, the cells in laboratory cultures developed a pentaradiate form on which the spines were particularly well developed. Table 9 shows that clone HC 18 was either predominantly triradiate or ca. half triradiate and half tetraradiate, and that pentaradiate cells were rare.

I completed the analysis on the radiation of the cells in the samples collected by Pauline Monck (Table 10). In the laboratory cultures, the radiation passed progressively from a dominant triradiate form to a predominance of dichotypical cells composed of one triradiate and one pentaradiate semicell after 27 and 20 days, followed by a predominance of pentaradiate cells after 34 and 27 days respectively in J.K. Henry Lake water and SPW medium. In Munday Lake water, no sample was available for day 27 and that may explain the apparent more direct transition from triradiate to pentaradiate dominance, without a tripentaradiate dominant phase in between.

Monck analysed the amount of phosphate and nitrate present in the medium contained in the biomonitors and in the aquaria at the beginning and at the end of her experiment (ca. 40 days). She found that whereas the nitrate content decreased, the phosphate content unexpectedly rose both inside and outside the biomonitors. This increase varied from four to 50 times, giving final PO_4^{-3} concentrations in the aquaria of 11, 17 and 126 $\mu g.l^{-1}$ for J.K. Henry Lake water, Munday Lake water and SPW medium respectively. The PO_4^{-3} concentrations inside the biomonitors were 27, 6 and 130 $\mu g.l^{-1}$, respectively. The concentration of calcium either increased or remained constant. The pH increased by 1.00-3.00 (between 5 and 8).

Variations of pH from 4.55 to 6.00 were observed in J.K. Henry Lake and no pentaradiate cells were seen (Table 10) and thus pH cannot be the only answer. The increase in PO_4^{-3} level is also very interesting and provides another possible explanation for the observed change from a dominance of tri- to pentaradiate cells. No relation between phosphate and radiation has ever been shown in the literature.

Changes in radiation in laboratory cultures of <u>Staurastrum polymorphum</u> have been reported by Brandham and Godward (1965), in response to change in temperature, but the controlled temperature conditions used in the present study with the laboratory cultures preclude such an interpretation. Many pentaradiate cells possessed two prominent spines at the base of each side of the process, similarly to <u>St.</u> <u>incisum</u> Wolle (1884;

p. 132, pl. 41 fig. 12-14)

2. IRRADIATION

Three different irradiations were tested, that is 75, 42 and 25 $\mu E.m^{-2}.s^{-1}$. Measurements of the cells after 10, 20 and 30 days of culture are given in Table 8. An analysis of variance on the ratio L/l (F=0.76, P=0.05) revealed no significant differences between the treatments and the time of sampling. There does not seem to be any morphological change linked with the treatments, as seen through microscope examination.

More tetraradiate cells were present than in the experiment with the different culture media (section F.1). However, no significant difference was found by the analysis of variance for triradiate cells (F=0.10; P=0.05), and this is likely due to the use of a stock culture with a higher proportion of tetraradiate cells (ca. 68% triradiate, 23% tetraradiate and 9% tri-tetraradiate). The radiation pattern stayed basically the same throughout the experiment.

3. TEMPERATURE

Temperatures of 15, 10 and 5°C were tested and an analysis of variance failed to reveal any significant differences in the L/l ratio (F=0.86; P=0.05) nor the number of triradiate cells (F=3.34; P=0.05) between the treatments and the time of sampling (Tables 8 and 9). Radiation also stayed unchanged throughout the experiment and the triradiate form was constantly dominant. The stock had ca. 80% triradiate, 12% tetraradiate and 8% tri-tetraradiate cells. The percentage of the triradiate form was slightly lower at 5°C with a slightly higher percentage of tetraradiate and tri- tetraradiate dichotypical cells. This is in keeping with Brandham and Godward's (1965) experiment on radiation and temperature. An analysis of variance failed to reveal any statistically significant difference.

The cultures at 5°C grew very poorly. After 20 days, many of the cells were dead so that counts for 20 and 30 days are based on 10 cells instead of 35.

4. PH

Two different pH values were tested, 4.62 and 6.20. The SPW medium had an original pH of 4.62, whereas a pH of 6.20 was obtained by adding $CaCO_3$ to the SPW medium. No significant differences were shown between treatments and sampling dates through an analysis of variance of the L/l ratio (F=2.68 P=0.05; Table 8).

Radiation was variable, the tetraradiate form being more abundant in the cultures of pH 6.20 (Table 9). It should be noted that this experiment was started with the same stock culture as for the experiment on irradiation, and thus contained a higher proportion of tetradiate cells originally (ca. 68% triradiate, 23% tetraradiate and 9% tri-tetraradiate). However, whereas after 10 days, the proportion of tri- to tetraradiate cells was ca. 1:1 for pH 6.20, it was of ca. 3:1 for pH 4.62. An analysis of variance showed that there was significant difference in the number of triradiate cells at different pH (F=44.92; P=0.05). pH was measured two days after day 30 and had increased markedly in both media. In the pH 6.20 culture, the average was 8.57 and in pH 4.62, the average was 8.49.

pH cannot explain the change in radiation pattern, since the final pH was the same in both sets of cultures and other media made with Como Lake water had a pH between 6.00 and 7.00. Possibly the addition of $CaCO_3$ to raise the pH to 6.20 may have played a role in the changes observed. I am not aware of any other workers noting a relation between pH and radiation of desmids. The only other instance in the present study where a complete reversal of radiation pattern was observed is in a culture of clone HC 18 in SPW medium diluted in half with distilled water, and grown in a 500 ml Erlenmeyer flask. After one month, the radiation percentage changed from 83.5% of triradiate cells to 99.5% of tetraradiate cells. These results agree with those of Brandham and Godward (1965), which related higher level of radiation to slow growth. In their study, however, low temperature was responsible for the slower growth. In the present study, the poorer nutritive value of the diluted medium is postulated as responsible for the slow growth. However, this does not explain fully the changes observed because a change in radiation pattern would also have been expected in Como Lake water, ECW (Table 3) or Sand SPW media, which were relatively low in nutrients and showed signs of slow growth and deterioration.

TABLE 8

AVERAGE CELL DIMENSIONS OF STAURASTRUM INFLEXUM (CLONE HC 18) IN DIFFERENT ENVIRONMENTAL CONDITIONS
(after 10, 20 and 30 days of culturing; 25 cells x 3 replicates; Av= Average; S.D.= Standard deviation)

Treatment	L (μm)						l(cp) (μm)						Is (μm)						L/l		
days of growth	10		20		30		10		20		30		10		20		30		10	20	30
	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.			
T=20° C; 16:8 L:D Irradiation= 45 μE. $m^{-2}.s^{-1}$																					
SPW	23	1.59	23	1.38	22	1.51	28	2.04	28	2.22	27	2.24	8	0.65	8	0.57	8	0.53	0.83	0.83	0.83
SW	22	1.55	22	1.32	21	1.38	30	4.59	28	2.26	30	3.51	8	0.61	8	0.48	8	0.49	0.73	0.79	0.72
Como Lake water	21	1.17	20	1.69	20	1.15	25	2.68	24	2.62	25	2.74	7	0.55	7	0.48	8	0.57	0.82	0.83	0.81
ECW	20	1.21	20	1.24	--	--	25	1.86	26	1.99	--	--	8	0.69	8	0.55	--	--	0.80	0.78	--
ECW-N	21	1.28	21	1.32	20*	1.60*	27	2.39	27	1.96	27	2.24	8	0.70	8	0.50	8	0.45	0.80	0.78	0.75
ECW-P	22	1.26	21	1.54	21	1.17	27	2.85	27	2.60	26	2.57	8	0.68	8	0.59	8	0.60	0.79	0.77	0.78
Steamed SPW	22	1.37	21	1.26	23	1.22	26	2.70	25	2.02	26	2.17	9	0.66	8	0.55	8	0.63	0.89	0.85	0.87
Sand SPW	--	--	22	1.35	21	1.33	--	--	26	2.09	27	2.60	--	--	8	0.57	8	0.45	--	0.84	0.79
SPW medium; 16:8 L:D Irradiation= 45 μE.m^{-2}.s^{-1}; pH= 4.62																					
15°C	22	1.71	22	1.85	22	1.62	26	2.22	25	2.58	26	2.62	8	0.62	8	0.72	8	0.59	0.83	0.85	0.83
10°C	23	2.00	23	1.40	23	1.78	27	3.92	27	3.03	26	3.04	8	0.67	8	0.60	8	0.67	0.84	0.83	0.87
5° C	21	1.49	21	1.78	21*	1.02*	24	2.33	24	2.00	23*	1.91*	8	0.77	8	0.84	8*	0.69*	0.89	0.89	0.89

TABLE 8 (cont'd)

Treatment	L (μm)						l(cp) (μm)						Is (μm)						L/l		
days of growth	10		20		30		10		20		30		10		20		30		10	20	30
	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.	Av	S.D.			
SPW medium; T= 20°C; 16:8 L:D; pH= 4.62																					
75 $\mu E.m^{-2}.s^{-1}$	23	1.26	24	1.49	23	1.49	28	2.59	27	2.18	26	2.34	8	0.55	9	0.54	8	0.66	0.85	0.88	0.90
42 $\mu E.m^{-2}.s^{-1}$	23	1.27	23	1.17	23	1.12	26	2.13	26	1.90	26	2.55	8	0.61	9	0.58	8	0.57	0.85	0.88	0.90
25 $\mu E.m^{-2}.s^{-1}$	24	1.14	23	1.13	23	1.60	28	2.25	26	2.11	25	2.56	9	0.68	9	0.57	8	0.57	0.85	0.88	0.90
SPW medium; T= 20°C; 16:8 L:D; Irradiation= 45 $\mu E.m^{-2}.s^{-1}$																					
pH 6.20	23	1.31	23	1.50	22	1.39	27	2.13	26	2.77	25	2.27	8	0.69	8	0.62	8	0.75	0.85	0.89	0.90
pH 4.62	22	1.37	23	1.18	23	1.22	26	1.91	26	2.62	26	2.57	8	0.50	8	0.57	8	0.74	0.87	0.89	0.91

* 2 replicates

TABLE 9

CELL RADIATION OF STAURASTRUM INFLEXUM (CLONE HC 18) IN DIFFERENT ENVIRONMENTAL CONDITIONS (after 10, 20 and 30 days of culturing; + 3-rad. = triradiate; 4-rad. = tetraradiate; 3-4-rad. = dichotypical cell with one semicell triradiate and the other tetraradiate.)

Treatment	Percentage after 10 days			Total counted	Percentage after 20 days			Total counted	Percentage after 30 days			Total counted
	3-rad.$^+$	4-rad.$^+$	3-4-rad.$^+$		3-rad.	4-rad.	3-4-rad.		3-rad.	4-rad.	3-4-rad.	
T=20°C;16:8 L:D; Irradiation=45μE.m^{-2}.s^{-1}												
SPW	80.2	12.3	7.5	---	---	---	---	---	83.6	3.6	11.8	110
SW	---	---	---	---	---	---	---	---	---	---	---	---
Como Lake water	---	---	---	---	---	---	---	---	90.9	2.9	6.2	242
ECW	87.5	6.7	5.7	297	91.3	6.3	2.8	316	---	---	---	---
ECW-N	93.2	3.5	3.3	665	95.1	1.9	3.0	570	---	---	---	---
ECW-P	91.4	5.1	3.5	603	90.8	4.8	4.4	543	92.5	4.5	3.0	508
Steamed SPW	89.5	5.5	5.0	383	85.7	8.1	6.1	326	76.3	14.9	8.9	389
Sand SPW	82.7	14.8	2.5	81	93.1	6.6	0.5	421	97.1	1.3	1.6	380
SPW medium;16:8 L:D; Irradiation =45μE.m^{-2}.s^{-1}; pH=4.62												
15°C	86.7	8.1	5.1	349	80.0	7.9	12.0	401	84.6	6.6	8.8	418
10°C	82.1	11.5	6.4	590	86.8	8.3	4.9	456	83.2	9.9	6.8	558
5°C	78.5	11.6	9.8	617	81.7	9.9	8.4	407	77.1	11.5	11.4	384

TABLE 9 (cont'd)

Treatment	Percentage after 10 days			Total counted	Percentage after 20 days			Total counted	Percentage after 30 days			Total counted
	3-rad.+	4-rad.+	3-4-rad.+		3-rad.	4-rad.	3-4-rad.		3-rad.	4-rad.	3-4-rad.	
SPW medium; T= $20^{o}C$;16:8 pH=4.62												
75 $\mu E.m^{-2}.s^{-1}$	68.7	23.5	7.8	520*	61.9	28.0	10.2	619	61.0	26.4	12.6	647
42 $\mu E.m^{-2}.s^{-1}$	66.3	25.9	9.9	591	61.8	26.2	12.0	644	64.4	24.1	11.4	617
25 $\mu E.m^{-2}.s^{-1}$	63.7	27.4	8.9	697	62.1	23.2	14.7	640	63.7	24.1@	12.1	669
SPW medium; T= $20^{o}C$;16:8 L:D Irradiation=45 $\mu E.m^{-2}.s^{-1}$												
pH 6.20	44.8	47.4	7.8	724	51.1	46.5	5.8	757	45.2	47.9	6.8	930
pH 4.20	60.8	29.1	10.1	650	64.8	25.8	9.3	651+	62.6	30.5	8.8	658

* 5-radiate = 0.2%

@ 5-radiate = 0.1%

\+ 3-5-radiate = 0.2%

TABLE 10

CELL RADIATION OF STAURASTRUM INFLEXUM (CLONE HC 18) IN DIFFERENT MEDIA AND IN THE FIELD
(Culture data from the present study, field data from Monck (unpublished))

Medium	Age of culture	Radiation (%)										Total
	(days)	3	4	5	6	7	3-4	3-5	3-6	4-5	4-6	counted
J.K. Henry Lake water	0	88.9	11.1	---	---	---	5.6	---	---	---	---	36
	13	76.4	1.8	1.8	---	---	10.9	9.1	---	---	---	55
	20	44.3	6.6	7.6	---	---	6.6	34.0	---	---	---	106
	27	16.9	1.4	25.4	---	---	1.4	47.9	---	7.0	---	71
	34	16.0	4.3	47.9	---	---	4.3	24.5	---	3.2	---	94
	41	19.5	---	54.9	0.9	0.9	---	23.9	---	1.8	---	113
Munday Lake water	10	76.4	7.9	---	---	---	9.0	4.5	---	2.3	---	89
	13	47.8	2.2	8.7	---	---	8.7	30.4	---	2.1	---	46
	20	56.6	7.1	8.1	---	---	3.0	22.2	---	3.0	---	99
	34	15.7	1.0	54.9	---	---	2.9	21.6	---	3.9	---	102
	41	17.6	2.8	54.6	0.9	---	0.9	19.4	---	3.7	---	108
SPW medium	10	52.9	8.3	2.5	0.8	---	6.6	22.3	0.8	5.0	0.8	121
	13	28.7	6.6	7.8	---	---	8.4	23.4	0.8	4.2	---	167
	20	5.0	5.0	26.3	---	---	8.8	43.8	---	11.3	---	80
	27	8.3	2.5	47.1	---	---	0.8	37.2	---	4.1	---	121
	34	5.3	4.6	61.4	---	---	3.0	18.2	0.8	6.8	---	132
	41	2.9	1.9	66.0	---	---	3.9	15.5	---	9.7	---	103
J.K. Henry Lake	8-VI-81	68.9	13.7	---	---	---	17.5	---	---	---	---	---
	24-VII-81	97.4	0.7	---	---	---	1.9	---	---	---	---	---

G. SUMMARY OF RESULTS AND DISCUSSION

Neither laboratory nor field studies of morphological variation in desmids are perfect. Laboratory cultures cannot reproduce field conditions. Abnormalities of development are more commonly observed in culture than in nature. Furthermore, it has been shown that Staurastrum cells in culture are often stouter and may have shorter processes than in cells found in the field (Mix 1965, Förster 1967, Naef et al. 1978, Brook 1982, present study). Clonal cultures have however the advantage of providing genetically homogenous material.

Peterfi (1972) says that:

> "...one of the ways to establish the range of individual variation of Desmids would be that of clonal cultures; however, due to the fact that most Staurastra cannot be cultivated with usual methods, the only way remains the study of natural populations, although such observations cannot be carried out systematically, due to the scarceness of suitable populations, especially of rare species."

Peterfi's statement that most "Staurastra cannot be cultivated by usual methods" is very ambiguous. Work by Winter and Biebel (1967), Mix (1965), Förster (1967), Pickett-Heaps (1974), Starr (1978) have proved that Staurastrum can be cultivated. However, none of these authors has done extensive culturing of species showing different morphological characters.

It is true that a problem arises with natural populations. Morphological studies of desmid taxa done with field material rely on the presence of an abundant population of the taxon. Rare taxa are ignored and the only practical way of study is by having them multiply in culture and hopefully relate the clonal culture results to field material.

In this study, four hundred and ninety-eight clones were transferred to culture tubes from 1080 cells isolated in well slides. These cells represented mostly the genus Staurastrum although two taxa of the closely related genus Staurodesmus were also studied. A few other genera of desmids were isolated: Bambusina, Closterium, Cosmarium, Desmidium, Euastrum, Hyalotheca, Micrasterias, Netrium, Pleurotaenium, and Xanthidium, but were not investigated.

Of the 498 clones transferred from well slides to culture tubes, about 310 grew including 237 clones of Staurastrum and Staurodesmus. The rate of success of the isolation process was 310/1080 or 29%.

Twenty-eight taxa of Staurastrum and Staurodesmus were isolated. Some of the cultures grew slowly or had many abnormal cells and when repeated transfer into fresh medium failed to restore the health of the cultures, they were discarded. Of the remaining clones, 136 were measured and/or observed for morphological variation and percentage of radiation. Some species were represented by only one clone, others by over 20 clones.

V. <u>DESCRIPTION AND VARIATION OF SELECTED STAURASTRUM AND STAURODESMUS TAXA</u>

A. <u>INTRODUCTION TO TAXONOMIC TREATMENT AND KEY</u>

The results presented in Sections A to F are preliminary analyses and experiments which are used as a background for the study of the taxa presented in Chapter V. In Chapter V, observations made on the clonal cultures isolated from field samples and on the material collected in the field are compared with the literature.

The taxa have been arranged in groups of similar morphology and the two taxa of <u>Staurodesmus</u> are treated at the end. The original descriptions and illustrations of the taxa isolated in culture, and of the varieties and forms belonging to the same species, are given whenever possible. Each of these is examined in regard to the variation observed in clonal cultures and a literature review. Related species are also discussed. The taxonomic treatment is very conservative and it is considered a priority to fit specimens to existing taxa, rather than describe new taxa on minor variations. The volume by Prescott <u>et al.</u> (1982) on <u>Staurastrum</u> (including <u>Staurodesmus</u>) became available at the last stage of completion of this thesis in December 1983 (despite the 1982 publication date). Since it constitutes a major and long awaited contribution to the taxonomy of <u>Staurastrum</u>, the book was examined and notes were added to my work under relevant taxa. For example, the synonymy between <u>St. proboscideum</u> (Brébisson) Archer and <u>St. borgeanum</u> Schmidle and the consequent new combinations (St. proboscideum f. minus (Schmidle) Prescott, Bicudo and Vinyard and St. proboscideum var. compactum (Grönblad) Prescott, Bicudo and Vinyard) proposed by Prescott et al. (1982) were already included in my thesis and minor changes had to be made. There are also disagreements between my work and Prescott and coworker's and these are discussed under the appropriate taxa.

Data on measurements and radiation (Tables 11-30) as well as SEM and light microscope photographs (Plates 1-18) follow each taxon studied in clonal culture. Drawing plates (Plates A-R) are given in Appendix D. Abbreviations were detailed in Chapter III, Section B.6. Figure 1 in the introduction illustrates the main terms used.

A key to the taxa studied in clonal cultures is given hereafter (Staurastrum is abbreviated as St. and Staurodesmus as Std.):

1a. Cell with the angles not extended into processes..........2

2a. Angles not tipped with spines........................3

3a. Cell wall ornamented with granules..............4

4a. Semicell pyramidal

St. muricatum var. muricatum

4b. Semicell elliptic to oval

St. alternans var. alternans

3b. Cell wall ornamented with spines................5

5a. Spines covering most of the cell except the isthmus

St. brebissonii var. brebissonii

5b. Spines arranged in a regular pattern; only two of spines on the front of the semicell

St. gladiosum var. gladiosum

6a. Cell wall ornamented with granules

St. avicula var. avicula

6b. Cell wall smooth................................7

7a. Apex convex; spines when present straight or convergent

Std. mucronatus var. delicatulus

7b. Apex concave or straight; spines when present divergent or upwardly directed

Std. dejectus var. dejectus

1b. Cell with angles extended into processes..................8

8a. Cell with accessory processes........................9

9a. Accessory processes apically inserted only.....10

10a. One accessory process at each angle

St. furcigerum var. furcigerum

10b. Two accessory processes at each angle

St. furcigerum f. eustephanum

9b. Accessory processes angular as well as apical

St. senarium var. senarium

8b. Cell without accessory processes....................11

11a. Processes divergent..........................12

12a. Processes deeply undulated

St. crenulatum var. *crenulatum*

12b. Processes denticulated..................13

13a. Base of semicell swollen

St. manfeldtii var. *parvum*

13b. Base of semicell not swollen but slanted

St. tetracerum var. *tetracerum*

11b. Processes convergent..........................14

14a. Cell usually pluradiate

15a. Cell about as long as wide

St. sexcostatum var. *productum*

15b. Cell wider than long...............16

16a. Cell small; width with processes under 50 μm

St. arachne var. *arachne*

16b. Cell bigger; width with processes over 50 μm...................17

17a. Typically six or seven processes; strong double verrucae on base of processes

St. ophiura var. *ophiura*

17b. Typically five or six processes; double verrucae on base of processes not as strong when present

St. pentacerum var. *pentacerum*

14b. Cell tri- or tetraradiate................18

18a. Processes tipped with two strong spines

St. grallatorium var. *forcipigerum*

18b. Processes not tipped with two strong spines........................19

19a. Subapical spines or double verrucae present

St. vestitum var. *vestitum*

19b. No subapical spines or double verrucae........................20

20a. Cell typically twisted at the isthmus; apical double verrucae rarely present

St. inflexum var. *inflexum*

20b. Cell not twisted at the isthmus; apical double verrucae usually present

St. proboscideum f. *minor*

B. STAURASTRUM BREBISSONII VAR. BREBISSONII

St. brebissonii (Brébisson) Archer in Pritchard 1861 (p. 739)

Basionym: St. pilosum Brébisson 1856 (p. 141; pl. 2, fig. 49)

Pl. A Fig. 1:

De Brébisson's description is:

> "S. majus, hispidum; hemisomatiis ovato-lanceolatis, a latere secundario triangularibus, angulis rotundatis.
> "Falaise. Rare.
> "Les aiguillons ou poils dont la surface de cette espèce est couverte sont plus longs et plus nombreux vers les angles. La face des hémisomates où se trouve la suture est assez convexe, de sorte qu'un vide prononcé se trouve entre les angles en regard, ce qui n'a pas lieu dans le St. hirsutum dont les hémisomates sont presque contigus dans toute la face de la suture. Le Phycastrum pilosum Naegeli l.c. t. VIII, A4, ne peut se rapporter ici. Ses poils sont plus épars et terminés par un globule."

St. brebissonii was first described under the name St. pilosum by de Brébisson 1856 but was later transferred to St. brebissonii since Phycastrum pilosum (named Staurastrum pilosum by Archer in Pritchard 1861, p. 739), had already been used by Nägeli 1849 (p. 126; pl. 8A, fig. 4) for a different taxon.

This species was not common in the Lower Fraser Valley. It was found in Jacobs and Lost Lakes. Stein and Borden (unpublished) list eight records of St. brebissonii var. brebissonii for British Columbia, including Lost and Munday Lakes and three records for the variety brevispinum W. West but none from the lower mainland near Vancouver. St. erasum (discussed later) is not recorded. St. brebissonii was first found in Normandy (France) but has since been reported from South America to the Arctic.

Clone examined: HC 70 from Jacobs Lake, 26-VII-79 (see Table 11).

In clone HC 70, the semicells are oval to oval-lanceolate in shape with a wide-open acute sinus and short spines forming concentric rings around the angles, about three quarters of the way down the semicell, the area just above the isthmus being free of spines (Pl. 1 Fig. 1-3). The centre of the apex where the concentric rings of spines meet, is free of ornamentation (Pl. 1 Fig. 4). The spines vary somewhat in length (Pl. 1 Fig. 4, 5) and tend to be longer at the angles (Pl. 1 Fig. 6), measuring about 1.5-3 µm. Their extremity is obtusely rounded or truncate (Pl. 1 Fig. 5-7). On Pl. 1 Fig. 6 and 7, pore openings can be distinguished on the cell wall between the spines. The dimensions of the clone are given in Table 11. The cells of clone HC 70 are on the average slightly longer than wide as shown by the L/l ratio. Only triradiate cells were seen in culture and field material (Table 11).

West _et al._ (1923; p. 62) state that there is a need for good figures of this taxon and that the interpretations given by different authors vary considerably. This variation is mostly observed in the shape of the semicell and sinus. Croasdale (1973) for example, shows in her fig. 14, a cell with rounded angles and sinus, whereas the alga in fig. 13 has definitely elongated angles and acute sinus. Thomasson (1952) shows an alga with rounded sinus in fig. 19, but in 1959, he represents a specimen with acute sinus (fig. 5). These variations are important in the distinction between _St. brebissonii_ and _St._

erasum Brébisson as will be discussed later.

Most authors show an apex free of spines in vertical view (West et al. 1923, pl. 138 fig. 1; Lowe 1923, pl. 4 fig. 12; Grönblad 1942, pl. 4 fig. 15, 18; Croasdale 1957, pl. 5 fig. 89; 1965, pl. 8 fig. 5, 6; Förster 1970, pl. 27 fig. 15; Coesel 1979, pl. 26 fig. 6, 7), although in Croasdale (1973, pl. 18 fig. 13, 14), the apex is entirely covered with sparse spines. The length of the spines also seems to vary slightly, as will be discussed under var. brevispinum W. West.

1. Proposed synonyms of St. brebissonii var. brebissonii

St. brebissonii ?forma minor Boldt 1888

St. brebissonii var. brevispinum W. West 1892

St. erasum de Brébisson 1856.

a) St. brebissonii ?forma minor Boldt 1888 (p. 36; pl. 2, fig. 45) Pl. A Fig. 2:

"...Long. 43,2-45,6 μ; lat. 38,4-42 μ; lat. isthmi 13,2-15,6 μ..."

The type locality of this forma is Greenland. No further record was found in the literature, although Grönblad (1942) places with f. minor a record by Borge (1930) measuring : L(ssp) = 44.5-54.3; l(ssp) = 40-57.2; l(csp) = 44.8-65.8; Is = 13-20; Sp = 2.5-4 μm. This is too big to be f. minor. Furthermore, Borge notes that his taxon corresponds well to West et al.'s (1923; pl. 138, fig. 1) St. brebissonii var.

brebissonii.

Neither de Brébisson (1856) nor Archer (1861) gave dimensions for the type species. If one accepts West et al.'s (1923) dimensions for the type species (L(sp):34-48; l(sp): 40-62; Is: 13; Sp (at angles): 2.5 µm), Boldt's specimens are included in the species range and there is no need for this new forma. It is proposed to include the forma, which was indeed published by Boldt preceded by a question mark, as synonym of variety brebissonii .

b) St. brebissonii var. brevispinum W. West 1892b (p. 731; pl. 9, fig. 26) Pl. A Fig. 3 :

> "Var. spinis brevioribus et validioribus.
> "Long. 49 µ; lat. s. spin. 42.5 µ; lat. c. spin. 45 µ; lat. isthm. 17.5 µ."

W. West first recorded this alga from the Lake District in England. It has been found in North America and Europe. Although W. West does not give the length of the spines of the alga, it can be calculated from the difference between the width with and without spines: the angular spines measure ca. 1.25 µm. Cells of clone HC 70 have angular spines of ca. 1.5-3 µm, which is slightly longer but similar to W. West's dimensions for var. brevispinum. Růžička (1957) found specimens belonging to var. brevispinum with maximum spine length of 1.5 µm. West et al. (1923; p. 62) give 2.5 µm for the length of the angular spines in the type species.

From the study of clone HC 70, the length of the spines appears to be a feature which shows considerable variation and thus is not a good taxonomic criterion (Pl. 1 Fig. 5, 6). Comparison of published data for both varieties brevispinum and brebissonii show that the variations in the length of the spines underlying the creation of var. brevispinum are minute. Published illustrations of these two varieties are often impossible to distinguish from each other. For example, Croasdale (1973; pl. 18, fig. 13) shows a cell of St. brebissonii with spines which appear shorter than in Schumacher's (1969; fig. 101) illustration of var. brevispinum. Croasdale describes her specimen has having short spines.

In the light of the difficulties involved in distinguishing between the two taxa, and of the variability of the distinctive characteristic, I propose that var. brevispinum be considered as a simple variation of St. brebissonii and not as a given taxonomic unit.

c) St. erasum Brébisson 1856 (p. 143; pl. 1, fig. 28) Pl. A Fig. 4 :

> "S. granulosum; hemisomatii ovoideis granulosis, e dorso convexis, angulis rotundatis subspinulosis.
>
> "Falaise. Rare.
>
> "Cette espèce pourrait être placée également près des St. rugulosum, dilatatum et margaritaceum auxquels elle ressemble par sa surface granulée. Elle s'en distingue par quelques épines très courtes, manquant quelquefois, qui se trouvent au sommet de ses angles et un peu au-dessous."

St. erasum and St. brebissonii (= St. pilosum Brébisson) were both described by de Brébisson in 1856 (Pl. A Fig. 1, 4). The type locality of St. erasum is Normandy (France), but further publications list the species from Argentina to the Northwest territories.

Although no dimensions are given for either species, the difference shown in the shape of the semicell seems to agree with Grönblad's analysis of the species which is discussed hereafter.

Grönblad (1927) recognizes that the original illustration of St. brebissonii has lead to misinterpretation and indeed that the St. brebissonii concept seems to have taken many forms in the literature. Grönblad decides to abide by the description of West et al. (1923) who say that the depressed semicells, open sinus and longer spines at the angles are the main taxonomic characteristics of the species. These features are fairly well defined in the original figure of each taxon (Pl. A Fig. 1, 4). St. brebissonii also usually has fewer and shorter spines than St. erasum. Grönblad (1942) later reviewed his decision and established the following distinctive factors between St. brebissonii and the closely related St. erasum. St. brebissonii is larger with a width of about 70 µm compared to 40 µm for St. erasum. It is also furnished with spines, while St. erasum has granules on the semicells and short spines at the angles. The semicell of St. brebissonii is oval-lanceolate with elongated angles while it is elliptic with rounded angles in St. erasum. Croasdale (1962; pl. 7, fig. 131), St. erasum morpha parva has definitely pointed as opposed to rounded angles as shown by de Brébisson (1856, fig. 28; Pl. A Fig. 4) and as emphasized by Grönblad (1942).

It may sometimes be very difficult to establish a distinction between these two similar species and that may explain the fewer records of _St. erasum_. Plate 1 Fig. 8 shows one isolated semicell and one cell from which one semicell became folded during the processing of the sample for SEM observation. Although the isolated semicell would appear to have elongated angles, the other semicell would better be described as elliptic with rounded angles.

Original descriptions of _St. erasum_ and _St. brebissonii_ are not explicit enough and refer to characteristics which are too variable to permit a clear distinction between the two species. Both species were validly published in the same publication, that is on the same date, thus the principle of priority does not apply. There have been fewer records of _St. erasum_ than of _St. brebissonii_ , and I suggest that _St. erasum_ be included as a synonym of _St. brebissonii_ var. _brebissonii_.

2. Other infraspecific taxa of _St. brebissonii_

The following taxa appear distinct from _St. brebissonii_. They do not present any taxonomic characters observed in variations of clone HC 70 and thus there is no reason not to accept them.

St. brebissonii var. _heteracanthum_ W. et G.S. West 1896b

St. brebissonii var. _paucispinum_ Smith 1922

St. brebissonii var. truncatum Grönblad 1926

St. brebissonii var. laticeps Grönblad 1942

St. brebissonii var. brasiliense Grönblad 1945

St. brebissonii var. curvispinum Grönblad 1945

St. brebissonii var. maximum Cedercreutz 1932

a) St. brebissonii var. heteracanthum W. et G. S. West 1896b (p. 260; pl. 16, fig. 26) Pl. A Fig. 5:

"Minus, semicellulis spinis ad angulum unumquenque paucioribus, cum spinis tribus validioribus quam spinae reliquae; a vertice lateribus subrectis.

"Long. 35 μ; lat. sine spin. 35 μ, cum spin. 50 μ; lat. isthm. 11.5 μ."

This taxon was first found in North America. No further records were found. With its spines grouped at the angles, this taxon differs considerably from the type species.

b) St. brebissonii var. paucispinum Smith 1922 (p. 350; pl. 10, fig. 25; pl. 11, fig. 1-5) Pl. A Fig. 6 :

"Cells small, with three or four large spines at the angles and one or two small spines on the apex of the semicells just within the angles.

"Length 31-34 μ; breadth (without spines) 32-40 μ, (with spines) 45-52 μ; breadth isthmus 8.5-10 μ.

"This variety is quite similar to the variety heterocanthum (sic) but differs in the possession of only one or two smaller spines at the cell angles and in a general occurrence of four large spines at the angles."

Smith first found this taxon in the Muskoka area of Ontario (Canada). No further record was found. This taxon differs significantly from the type species. Only angular spines are present and the spine pattern is not characteristic of St. brebissonii. Only the shape of the semicell and of the isthmus are similar. It is very close to var. heteracanthum . The difference between the two taxa rests solely on minor variation of spine characteristics. The description of that variety could possibly be widened to accommodate the different features of var. paucispinum, that is the presence of "only one or two small spines at the cell angles" and the " general occurrence of four large spines at the angles." (Smith 1922). A more thorough investigation of both taxa is necessary.

c) St. brebissonii var. truncatum Grönblad 1926 (p. 27; pl. 2, fig. 85, 86) Pl. A Fig. 7:

> "(syn.=? S. pilosum loc. cit. (W & W, Mngr.V) quoad pl. 138 f. 1). Differt a forma typica semicellulis fere trapeziformibus apice truncata dorso altius convexo; membrana spinis densius obsessa. Long. 41, lat. 46, isthm. 17 μ..."

This variety is not common; Grönblad (1926) first found it in Europe and Croasdale (1957) recorded it in Alaska. It differs from the type by the elevated straight apex which gives a trapeziform appearance to the semicell.

d) St. brebissonii var. laticeps Grönblad 1942 (p. 41: pl. 4, fig. 16, 17) Pl. A Fig. 8:

> "Semicellulae latissimae lateribus basalibus convexis usque ad angulos apicales protractos divergentesque; apice subrecto (interdum medio protuso); a vertice visae triangulares lateribus retusis angulis subprotractis angustis. Membrana aculeolis parvis in ordinibus concentricis dispositis, in angulis ipsis aculeis nonnullis maioribus. Long. 53 lat. 70 ist. 19 μ."

This taxon was first found by Grönblad in Swedish Lappland and later (Grönblad 1952) in West Greenland. The diverging angles of this variety are very distinctive. The taxon is similar to St. brebissonii var. brebissonii in the open sinus, concentric disposition of the short spines around the angles and in the longer angular spines.

e) St. brebissonii var. brasiliense Grönblad 1945 (p. 24; fig. 198) Pl. A Fig. 9:

> "Semicellulis latioribus, apice medio convexo, angulis quasi protractis; aculeis angulorum curvatis. Sine spin. long. 61, lat. 59, ist. 17."

This taxon was first found in Brazil and has also been recorded in North America and Europe. It has long curved angular spines.

f) St. brebissonii var. curvispinum Grönblad 1945 (p.24; fig. 199) Pl. A Fig. 10:

> "Cellulis non depressis, semicellulis suboblongis, sinu late aperto, aculeis numerosioribus, omnibus curvatis. Sine spin. long. 95, lat. 84, ist. 23."

This variety was first found in Brazil and appears rare. Spinal features are similar to those of var. brasiliense . The spines are however more numerous, as stated by Grönblad and shown in his fig. 199 (Pl. A Fig. 10). The semicells of var. *curvispinum* are also bigger than var. *brasiliense*.

g) *St. brebissonii* var. *maximum* Cedercreutz 1932 (p. 245; textfig. 14, 15).

Neither de Brébisson nor Archer in the description of the species, gave any dimensions for *St. brebissonii*. West *et al*'s (1923) dimensions for *St. brebissonii* are given under *St. brebissonii* f. *minor* (p. 90). Unfortunately, the original description for var. *maximum* was not available, but Thomasson (1952) gives Cedercreutz's dimensions as: "long. 87 μ, lat. 87 μ", which indicates it is definitely larger than the type species. The dimensions of Thomasson's specimens from Scandinavia are between var. *maximum* and var. *brebissonii*. Grönblad (1936) reported a specimen from Russia which is in the dimension range of var. *maximum*.

Size is not usually a good taxonomic criterion, although the variation here reported is almost a doubling in size and can hardly be ignored. Cedercreutz's variety appears to be a distinct entity from *St. brebissonii* var. *brebissonii*.

TABLE 11
CELL DIMENSIONS AND RADIATION OF ST. BREBISSONII
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(csp) (µm) Average	Range	S.D.	C.V.	l(csp) (µm) Average	Range	S.D.	C.V.	Is (µm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3
70	Jacobs 26-VIII-79	41	35-45	2.37	5.71	37	33-42	2.36	6.38	14	12-17	1.26	9.03	1.12	100

Field material

Source	L(csp) (µm)	l(csp) (µm)	Is (µm)	L/l	Radiation 3
Jacobs 26-VII-79	38	36	9	1.05	X

Plate 1

St. brebissonii var. *brebissonii*

SEM photographs

1-8. Clone HC 70

1, 3. Cell in front view showing the shape and the spine pattern

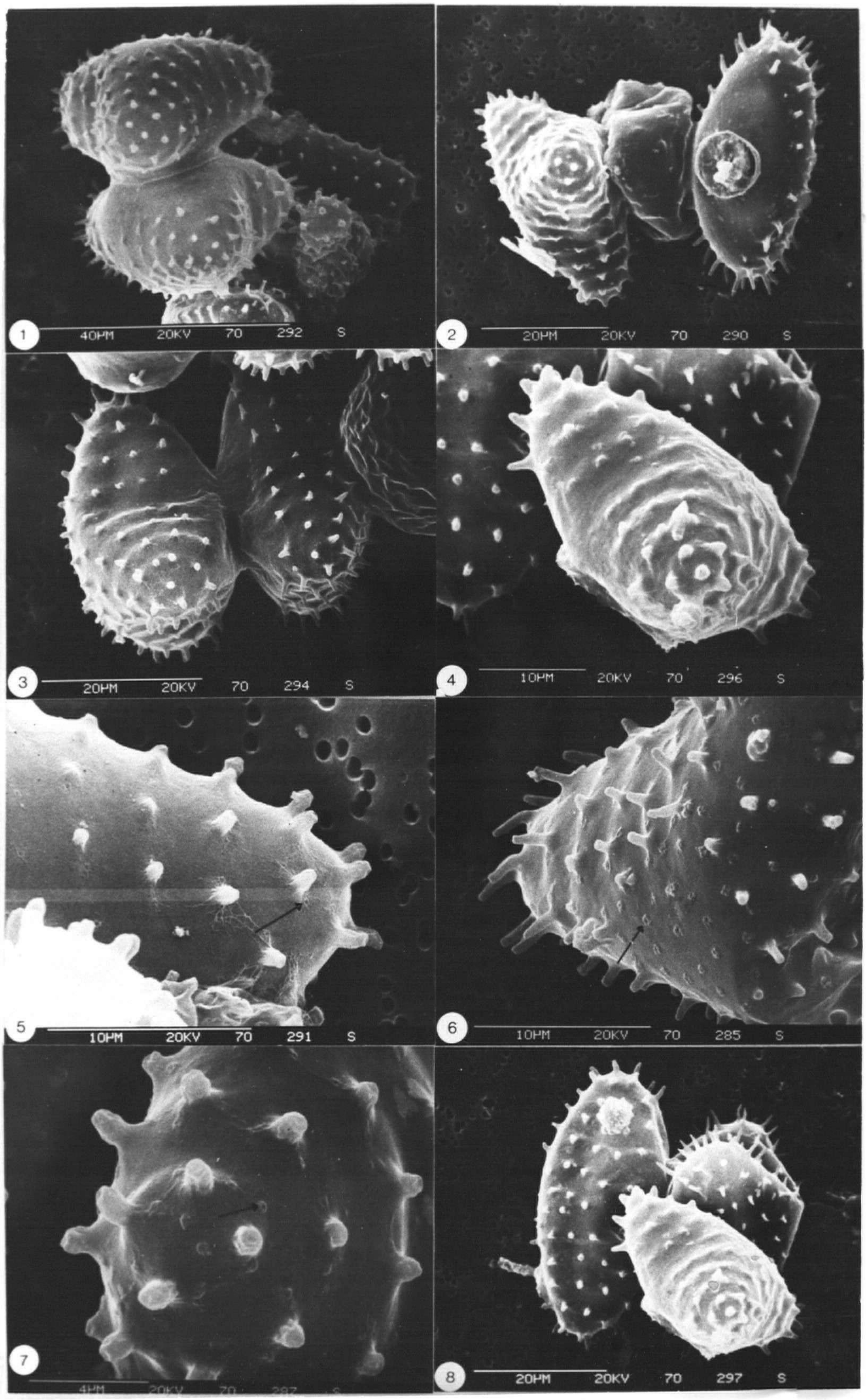
2. Two semicells: left, in front view; right, in basal view showing the spine pattern above the isthmus

4. Isolated semicell in front view (enlarged view of Fig. 8)

5-7. Detailed view of angular spines; the arrow indicates the pore openings

8. Isolated semicell with elongated angles and whole elliptic cell (one semicell folded) with rounded angles

119 A



1
40PM 20KV 70 292 S
2
20PM 20KV 70 290 S
3
20PM 20KV 70 294 S
4
10PM 20KV 70 296 S
5
10PM 20KV 70 291 S
6
10PM 20KV 70 285 S
7
8
20PM 20KV 70 297 S

C. STAURASTRUM GLADIOSUM VAR. GLADIOSUM

St. gladiosum Turner 1885 (p. 938; pl. 16, fig. 21) Pl. A Fig. 11:

> "Species with reniform segments; spines strong, arrayed in series, a few smaller ones scattered; end view triangular, with gently concave sides; ends broadly rounded with six to eight large spines at each; sinus open, expanding rapidly...
>
> "Long. 49μ = .0019 in.; lat.= long.; lat. isthmi 11-12 μ = .00043-47 in."

From the literature, St. gladiosum appears to be a common species which has been reported from different areas of the world. In the present study, St. gladiosum was found in Jacobs, Lost, Munday, Como and Placid Lakes, although it was never very abundant in any of them. Stein and Borden (unpublished) list 35 records of St. gladiosum for British Columbia, including Jacobs, Munday, Lost and Como Lakes; no varieties are recorded. St. teliferum has been recorded 12 times, including Jacobs creek, Como, Lost and Munday Lakes. St. claviferum was found once in the Nanaimo district.

Clones examined: HC 71, 110 from Lost Lake 5-IX-79; HC 496 from Munday Lake 1-XI-80; HC 323 from Como Lake 27-VI-80. Clones discarded because many cells were deformed: HC 132, 135, 148 from Lost Lake, 5-IX-79 (Table 12).

Clones of St. gladiosum have oval semicells with rounded angles, slightly convex apex and an open acute sinus as seen in front view (Pl. 2, Fig. 1, 5). The cells are almost as long as broad so that the L/l ratio is close to 1 (Table 12). A series of strong spines, ca. 3-8 μm are present. The spines increase gradually in length towards the cell angles (Pl. 2, Fig. 2). While the pattern of spines as well as their length and stoutness, varies from cell to cell, it always assumes an orderly arrangement. In front view, there are 11-15 spines lining the margin of the apex between the angles (Pl. 2 Fig. 1,5). Two rows of spines are usually present on the front of the semicell, the one closer to the apex running from one angle to the other, whereas the second row just below is restricted to the angles and usually has a gap in the middle (Pl. 2 Fig. 3, 4). The rest of the semicell is free of ornamentation. The spines are widely spaced and not as numerous as in St. brebissonii var. brebissonii. When observed with the light microscope (100 x) or SEM, the front view may show two diverging angular spines, one above the other (Pl. 2 Fig. 3, 6).

The vertical view shows straight to slightly concave margins. The regularly disposed apical spines show some variation in their arrangement (Pl. 2 Fig. 3, 4; Pl. B Fig. 8, 9). There are three apical spines just inside the margin, with the central spine usually placed slightly above the other two and closer to the centre of the apex. Generally, there is a ring or triangle of 12 spines surrounding the centre of the apex, which usually shows some pore openings (Pl. 2 Fig. 4). At high magnification (6700 x) the pore openings appear slightly elevated with an opening in their centre (Pl. 2, Fig. 2). Midway between the angles, on the subapical margin, there is usually an area free of spines bordered by the spines located closer to the angles (Pl. B Fig. 8, 9). The width of this area varies slightly so that, at times, it appears only as a slightly wider space between the spines, halfway between the angles.

Only triradiate cells of St. gladiosum have been found in clonal cultures and field material. No other pattern of radiation or dichotypical cells have been observed. The same is true for literature reports consulted.

Dimensions obtained for clonal cultures and field specimens are given in Table 12. Both in clonal culture and field material, the cells are about as long as broad. The spines of field material are longer (up to 8 µm) than cultured material (up to ca. 6 µm). In field material, the exact point of insertion of the spines is difficult to distinguish because it is obscured by the protoplasm content of the cells.

Variation in size is observed among clonal cultures, clone HC 71 being the largest (46 x 47 µm), followed by clone HC 496 (39 x 39 µm) and clone HC 110 (38 x 35 µm). Despite the difference in size, the L/l ratios are similar. In the field, cells are slightly bigger, with most cells above 40 µm and one specimen above 50 µm in length and width (Table 12). A cell collected at the same time and place as clone HC 71 measured 38 x 38 µm.

Illustrations of St. gladiosum var. gladiosum in the literature basically agree with Turner's original drawing as well as with the findings of the present study. Brown (1930; pl. 14, fig. 84, 85) and Hinode (1962; fig. 92, 93) present only one row of spines lining each of the three sides of the semicell in apical view. There are no other spines between the central ring and the margin of the semicell. Prescott (1940; fig. 7, 8) represents the subapical spines covering the whole margin of the apical view, except for one side where there is a gap halfway between the angles. He also shows an apical ring of short spines which, contrary to Turner's original figures, is composed of more than three spines between each angle. Krieger (1932; pl. 15, fig. 14), Scott and Prescott (1961; pl. 56, fig. 1), Hinode (1971; fig. X:3) and Croasdale and Grönblad (1964; pl. 18, fig. 14) illustrate two rows of apical spines in vertical view. In Croasdale and Grönblad (1964) however, the row of spines closer to the margin is missing on one side, so that the apical ornamentation is composed of one central triangle of spines and one row of spines between the margin and this central triangle, on two sides only. This variation has been observed in clonal culture (Pl. 2 Fig. 7, 8).

1. Proposed synonyms of St. gladiosum var. gladiosum

   St. breviaculeatum Smith 1924b

   St. claviferum W. et G.S. West sensu Bourrelly 1966

a) St. breviaculeatum Smith 1924b (p. 78; pl. 70 fig. 10-18) Pl. A Fig. 12:

> "Cells small, length and breadth about equal, deeply constricted, sinus acute-angled and with apex subacuminate, isthmus narrow; semicells transversely elliptic, dorsal margin sometimes flattened in the median portion; lateral angles broadly rounded and bearing four short quadrately arranged divergent spines; cell body with two transverse rows of 4-7 spines, the lower row half way between the isthmus and the cell apex, the upper midway between the lower row

and the apex; cell apex with median portion bare and with margins towards the angles with 3-4 outwardly pointing spines. Vertical view triangular, sides of cells emarginate and angles broadly rounded and bearing four quadrately arranged short divergent spines; center of cell body with a triangular ring of spines, the sides of the triangle lying parallel to the margins of the cell and each side composed of three outwardly facing spines, angles of the central triangle connected to the corresponding angle of the cell by a short row of spines; lateral margins of cells with 6-8 erect spines and a second arcuate intramarginal row of spines that are of similar size and arrangement; outline of cell slightly emarginate between adjacent spines. Chloroplast with a small central mass and two laminate blades running to each angle of the cell; pyrenoid single and central... "Cells 38-46 μ long with spines, 36-42 μ long without spines; breadth with spines 37-55 μ, without spines 34-44 μ; isthmus 9-13 μ broad; spines 2-5 μ long."

St. breviaculeatum has been found in Canada and the United States but does not seem to have been reported in Europe. Smith's figures 10-15 represent the type species, while figures 16-18 are of a forma with shorter spines (Pl. A Fig. 12). Smith's taxon presents basically the same feature as St. gladiosum var. gladiosum ; the shape of the cell, dimensions and spine pattern are similar. Smith notes the presence of two sets of two spines at each angle and, although this characteristic is distinguished on his fig. 11, it is not as obvious on fig. 10 on the right side of the upper semicell and certainly not on fig. 16 and 17. Plate 2 Fig. 3, 5 and 6 of clones HC 71, 148 and 496 illustrate a similar appearance of the spines at the angles. In Pl. 2 Fig. 6, the level of focus permits only two spines to be seen in front view. Smith's illustrations (fig. 10, 11) probably represent two spines overlapping each other at each angle; that is, one spine behind the other. Other publications of the species since Smith, do not show Smith's pattern as illustrated in his fig. 11 (see Taylor 1935b, pl. 2 fig. 5; Prescott 1966, pl. 8 fig. 10, 11; Thomasson 1962, fig. 35, 36).

Smith states that St. breviaculeatum differs from the St. teliferum-setigerum group by having shorter angular spines which are also the same size as those on the cell body. Although the difference is slight, specimens observed throughout this study usually had spines which show a gradual elongation towards the angles (Pl. 2 Fig. 3, 5). Observation and measurement of the spines on Smith's figures 11-14, prove that his specimen also showed this slight difference of the spine length at the angles.

West et al. (1923, p. 53) distinguish St. setigerum from other spiny Staurastrum by the presence of two kinds of spines: delicate ones on the body of the semicells and stouter ones at the angles. Whereas this is probably the characteristic Smith was trying to emphasize, his statement that all the spines in St. breviaculeatum are of equal length appears inaccurate based on his own illustrations.

The spine pattern of St. breviaculeatum in apical view cannot really be distinguished from that of St. gladiosum. There is a central ring or triangle of spines with an "arcuate" row between the margin and the central triangle. This is very similar to the observations of this study of three apical spines with the centre one inserted slightly more towards the apex and a central triangle of spines. The spine pattern of St. breviaculeatum in front view also corresponds to observations from the present study. Since there does not seem to be any well defined taxonomic criterion to distinguish between St. gladiosum Turner and St. breviaculeatum G.M. Smith, I propose St. breviaculeatum as a synonym of the older St. gladiosum.

Prescott et al. (1982) propose to include St. breviaculeatum as a synonym of St. claviferum W. et G.S. West 1896b but I do not agree with them. The spines in St. claviferum are more numerous than in St. breviaculeatum and in vertical view, they are not regularly arranged. Whereas there are "two transverse rows of 4-7 spines" (Smith 1922) on the cell body of St. breviaculeatum in front view, there are two to four rows of spines in West and West's figure. In apical view, the spines are said to be irregularly arranged ("cum spinis brevibus subirregulariter ordinatis") by the Wests (1896b), whereas Smith describes an orderly arrangement of a central triangle of spines connected to each angle by one row of spines. Prescott et al. (1982; p. 159 pl. 371 fig. 6) give only Smith's figures of St. breviaculeatum and not the original illustrations by West and West for St. claviferum.

Two varieties of St. breviaculeatum have been described, but no conclusions can be made until thorough comparisons with other related species is carried out.

i. St. breviaculeatum var. karelicum Grönblad 1936 (p. 10; fig. 23-24) Pl. B Fig. 1:

> "Differt a fronte visum angulis plus rotundatis, semicellulis ellipticis, spinis plus numerosis; a vertice lateribus retusis; itaque cellulis minoribus.

Long. 25, lat. 25, ist. 9 μ."

The spine pattern of this variety found in North Russia differs considerably from that described by Smith (1924) for the species. The spines are more numerous in front view but the apical spines are less numerous and form only one arcuate ring as seen in apical view. Grönblad's (1936) description does not stress the obviously shorter spines illustrated by him, but from his figures (Pl. B Fig. 1), it appears to be one of the main characteristics of his taxon. St. breviaculeatum var. karelicum resembles St. teliferum f. obtusa W. West (1891; pl. 24, fig. 6), although the pattern of spines is different and it is smaller.

ii. St. breviaculeatum var. macracanthum Scott et Grönblad 1957 (p. 33; pl. 18, fig. 1, 2) Pl. B Fig. 2:

> "Differt spinis marginalibus et intramarginalibus (In aspectu verticali) multo longioribus, spinis angulorum robustioribus; sinu minus aperto. Long. csp. 39-41, ssp. 35-38, lat. csp. 42-49, ssp. 33-39, ist. 11-13."

This variety was first found in Mississipi (U.S.A.) and later reported by Förster (1972) from the same state. It is described as having longer marginal and intramarginal spines in apical view and stouter angular spines. As discussed previously, Smith's illustrations of St. breviaculeatum do show longer spines towards the angles. Neither his illustrations nor observations in the present study have shown that the angular spines are stouter; they are also directed toward the isthmus.

The sinus is not as open as in *St. breviaculeatum* and *St. gladiosum* and has straight margins. This taxon is transferred to *St. claviferum* by Prescott *et al.* (1982, p. 158) but as discussed previously, their interpretation is not accepted.

b) *St. claviferum* W. et G.S. West 1896b (p. 259; pl. 16 fig. 25) *sensu* Bourrelly 1966 (p. 114; pl. 20, fig. 5, 6) Pl. B Fig. 7:

The Wests' illustration of this species shows more numerous and shorter spines of a different pattern than observed in *St. gladiosum* var. *gladiosum*. West and West first found this taxon in the United States. It has since been found in the Trois-Rivières area (Québec, Canada) by Irénée-Marie (1949a) and in New Hampshire by Cushman (1905b). One report by Bourrelly (1966) from Algonquin Park (Ontario, Canada), appears to be more closely related to *St. gladiosum* than to *St. claviferum*.

2. Other infraspecific taxa of *St. gladiosum*

The taxonomic characteristics of the following varieties have not been observed in clonal cultures or field material and there are no reasons not to accept them at the present time.

St. gladiosum var. *longispinum* Turner 1892

St. gladiosum var. *delicatulum* W. et G.S. West 1900

a) *St. gladiosum* var. *longispinum* Turner 1892 (p. 112; pl. 17 fig. 2) Pl. A Fig. 14:

"Spinulis valde elongatis, longitudine irregularibus.

> "Long. 46, lat. 48, lat. isth. 13, long. spin. 9-17 μ..."

Turner describes the variety he found in India, as having long spines of variable length. As seen by his figures, the spines are longer at the angles, but their disposition is very much like the type species as well as the specimens observed in the course of this study. This variety should be compared to St. longirostratum Grönblad 1920 (pl. 1, fig. 20, 21). Grönblad describes his species as:

> "Cellulae mediocres medio sinu acuto extrorsum aperto regulariter ampliato profunde constrictae. Semicellulae a fronte visae depresse ellipticae, dorso convexo late arcuato, angulis rotundatis; a vertice visae triangulae lateribus medio leviter retusis, angulis rotundatis vel subtruncatis; membrana spinis longis in series regulariter dispositis armata, a vertice visa in area centrali triangula glabra, sed ceterum spinis in series tres cum marginibus parallelas dispositis (quarum una series in ipso margine, reliqui intra hos) instructa; a fronte in unoquoque angulo spinae singulae longiores et robustiores oblique (sub angulis in dorso) defixae conspiciuntur. Cum spin. long. 60, lat. 68, sine spin. long. 46, lat. 49, isthm. 18, spinae longiss. 15, spin. breviss. 8 μ."

Grönblad's illustrations of the species do show a front view with one angle protruding in the middle of the semicell. This is unfortunate since it does not show the spine pattern on the front of the semicell. Both species do show a characteristic of St. setigerum stressed by West et al. (1923) and mentioned earlier, that is stout angular spines and more delicate body spines. This is not a feature observed in the material found in the present study and more thorough investigation of the species complex having this feature would be necessary before drawing any conclusion. Grönblad (1948) expresses doubts about the validity of this species.

b) St. gladiosum var. delicatulum W. et G.S. West 1900 (p. 296; pl. 412, fig. 14) Pl. A Fig. 15:

> "Var. spinis delicatioriobus, interdum leviter curvatis, paucioribus inter angulos. Long. sine spin. 37.5 μ, cum spin. 44 μ; lat. sine spin. 38.5 μ, cum spin. 50 μ; lat. isthm. 14 μ."

This variety was first found in Malham tarn in West Yorkshire (England); Coesel (1979) found it in Holland. In apical view, the spines are less numerous than in the type species, with only a few scattered spines bordering the margin between the angles. In front view, the sinus is more widely open and more rounded than observed in the present study and correspond to Turner's figure of the type species (Pl. A Fig. 11). Coesel (1979; pl. 26, fig. 2, 3) shows one front view of the variety with a closed and rounded sinus and a second one with an acute and more open sinus.

3. Uncertain infraspecific taxon of St. gladiosum

Forma ornata Laporte 1931

Mention of this forma was found in Messikommer (1942; pl. 17, fig. 1), however the original description was not available. From Messikommer's figure, this forma appears to be based on the stouter and probably longer spines. The spine pattern is basically similar to the type species.

4. Taxa related to St. gladiosum

Although few varieties and formae of St. gladiosum have been described, some species are very closely allied to it and should be discussed here. Many well established species share the basic spine pattern observed in St. gladiosum. Some of them are also distinguished by other reliable taxonomic characteristics while in others, it is difficult to see the basis for the recognition of separate species.

St. teliferum Ralfs 1848

St. teliferum var. ordinatum Börgesen 1894

St. teliferum var. subteliferum (Roy et Bisset) Förster 1970

a) St. teliferum Ralfs 1848 (p. 128; pl. 22 fig. 4, pl. 34 fig. 14) Pl. B Fig. 3 :

> "...segments reniform, bristly; end view triangular, with concave sides and broadly-rounded bristly angles..."
>
> "Frond about as large as that of Staurastrum hirsutum, deeply constricted at the middle; segments twice as broad as long, somewhat reniform, and furnished with scattered spines. End view triangular; the spines variable in number and confined to the angles.
>
> " Staurastrum teliferum differs from S. hirsutum in its longer spines, which are also fewer, stouter, and in the end view confined to the angles. It is a larger plant than S. Histrix ; its spines are more numerous, and the end margins in the front view are convex.
>
> "Length of frond 1/597 of an inch; breadth 1/643; breadth at constriction 1/2041; length of spine 1/4098; diameter of sporangium 1/738; length of spine of sporangium 1/2066."

The subsequent interpretations given to St. teliferum by different authors have varied widely. West et al. (1923) describe St. teliferum as, "one of the most widely distributed of the British Desmids". Such a statement may also hide a different fact, that it is indeed one of the most broadly interpreted species reported in Britain. West et al.'s figures (pl. 236, fig. 2-6) differ from Ralfs' (Pl. B Fig. 3) in having a more open sinus and by showing an apical ring of spines in vertical view. Ralfs shows only a few apical spines clustered around the angles, and states that it is "furnished with scattered spines."

Illustrations of the species by later authors do show, in apical view, a more or less well defined apical ring of spines as represented by West et al. and, furthermore, often have extra apical spines between the ring of spines and the margin of the semicell (Taylor 1935a, pl. 35 fig. 3; Croasdale and Grönblad 1964, pl. 18 fig. 15, 16; Messikommer 1938, pl. 10 fig. 106). Croasdale and Grönblad 1964 (p. 206 pl. 18 fig. 15, 16) do show some interesting variation in their specimens. Their fig. 16 illustrates, in apical view, one well-defined intramarginal ring of spines with a definite gap in its centre and the spines clustered around the angles. Their fig. 15 shows three intramarginal spines on two sides of the semicell in apical view; however, the third side has two more or less defined rows of intramarginal spines. The space between the marginal spines is wider halfway between the angles, but there is no well defined gap. Croasdale and Grönblad note: "...spines to some extent grouped at angles." Their findings are in keeping with the variation in the width of the central gap between marginal spines observed in apical view in clones HC of St. gladiosum (Pl. 2 Fig. 3, 4). This also shows a transition between the species St. teliferum pictured by West et al. (1923) and St. gladiosum Turner. A careful observation of Turner's figure of St. gladiosum shows that at least on the right side of the semicell shown in apical view in his figure 21 (Pl. A Fig. 11), there is a definite gap halfway between the angles, the spines close to the margin being intramarginal and not marginal. The species St. teliferum needs to be reevaluated as its common interpretation differs from the information which can be gathered from Ralfs' original figures.

b) St. teliferum var. ordinatum Börgesen 1894 (p. 27; pl. 2, fig. 23) Pl. A Fig. 13:

> "A forma typica differt spinis non sine ordine dispositis; semicellulae a fronte visae apicibus circiter 13 spinis ornatis, a vertice visae medio glabro ad marginem versus 12 spinis in orbem triangularum dispositis, margine etiam spinifera.
>
> "Long. = 38 μ; lat. sine spin. = 33 μ..."

This variety was first found in Greenland and has since been reported from Europe. This variety does differ from Ralfs' original illustrations of St. teliferum through the arrangement of the spines. Comparison of Turner's original figure of St. gladiosum (Pl. A Fig. 11) and of Börgesen's illustration (Pl. A Fig. 13) of St. teliferum var. ordinatum show that both in front and vertical views, the spines are similarly arranged. There are two rows of spines on the front of the semicell and in apical view, there is a central triangle of spines and lateral spines. However St. teliferum var. ordinatum has shorter spines and is slightly smaller than St. gladiosum. It seems to correspond more closely to St. gladiosum than to St. teliferum. Capdevielle and Couté (1980) published some detailed drawings and SEM photographs of St. teliferum var. ordinatum. The authors mention that their taxon differs from Börgesen's by being about as long as broad, a difference which is minimal since Börgesen's L/l ratio would be 1.15. They also note that the apical ring of spines in apical view is composed of 12 spines in their specimens and of nine in the variety. This is not accurate as Börgesen illustrates clearly a ring composed of three spines lining each three margins of the semicell plus one spine at the tip of each triangle. From their references, it seems that Capdevielle and Couté observed Förster's (1970; pl. 27, fig. 18) illustration of St. teliferum var. ordinatum. The spines closing the ring at each angle are placed slightly closer to the angle, which gives the impression that there are only nine central spines. The SEM photographs of Capdevielle and Couté show a less open sinus than in Börgesen's figure. Plate 27 fig. 18 in Förster (1970) and pl. 14 fig. 23 (left) in Růžička (1973) illustrate a sinus not as widely open as in Börgesen's figure. Růžička (1973, pl. 14 fig. 23; right) illustrates a sinus which is more widely open than in Capdevielle and Couté pl. 2, fig. 6-9 and in HC clones.

c) St. teliferum var. subteliferum (Roy et Bisset) Förster 1970 (p. 342; pl. 27, fig. 16, 17) Pl. B Fig. 4

Basionym: St. subteliferum Roy et Bisset 1886 (p. 238; pl. 268, fig. 1) Pl. B Fig. 5:

Roy and Bisset description follows:

> "Medium-sized, slightly longer than broad: semicells in front view regularly oval, with three stout spines on each side, 2-3 similar to and near to these on the face of the semicells, and two small spines close to the end; end view triangular, with three superposed stout spines terminating each angle, and two similar ones on each side of it; nearer the centre of the triangle is a circle of nine minute spines, sides concave; constriction acute, opening out widely. Membrane smooth. Long. 37 μ; lat. 35 μ; lat. of isth. 13 μ."

This taxon was first found in Japan. Förster (1970) recorded it from Germany. Förster (1970) transferred St. subteliferum in St. teliferum as a variety, on the basis of the arrangement of the spines. His figures (Pl. B Fig. 4) differ in many respects from those of Roy and Bisset's fig. 1 (see Pl. B, Fig. 5). Förster did not take into consideration the principal characteristic of the species; that is, the longer spines at the angles, which is very clearly shown on Roy and Bisset's figures, but is totally missing from Förster's figures.

St. subteliferum Roy et Bisset and St. teliferum var. subteliferum Förster do not seem to belong to the same taxon. Roy and Bisset's taxon is smaller than St. setigerum but the presence of two types of spines at the angles and on the body should justify its classification under that species. In size it is similar to St. setigerum var. occidentale W. et

G.S. West 1896b (p. 260; pl. 16, fig. 27), although it is a bit longer than broad. Furthermore, both taxa are very similar in apical view as pointed out by Smith (1924b). The semicells of St. subteliferum in front view are oval and not narrowly elliptic with elongated angles as in var. occidentale.

Roy and Bisset do not give the length for the two types of spines of St. subteliferum. It has been shown earlier that in St gladiosum, the spines are slightly longer at the angles. On this basis, St. subteliferum resembles St. gladiosum var. delicatulum which possesses long and curved spines and is of similar dimensions, although the spines are more regularly disposed in St. subteliferum.

d) Conclusion

I think that St. teliferum var. ordinatum and many publications of St. teliferum var. teliferum might be synonymous with St. gladiosum var. gladiosum. I agree with Förster that the features of St. subteliferum do not justify the naming of a separate species but I do not believe that Förster's specimens are the same as St. subteliferum. With its short spines, Förster's taxon is similar to St. teliferum var. ordinatum. A more thorough investigation is needed before making further conclusions about those taxa.

TABLE 12

CELL DIMENSIONS AND RADIATION OF ST. GLADIOSUM
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation; C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(csp) (µm) Average	L(csp) (µm) Range	L(csp) (µm) S.D.	L(csp) (µm) C.V.	l(csp) (µm) Average	l(csp) (µm) Range	l(csp) (µm) S.D.	l(csp) (µm) C.V.	Is (µm) Average	Is (µm) Range	Is (µm) S.D.	Is (µm) C.V.	L/l	Radiation (%) 3
71	Lost 5-IX-79	46	39-51	2.39	5.17	47	39-52	3.12	6.67	17	14-18	1.03	6.21	0.99	100
110	Lost 5-IX-79	38	32-53	4.09	10.90	35	29-52	4.24	12.25	14	12-20	1.38	10.12	1.08	100
496	Munday 1-XI-80	39	36-43	1.85	4.86	39	35-44	2.68	6.86	16	14-18	0.80	5.70	1.00	100
323	Como 27-VI-80	37	32-45	3.20	8.56	37	32-41	2.38	6.38	14	12-17	1.32	9.68	1.00	100

Field material

Source	L(csp) (µm)	L(ssp) (µm)	l(csp) (µm)	l(ssp) (µm)	Is (µm)	L/l	Radiation 3
Jacobs 22-VIII-79	44	41	47	38	14	0.93	X
Jacobs 26-IV-80	41	38	43	34	12	0.95	X
" "	52	44	51	39	--	1.03	X
" "	49	41	46	36	14	1.07	X
Lost 5-IX-79	38	38	41	32	12	0.93	X
Lost 18-VII-80	44	40	47	35	13	0.93	X
Lost 20-IX-80	44	44	42	34	16	1.05	X
Lost 11-X-80	44	42	44	35	17	1.00	X
Placid 8-VIII-80	43	37	46	37	16	0.93	X

Plate 2

St. gladiosum var. gladiosum

(marker= 10 μm unless indicated otherwise)

1. Clone HC 71, light microscope photograph; cell in front view showing the spine pattern

2-4. Clone HC 71, SEM photographs.

2. Detailed view of one angle showing the spines and the pores.

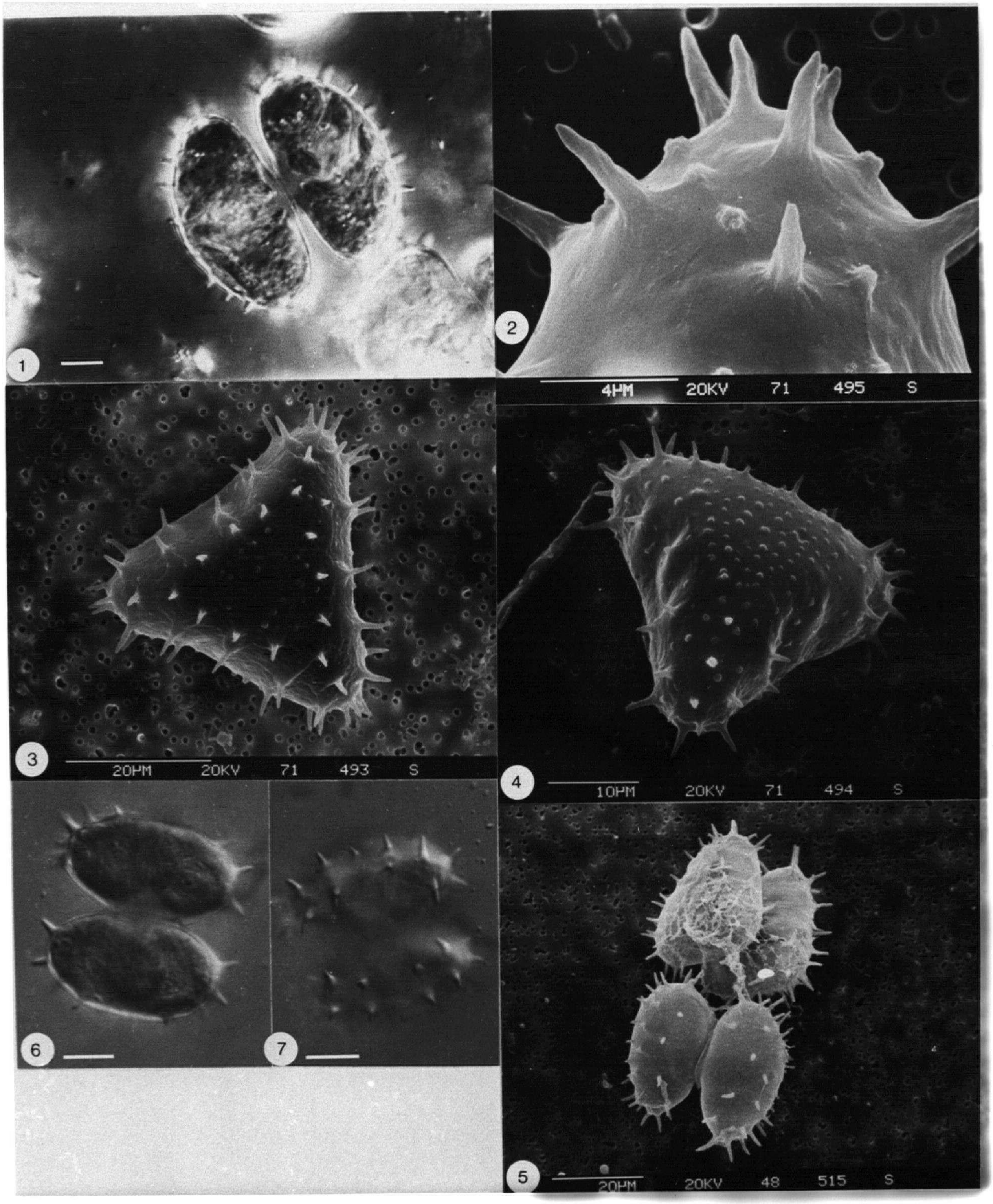
3. Cell in vertical view showing the spine arrangement

4. Isolated semicell viewed from the front and the apex showing the spine pattern

5. Clone HC 148, SEM photograph; two cells in front view

6, 7. Clone HC 496, light microscope photographs; Cells in front view showing the spine pattern

138A


1
2
4HM 20KV 71 495 S
3
20HM 20KV 71 493 S
4
10HM 20KV 71 494 S
6
7
5
20HM 20KV 48 515 S

D. STAURASTRUM ALTERNANS VAR. ALTERNANS

St. alternans Brébisson ex Ralfs 1848 (p. 132; pl. 21, fig. 7)

Pl. B Fig. 10:

> "...segments rough, narrow-oblong, and, from their twisted position, unequal in the front view; end view with the angles of one segment entire, and alternating with those of the other...
>
> "Frond rough with minute pearly granules, which, except on the margin, appear like puncta; segments two or three times longer than broad, oblong, twisted, so that in the front view one of them appears shorter on one side, in consequence of the blending together of two of the angles. The end view is triangular, with concave sides and very obtuse entire angles. The angles of the lower segment are seen alternating with those of the upper.
>
> "I formerly described this plant as the Staurastrum tricorne, but that species in the front view is prolonged at the sides into short processes; I am not certain that the two are distinct, but in doubtful points I think it right to defer to M. de Brébisson's opinion.
>
> " Staurastrum alternans may be known from S. dilatatum and S. punctulatum by its unequal segments in the front view and alternating angles in the end one.
>
> "I have gathered the sporangia at Penzance; they are orbicular and furnished with spines forked at the apex.
>
> "Length of frond 1/1037 of an inch; breadth 1/1106; breadth at constriction 1/3205..."

St. alternans was found in J. K. Henry, Como, Munday and Jacobs Lakes, but never in abundance. In Stein and Borden (unpublished), 22 records of St. alternans are listed for British Columbia, including Munday Lake. St. punctulatum var. punctulatum has 66 records, including Munday, Lost and Como Lakes.

Clones examined: HC 205 from J.K. Henry Lake, 18-IV-80; HC 438 from Munday Lake, 16-V-80 (Table 13).

Cells are about as long as wide with a L/l ratio of ca. 1 (Table 13). The semicells of St. alternans are usually elliptic-lanceolate in shape with rounded angles (Pl. 3 Fig. 1). Some semicells have a more elliptic and less lanceolate shape, the semicells appearing fuller (Pl. 3 Fig. 4). This is particularly true for clone HC 438 where the cells would be better described as oval rather than elliptic-lanceolate. The apex is slightly convex. Cells with semicells of slightly different width were observed in clonal cultures and field material.

The sinus is either acute (Pl. 3 Fig. 2, 3) or rounded (Pl. 3 Fig. 4). Many semicells alternate slightly (Pl. 3 Fig. 2, 4), but others have their angles lying exactly above each other (Pl. 3 Fig. 6).

Granules form concentric rows around the angles of the semicells (Pl. 3 Fig. 3). They cover most of the cell except for the area surrounding the isthmus (Pl. 3 Fig. 3, 4). Depending on the degree of development of the granulation, the sides and angles of the semicells will appear either smooth or granulate under the light microscope. No defined row of supraisthmial granules was seen.

The granulation varies considerably in coarseness (Pl. 3 Fig. 1, 5). Pl. 3 Fig. 9 is a close-up of a cell with heavy ornamentation where the rugged and irregular shape of these "granules" is easily observed. Lines of what may be mucilage seems to connect some granules together. Such particular ornamentation is also seen with the light microscope. The ornamentation appears like rounded flattened granules (Pl. 3 Fig. 8) or concentric rows of more delicate granules (Pl. 3 Fig. 7).

In apical view, the sides of the cells are slightly concave or almost straight (Pl. 3 Fig. 6). Also noticeable is the difference in protrusion of the angles. In Pl. 3 Fig. 6 the top semicell has rounded angles that are shorter and not as elongate as its sister semicell beneath it. The ornamentation covers the whole apex of the semicell even its central part. In Pl. 3 Fig. 6, a central rosette of granules is seen on the centre of the apex. The granulation, visible on the side of the semicells in apical view, gives an uneven appearance (Pl. 3 Fig. 6).

The dimensions of the clones are given in Table 13. All cells observed in field and clonal cultures were triradiate. Clones HC 205 and 438 were both observed with a light microscope, although only clone HC 205 was processed for SEM observation.

Illustrations of St. alternans in the literature, show a considerable degree of variation. Although St. alternans was described by Ralfs as having alternating semicells, West and West (1912) stress that this can not be a specific characteristic since it is common in other related Staurastrum. This characteristic was seen in all field specimens observed but varied in cultures as previously noted.

Many illustrations represent a perfect alternation between the two semicells in vertical view (Archer 1861, pl. 2 fig. 16, 17; West and West 1912, pl. 136 fig. 8; Allorge and Allorge 1931, pl. 12 fig. 14, 15; Croasdale 1962, pl. 7 fig. 125; Hinode 1971, fig. IX:21; Růžička 1973, pl. 14 fig. 20), while others illustrate some degree of twisting of the isthmus but not sufficient to have the angles alternate perfectly with each other (Förster 1965, pl. 8 fig. 15; Coesel 1979, pl. 24 fig. 4, 5). Most cells of clones HC 205 and 438 did show some degree of twisting, but rarely were the two semicells in perfect alternation with each other. Some authors show only a single semicell in apical view, which suggests that the semicells were not showing any degree of alternation and that the angles lay perfectly above each other (Taylor 1935a, pl. 35 fig. 6; Krieger and Scott 1957, pl. 5 fig. 2; Grönblad 1960, fig. 215, 216).

West and West (1912; pl. 136, fig. 8) show two cells with slightly different sinus shape. Figure 8a represents a close and acute sinus whereas the sinus in fig. 8a' is more widely open. Coesel (1979; pl. 24, fig. 4) illustrates an alga very similar to the Wests fig. 8a' and which also has a row of granules just above the isthmus whereas the cell in his fig. 4 has a less open and more rounded sinus. Such variation in the degree of opening of the sinus and in its shape from rounded to acute, occurs in the literature and has been observed to some extent in clones HC 205 and 438 (Pl. 3 Fig. 1, 4).

The presence of a well defined row of supraisthmial granules was never observed, but the width of the space free of ornamentation above the isthmus varies. Literature reports also represent this variation; for example Smith (1924b; pl. 6, fig. 4) represents a specimen where the ornamentation covers almost the whole isthmial area, whereas in Krieger and Scott (1957; pl. 5, fig. 2) and Růžička (1973; pl. 14, fig. 20), there is a wide area free of ornamentation above and below the isthmus.

Although specimens in clones HC 205 and 438 always show granulation on the centre of the apex in apical view, some authors represent the cells with a smooth apex (Krieger and Scott 1957, pl. 5 fig. 2; Croasdale 1962, pl. 7 fig. 125). The strength of the ornamentation also seems to vary, judging by its representation on drawings by different authors. Allorge and Allorge (1931; pl. 12, fig. 14, 15), Taylor (1935a; pl. 35, fig. 6) and Krieger and Scott (1957; pl. 5, fig. 2) represent the granules as small circles. Coesel (1979; pl. 24, fig. 4, 5) shows the granules by very delicate dots. A range of different intensity of granulation between these extremes are illustrated in other publications. These illustrations seem to agree with the important variation in the intensities of granulation observed in clones HC 205 and 438, from delicate granules to rugged prominent granules (Pl. 3 Fig. 4, 5, 7, 8).

1. Proposed synonyms of St. alternans var. alternans:

   St. alternans var. subalternans Maskell 1888

   St. punctulatum forma ellipticum Lewin 1885.

a) St. alternans var. subalternans Maskell 1888 (p. 22; pl. 4, fig. 38) Pl. B Fig. 11:

> "Frond small; segments in front-view sub-elliptical; when viewed slightly tilted (as in the figure) the third angles of the two segments are not exactly opposite. In end-view, segments triangular, sides concave, angles rounded; the frond being only slightly twisted, the angles of each segment are neither quite in correspondence nor quite alternate. Cytioderm punctate, the puncta transverse.
>
> "Long., 25 μ; lat., 26.7 μ..."

This variety was first found in New Zealand. No further records were found. Since it is based solely on the degree of torsion of the isthmus which is a highly variable characteristic as discussed previously, it can not be recognized as a true variety.

b) St. punctulatum forma ellipticum Lewin 1888 (p. 9; pl. 1, fig. 16)

The original description of this forma was not available and it appears to be rare. Krieger (1932; pl. 15, fig. 10; Pl. B Fig. 12) gives under the name var. ellipticum forma, a form with elliptic semicells, rounded angles and concave sides in vertical view. Although West and West (1912; p. 146) did not observe this taxon, they express the opinion that it may belong to St. alternans and their conclusion is accepted.

2. Other infraspecific taxa of St. alternans

A number of varieties and forms of St. alternans have been described in the literature and, based on observations of the present study and literature reports, there is no ground not to accept them. Some have been placed by other authors as synonyms of different taxa.

St. alternans var. pulchrum Wille 1879

St. alternans var. minus Turner 1892

St. alternans var. basichondrum Schmidle 1898

St. alternans var. basichondrum f. tetragonum Croasdale et Grönblad 1964

St. alternans var. divergens W. et G.S. West 1902a

St. alternans var. spinulosum Irénée-Marie and Hilliard 1963

a) St. alternans var. pulchrum Wille 1879 (p. 53; pl. 13, fig. 66) Pl. B Fig. 13:

"S. fere tam longum quam latum, sinu subrectangulo ampliato constrictum; semicellulae e basi angusta sursum valde dilatatae, subcuneiformes, dorso truncato l. late rotundato, angulis magis minus rotundato-obtusis; a vertice visae trigonae angulis rotundatis, lateribus retusis. Membrana granulata, margine granulato dentata.

"Long. 32; lat. 30; lat. isthm. 10 μ."

This variety is not common but has been reported in different areas of the world. Wille's plant is slightly longer than broad and has a subrectangular sinus with the base of the semicell slightly concave.

b) St. alternans var. minus Turner 1892 (p. 105; pl. 16, fig. 6) Pl. C Fig. 1:

"Multo minor quam F. typica.

"Long. et lat. 15, lat. isth. 9.5 μ."

This variety first described from East India, does not appear to have been recorded since. It has a rounded sinus and the granulation is restricted to the angles. It resembles St. striolatum (Nägeli) Archer, which, according to West and West (1912; p. 178), measures 19-28 by 18-28 μm with an isthmus 6-10 μm wide.

c) St. alternans var. basichondrum Schmidle 1898 (p. 58; pl. 3, fig. 6) Pl. C FIg. 2:

This variety was found in northern areas. Only the illustration of this taxon was available. Croasdale (1962) reports this taxon as var. basichondrum Schmidle 1898, although Schmidle reports it in the legend as St. alternans v. In West and West (1912; p. 170), it is listed as a record of St. alternans. Apart from the naked apex in apical view and the row of supraisthmial granules in front view, the main difference from the type species seems to be the shape of the sinus. Some illustrations of St. alternans (West and West 1912, pl. 126, fig. 8a'; Coesel 1979, pl. 24 fig. 24) show a wide open sinus ending in a small acute notch and are similar to var. basichondrum. The distinction between the species and its variety appears to be based on slight variations and more thorough investigation may prove that there is no ground to separate these taxa.

Croasdale (1962) and Croasdale and Grönblad (1964) represent cells of var. basichondrum with fairly elongated angles which form short processes with rounded extremities. The sinus is very definitely rounded and differs from Schmidle's fig. 6 (Pl. C Fig. 4). Croasdale (1962) expresses some doubts about her classification.

d) St. alternans var. basichondrum f. tetragonum Croasdale et Grönblad 1964 (p. 194; pl. 18, fig. 4, 5) Pl. C Fig. 5:

> "Cellulae 34 μ x34 μ, isth. 19 μ et 38-40 μ x39-42 μ, isth. 16-17 μ. Semicellulae a vertice visae tetragonae.
>
> "Semicells tetragonal in vertical view. The plants appeared in two morphae: Fig. 4 shows a small angular plant 34 μ x 34 μ, isth. 9 μ (Sta. 21), and Fig. 5 shows a larger plant with rounded angles, 38-40 μ x39-42 μ, isth. 16-17 μ (Sta. 16). This identification is uncertain. Except for the supraisthmial circle of granules and the somewhat irregular granulation in vertical view these plants might be classified as S. dilatatum Ehr. Except for the larger size and more extended angles they might be classified as S. margaritaceum (Ehr.) Menegh."

A minor contradiction is present. In their Latin description, Croasdale and Grönblad state a width of "19 μ" for the isthmus of the smaller form, while in the English version, they quote the isthmus as being "9 μ" wide. Measurements of fig. 4 suggest that the 9 μm figure is the right one, although Prescott et al. (1982) report the isthmus as 16-19 μm wide.

Croasdale and Grönblad are dubious about their identification of this specimen, thinking that it may be better placed under St. dilatatum Ehrenberg or St. margaritaceum (Ehrenberg) Meneghini. The reason for not naming it St. dilatatum is the presence of a circle of supraisthmial granules and the slightly irregular granulation in vertical view. The figure of Ralfs (1848; pl. 21 fig. 8c; Pl. B Fig. 11, left) of St. alternans shows a ring of granules above the isthmus in vertical view. Similarly Coesel (1979, pl. 24 fig. 5) also represents a form of St. alternans with supraisthmial granules.

Notwithstanding where it should be classified, f. tetragonum would certainly better be termed only as facies 4 in keeping with Grönblad and Růžička's (1959) recommendations.

e) St. alternans var. divergens W. et G.S. West 1902a (p. 177; pl. 21, fig. 18) Pl. C Fig. 3:

> "Var. minor, apicibus semicellularum concavis, angulis levissime dilatatis (subcapitatis) sursum leviter divergentibus; a vertice visis ut in forma typica sed angulis levissime subcapitatis.
>
> "Long. 17 μ; lat. 17-18 μ; lat. isthm. 5.5 μ..."

This variety first found in Ceylon, was later renamed St. striolatum var. divergens W. et G.S. West (1912; p. 178, pl. 128 fig. 6).

f) St. alternans var. spinulosum Irénée-Marie and Hilliard 1963 (p. 113; pl. 1, fig. 3) Pl. C Fig. 4

> "Varietas separata a typo granulibus mutantis in curtas et tenues spinas longiores ad apices quarumque appendicium...
>
> "L. 23-24.5 μ; W.(cp) 30-31 μ, (sp) 27.5-28 μ; Is. 9-9.6 μ."

This species is distinguished by its "short and slender thorns which are longer at the end of each process". These thorns are grouped around the angles. This pattern of ornamentation differs from St. alternans var. alternans.

3. Taxa related to St. alternans

The following taxa are closely related to St. alternans

St. punctulatum Brébisson ex Ralfs 1848

St. punctulatum var. subproductum W. et G.S. West 1912

St. punctulatum var. striatum W. et G.S. West 1912

a) St. punctulatum Brébisson ex Ralfs 1848 (p. 133; pl. 22, fig. 1) Pl. C Fig. 6:

> "...segments rough with puncta-like granules, elliptic, equal; end view with broadly rounded angles and slightly concave sides...
>
> "Frond larger than that of Staurastrum alternans, rough with minute pearly granules which appear like puncta; segments twice as broad as long, elliptic; end view triangular with very blunt angles.
>
> " Staurastrum punctulatum may be distinguished from S. alternans by its equal and more turgid segments in the front view, and in an end one by its less concave sides. S. rugulosum agrees with it in size and partly in form, but in that species the pearly granules are larger and fewer, and at the angles appear like little spines.
>
> "Length of frond 1/704 of an inch; breadth 1/881; breadth at constriction 1/2270."

St. punctulatum is a common species which was found in many regions of the world. St. alternans is closely related to St. punctulatum. It is on the basis of Ralfs' distinction between St. alternans and St. punctulatum that clone HC 205 and 438 as well as field material have been placed under St. alternans. Contrary to Ralfs' concept, some literature records do seem to show narrowly-elliptic semicells and end views with concave sides for cells which are identified as St. punctulatum (Scott and Prescott 1958, pl. 14 fig. 18; 1961, pl. 52 fig. 14). These could probably be placed in St. alternans, but since the distinction between the two species is poorly defined, it may be better to wait for a complete reevaluation of these taxa.

b) St. punctulatum var. subproductum W. et G.S. West 1912 (p. 182; pl. 127, fig. 15) Pl. C Fig. 7:

Syn.: St. punctulatum forma G.S. West 1899 (p. 219)

> "Cells proportionately wider, lateral angles of semicells very slightly produced; vertical view with faintly convex sides and almost imperceptibly produced angles.
>
> "Length 31 μ; breadth 31 μ; breadth of isthmus 8.5 μ."

This variety was first reported as a forma of St. punctulatum from Cambridgeshire (England) by G.S. West and has since been found in many areas of the world. It is about as long as broad with the angles slightly extended or produced, and has slightly convex sides in vertical view, with almost imperceptibly extended angles. Clones HC 205 and 438 differ from St. punctulatum var. subproductum by the less convex apex, the more narrowly elliptical cells, the usually slightly concave and occasionally straight sided vertical view and the less open sinus (although see Pl. 3 Fig. 4). These differences are sufficient to distinguish the two taxa and they are accepted for the time being.

c) St. punctulatum var. striatum W. et G.S. West 1912 (p. 186; pl. 128, fig. 5, 6) Pl. C Fig. 8:

Syn.: St. striatum (W. et G.S. West) Růžička 1957 (p. 157; pl. 148, fig. 53-55)

> "Semicells more distinctly rhomboid than in the type; granules most minute, fewer in number, and arranged in somewhat distant series around the angles. Zygospore exactly like that of var. pygmaeum.
>
> "Length 29-31 μ; breadth 29-31.5 μ; breadth of isthmus 9.5-11.5 μ; diam. zygosp. without spines 36-37 μ; with spines about 67 μ."

This taxon is very similar in shape to var. subproductum ; however it differs by the slightly different shape of the semicells and the less numerous and more distant rows of granules. The variety was raised to species level as St. striatum (W. et G.S. West) Růžička 1957. Růžička illustrates three extremes of the range of variation he observed with this taxon, from a cell of oval shape with broadly rounded angles (fig. 53) to a cell with well produced angles forming short processes (fig. 55). Similar variation was observed in clones HC 205 and 438 but not to the same extent. A form with widely rounded angles and straight sides as in Růžička's fig. 53 was observed (Pl. 3 Fig. 6, top semicell). Cells with short processes were never seen. The most common specimens had elongated angles but the reduction in width from the body of the semicell to the angle was relatively slight and gradual, and the angles never formed as narrow and elongated processes as shown by Růžička (fig. 55). Supraisthmial granules which were observed by Růžička, were never seen.

d) Discussion

St. alternans and St. punctulatum are closely related species which are also very commonly reported in the literature. St. punctulatum does comprise a number of varieties which may need to be reclassified. A few other species such as St. striatum are also closely allied to these taxa. Ruzicka's thorough discussion and inclusion of variation observed in this taxon is a first step toward a more natural classification of this group of Staurastrum taxa. The variation in the shape of the cell is often a very gradual process, from rounded angles to short processes, from elliptical to oval to pyramidal semicells. The features differentiating these species are often difficult to describe and somewhat variable. Usually the descriptions of the taxa are brief and barely adequate and take little account of variation. This makes it more difficult for today's taxonomists; they may have only a vague idea of the original concept and furthermore, are faced with specimens varying only slightly from the type species, but which may have been placed in a different variety, form or even species. As Teiling (1967) pointed out, sometimes the description of new taxa is the result of the unavailability of the large body of literature involved. A compilation of publications of desmids taxa or more specifically of Staurastrum taxa such as Nordstedt's would be invaluable, but it is a major undertaking.

In this study, clones HC 205 and 438 are described in what is believed to be the original concept of _St. alternans_ var. _alternans_ and _St. punctulatum_ var. _punctulatum_. Since Ralf's illustration of _St. alternans_ in particular is very poor, the description and illustration of this taxon by West _et al._ (1923) is used to complement Ralfs' description.

Table 13

CELL DIMENSIONS AND RADIATION OF ST. ALTERNANS
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(csp) (µm) Average	Range	S.D.	C.V.	l(csp) (µm) Average	Range	S.D.	C.V.	Is (µm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3
205	J.K. Henry 18-IV-80	35	28-38	1.84	6.31	35	32-38	1.65	4.44	12	11-14	0.62	6.01	1.00	100
438	Munday 16-V-80	33	31-36	1.00	4.66	33	30-37	4.34	13.36	11	11-12	0.49	4.26	1.01	100

Field material

Source	L(csp) (µm)	l(csp) (µm)	Is (µm)	L/l	Radiation 3
Munday 16-V-80	39	35	12	1.12	X
Munday 20-IX-80	35	36, 39*	12	0.97, 0.89	X
Como 27-VI-80	37	36	11	1.03	X
Jacobs 8-VIII-80	37	36	11	1.03	X
Jacobs 14-VI-79	35	33	9	1.06	X
Jacobs 7-VI-80	34	28	10	1.22	X

* Dichotypical cell

Plate 4

St. alternans var. alternans

(marker= 10 μm unless indicated otherwise)

1-6, 9. Clone HC 205, SEM photographs

1, 2, 4. Cells in front view showing the shape and ornamentation of the cells

3. Detailed view of the angles in front view showing the ornamentation

5, 6. Cells in vertical view showing the apical ornamentation

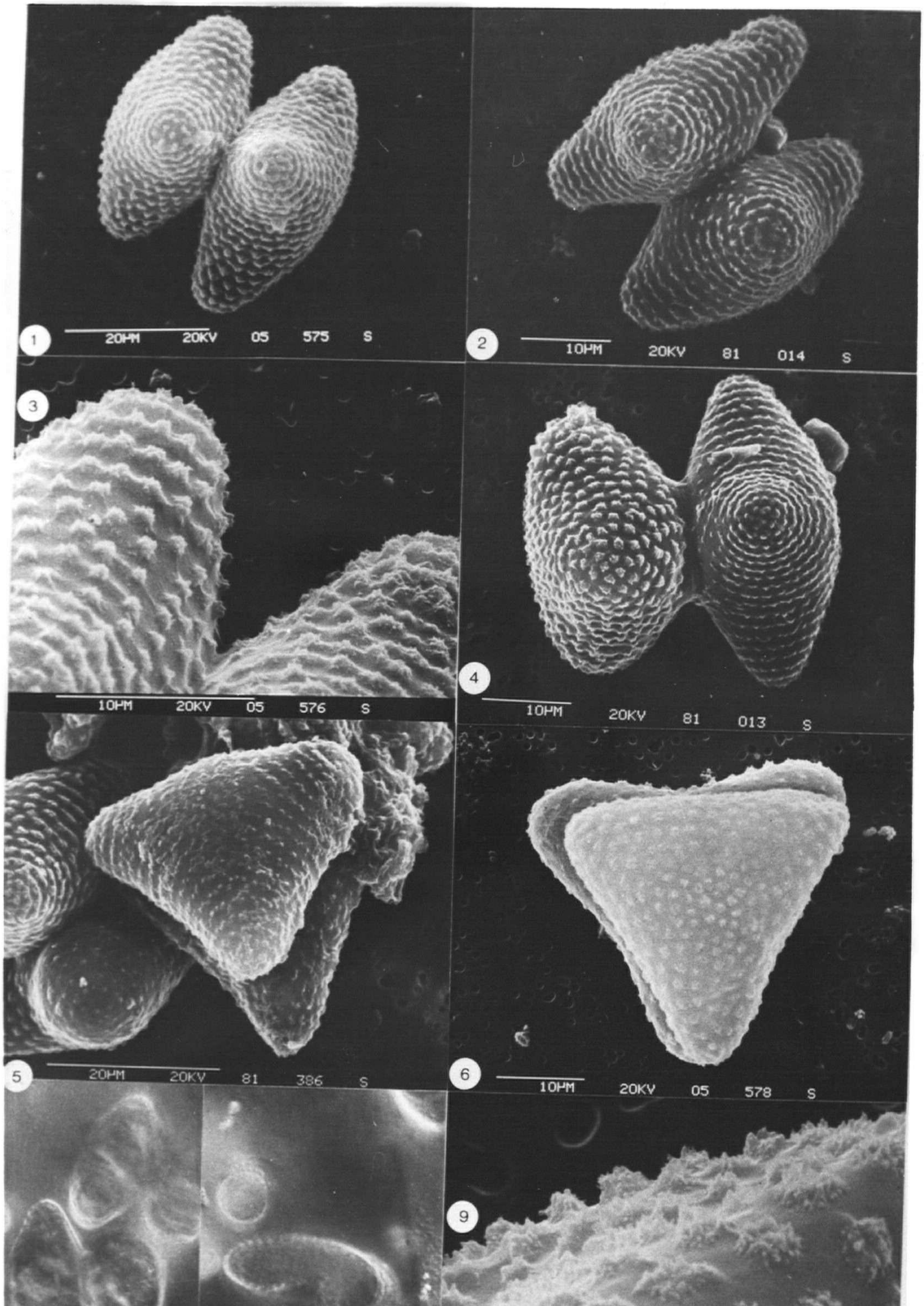
9. Detailed view of the ornamentation

7, 8. Clone HC 205; light microscope photographs

7. Cell in front view with delicate granules

8. Cell in front view with coarse granules.

155A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2
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3
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4
10PM 20KV 81 013 S
5
20PM 20KV 81 386 S
6
10PM 20KV 05 578 S
7
8
9
2PM 20KV 05 580 S

E. STAURASTRUM MURICATUM VAR. MURICATUM

St. muricatum Brébisson ex Ralfs 1848 (p. 126; pl. 22, fig. 2)

Pl. C Fig. 9:

> "...segments semiorbicular, rough with conic granules; end view triangular, with convex sides and broadly rounded angles.
>
> "Frond deeply constricted at the middle, nearly equal in length and breadth, rough with minute conic granules or spines. End view triangular, its sides convex and angles broadly rounded.
>
> " Staurastrum muricatum is larger than S. hirsutum, and not hirsute, but rough with stout short granules or spines; in the end view also the sides are more convex.
>
> "Length of frond 1/409 of an inch; breadth 1/474."

First described by de Brébisson 1835 (p. 66) as Binatella muricata, St. muricatum was later tranferred to the genus Staurastrum by de Brébisson in Meneghini 1840 (p. 226). Ralfs (1845) illustrates both St. hirsutum (fig. 1a, b, c) and St. muricatum (fig. 1d, e) under the name St. muricatum (see Pl. C Fig. 10) but Ralfs (1848; p. 126, pl. 22 fig. 2-3) divides St. muricatum sensu Ralfs 1845 into two different taxa, St. hirsutum and St. muricatum .

St. muricatum was quite abundant among populations of Sphagnum or aquatic vascular plants in Munday and Lost Lakes. The species has been previously found in Munday and Lost Lakes and 20 records are noted for British Columbia by Stein and Borden (unpublished). St. arnellii and St. botrophilum were each recorded twice, but not in the lower Fraser Valley.

Clones examined: HC 275, 276, 283, 284 from Munday Lake, 16-V-80; HC 408-411, 414, 415, 417, 418 from Lost Lake, 18-VII-80; HC 492 from Lost Lake, 20-IX-80 (Table 14).

St. muricatum grows very well in culture and 26 clonal cultures were successfully established. Of these, 13 clones were measured and observed, nine from Lost Lake and four from Munday Lake.

The semicells are elliptical to subelliptical to more or less pyramidal in front view (Pl. D Fig. 1, 2). The apex is strongly convex and the angles at the base of the semicells are well rounded. The sinus is open and acute or slightly rounded (Pl. D Fig. 1, 2).

The semicells are ornamented with conical granules disposed in concentric rows around the angles (Pl. 4 Fig. 1, 2). The space between the rows of granules is relatively wide. The degree of development of the granulation varies (Pl. 4 Fig. 1-4). This variation is mostly obvious at the angles: some angles appear rounded while others have a rough outline due to the presence of big conical granules (Pl. 4 Fig. 4). The granules were usually coarser in field than in culture material.

In apical view, the sides of the cell are slightly concave, straight or slightly convex. The granules may either cover the whole apex (Pl. 4 Fig. 5) or leave a small central area free of granules (Pl. 4 Fig. 6).

One semicell observed with the SEM microscope from the side of the isthmus (basal view) shows the granulation covering the underside of the angles around the isthmus (Pl. 4 Fig. 5).

The great majority of the cells were triradiate, but in two clones (HC 275, 276), tetraradiate cells made up 1.8 and 2.3% of the cells counted. All cells from field material were triradiate (Table 14).

All the clones had similar dimensions, but the clones from Munday Lake were slightly larger. The L/l ratio was just above 1, indicating a cell slightly longer than wide. Field measurements were in the same range as measurements of clonal cultures (Table 14).

1. Proposed synonyms of St. muricatum var. muricatum

St. muricatum var. denudatum Brébisson 1856

St. muricatum var. denudatum Brébisson 1856 (p. 141):

> "...la variété denudatum, que j'ai recueillie près de Falaise, diffère du type par sa surface à peine hispide ou chargée d'un petit nombre d'épines très courtes."

The distinctive characteristic of this variety is the finer granulation. This feature has been shown to be very variable in clonal cultures and is not a good taxonomic characteristic. Thus this variety is better considered only as a minor variation of St. muricatum var. muricatum.

2. Other infraspecific taxa of St. muricatum

The following taxa present characteristics which have not been observed in this study and there is no ground not to accept them. Some taxa have already been placed by other authors as synonyms of different species.

St. muricatum var. acutum W. West 1890

St. muricatum var. borholmiense Gutwinski 1890

St. muricatum var. australis Raciborski 1892

St. muricatum var. subturgescens Schmidle 1893

a) St. muricatum var. acutum W. West 1890 (p. 294; pl. 5, fig. 14) Pl. C Fig. 11:

> "Var. spinis brevibus (nec granulis), semicellulis truncato-pyramidatis.
>
> "Long. 62-70 μ; lat. 48-52 μ..."

This variety, distinguished by the pyramidal-truncate shape of the semicells and the presence of spines instead of granules, was placed as a synonym of St. pyramidatum W. West 1892a (p. 179). The distinctive pyramidal shape may justify such a move. The type specimen of St. muricatum var. acutum was found in North Wales whereas that of St. pyramidatum was found in West Ireland.

b) St. muricatum var. borholmiense Gutwinski 1890 (p. 71) Synonym: St. muricatum forma Nordstedt 1888 (p. 203; fig. 19, 20).

Gutwinski did not give a diagnosis or description of this taxon, although he referred to Nordstedt's publication. This variety is recognized by West et al. (1923) as a synonym of St. hirsutum.

c) St. muricatum var. australis Raciborski 1892 (p. 383, pl. 7

fig. 19) Pl. B Fig. 6:

> "Minor, granulis paucioribus; area suprabasalis et apicalis glabrae. Long. cell. 30 μ; lat. cell. 25 μ; lat. isthmi 14 μ."

This taxon is smaller than var. muricatum and has reduced ornamentation and a closed sinus. It appears to be more closely related to St. arnellii, which is discussed later, than to St. muricatum.

d) St. muricatum var. subturgescens Schmidle 1893 (p. 554; pl. 28, fig. 20) Pl. C Fig. 12:

> "48 μ longum, 42 μ latum, incisura profunda, ampla, intus rotundata, extus ampliata, semicellulis ellipticis, granulatis (granulis acutis parvis in series circulares dispositis) e vertice visis triangularibus, angulis late rotundatis, lateribus concavis, medio parva areola triangulari nuda.
>
> "Diese Pflanze nimmt, was Granulation und Zellform anbelangt, die mitte ein zwischen Staur. muricatum Breb. (sic) und Staur. turgescens De Not. Mit der typischen Form selten."

The rounded and elongated isthmus shown in the original figure and the concave sides in apical view, distinguish this taxon from St. muricatum. The regular granulation, more elongated semicell, as well as the shape of the sinus separate it from St. turgescens de Notaris. This taxon appears to be more closely related to St. muricatum than to St. turgescens.

3. Uncertain infraspecific taxa of St. muricatum

The original publications of the following varieties were not available or the description was so sketchy that no conclusion could be drawn.

St. muricatum var. trapezicum Gutwinski 1890

St. muricatum var. turgescens Schmidle ?

St. muricatum var. dimidiatum Comère 1901

a) St. muricatum var. trapezicum Gutwinski 1890 (p. 72):

"Semicellulae perfecte trapezicae, dorso truncato. Lg. 42-43 μ; lat. 36 μ; isth. 12 μ; lat. ap. 22 μ."

Gutwinski does not provide a picture of his variety. Many trapezoid taxa have been described. Without a more detailed description and an illustration, it is difficult to know what alga Gutwinski is referring to.

b) St. muricatum var. turgescens Schmidle ?

Cedergren (1926, p. 312) refers to a variety turgescens Schmidle, but probably means var. subturgescens Schmidle 1893. Her bibliography does not cite any of Schmidle's publications. No mention of var. turgescens was found in Norstedt (1896, 1908) or in other publications.

c) St. muricatum var. dimidiatum Comère 1901 (pl. 12 fig. 13)

This variety was noted in Nordstedt (1908) but the original publication was not available.

4. Species related to St. muricatum

The following species are closely related to St. muricatum

St. hirsutum (Ehrenberg) Brébisson ex Ralfs 1848

St. botrophilum Wolle 1881

St. trapezicum Boldt 1888

St. arnellii Boldt 1885

a) *St. hirsutum* (Ehrenberg 1834) Brébisson ex Ralfs 1848 (p. 127; pl. 22, fig. 3) Pl. C Fig. 13:

> "...segments semiorbicular, rough with numerous hair-like spines; end view with three rounded angles and straight or slightly convex sides...
>
> "Frond variable in size, about equal in length and breadth, deeply constricted at the middle; segments semiorbicular, hirsute rather than spinous; hairs numerous, scattered. End view triangular; the sides straight or slightly convex, and the angles broadly rounded.
>
> "I have gathered sporangia at Dolgelley and Penzance. They are orbicular, their spines short, and branched at the apex.
>
> "The hair-like spines are characteristic of this species.
>
> "Length of frond from 1/676 to 1/468 of an inch; breadth from 1/833 to 1/680; breadth at constriction 1/2300; diameter of sporangium from 1/744 to 1/480; length of spine of sporangium 1/2040."

St. hirsutum is considered by Ralfs (1848) and West *et al.* (1923; p. 68) to be closely related to *St. muricatum*. West *et al.* note that there are intermediate forms between the two species. Although the stoutness of the conical granules varied, no hair-like spines, characteristic of *St. hirsutum*, were ever observed in culture in the present study. As previously mentioned, granules tended to be more developed in field material. They were usually ca. 1 µm long or less, but short conical spines as long as 2.7 µm were encountered. The wide open sinus and more elliptic semicells of _St. muricatum_ also differentiate it from _St. hirsutum_. _St. hirsutum_ appears to be a species distinct from _St. muricatum_.

b) _St. botrophilum_ Wolle 1881 (p. 2; pl. 6, fig. 13) Pl. C Fig.15:

> "St. mediocre, paulo longius quam latius, distincte granulosum; granulis in series regulares ordinatis; a fronte, semicellulis triangularibus, angulis inferioribus rotundatis subito in dorsum late truncatis, a lateribus, late ellipticis divergentibus, a vertice, triangularibus. Diam. .0015"-.0016"...
>
> "This form belongs to a class like _St. pygmaeum_, Bréb., _St. punctulatum_, Bréb., _St. rugulosum_, Bréb., etc., but is separated by the Cosmarium-like, truncate form as seen in front view."

St. botrophilum was the object of a good review by Brook and Williamson (1983). These authors are convinced that the Taylor (1935a, pl. 33 fig. 11, 13) and Croasdale and Grönblad (1964, pl. 18 fig. 1) records of _St. botrophilum_ represent instead _St. muricatum_. However, at least in Taylor's figure, the sinus is definitely closed, a characteristic that distinguishes it from _St. muricatum_. _St. botrophilum_, in Grönblad 1920 (p. 58; pl. 2, fig. 34, 35), may be better placed in _St. muricatum_ because of its open sinus. Wailes' (1930, fig. 26) report of _St. botrophilum_ from Mount Ferguson (British Columbia) does appear to fit very well the description of that species.

c) St. trapezicum Boldt 1888 (p. 35; pl. 2, fig. 46) Pl. C Fig. 16:

> "S. fere tam latum quam longum vel paullo longius, profunde constrictum, sinu profundo acutangulo; semicellulae a fronte visae subtrapezicae, dorso lateribusque levissime concavis, ventre convexo, angulis inferioribus rotundatis, superioribus obtusangulis, membrana aculeis in seriebus verticalibus ordinatis instructa; a vertice visae trigonae, lateribus leviter retusis.
>
> "Long. 43,2-50,4 μ; lat. 42-43,2 μ; lat. isthmi 15,6-19,8 μ; lat. apic. 16,8 μ."

This species is very similar to St. hirsutum and St. botrophilum, although its cells are more depressed and the bases of its angles are more elongated. The record of Thomasson (1959) of St. trapezicum from Argentina may be better named St. muricatum : the cells do show a somewhat pyramidal shape but the bases of the angles are more rounded, not as wide, and the sides of the semicells are more convex.

d) St. arnellii Boldt 1885 (p. 112; pl. 5, fig. 21) Pl. C Fig. 14:

> "S. parvum, diametro circiter quinta parte longius, profunde constrictum sinu lineari angusto extremo ampliato; semicellulae trapezicae, e basi recta sursum angustatae, lateribus modice convexis, angulis superioribus obtusis, inferioribus late rotundatis, margine granulato-dentatae, ad marginem versus granulatae, granulis et a fronte et a vertice radiatim concentriceque dispositis, intima in serie et ad basin semicellularum singulis, ceteris in seriebus binis; e vertice conspectae triangulares, angulis obtuse rotundatis, lateribus in medio leviter retusis.
>
> "Long. 36-38,4 μ; lat. 31,2-32,4 μ; lat. isthm. 12 μ."

St. arnellii is smaller than St. muricatum, its semicells are more truncate-pyramidal in shape and its sides, in end view are free of granules. The interpretation of this taxon in the literature varies. West et al. (1923; p. 80) note the presence of emarginate granules in the middle of the margin in apical view. Their cells also seem more depressed than in Boldt's illustration of St. arnellii and have a more widely open sinus. However Förster (1970, pl. 27 fig. 13) shows elliptic semicells without emarginate granules. St. arnellii is very similar to St. botrophilum but it is bigger and has a closed sinus. The strong affinity between the two species would seem to justify the transfer of St. arnellii as a variety of St. botrophilum. However a more thorough study of the two species would be necessary before doing so.

5. Conclusion

The group of Staurastrum with pyramidal-truncate to subelliptic shaped semicells ornamented with granules to spines comprises a number of different species. Other Staurastrum include numerous varieties and forms of one major species. In the present case, there is not one or two principal species under which all the variations are described varieties or forms, but a group of species.

These species can be subdivided into three sub-groups. The first one contains species with semicells of definite pyramidal-truncate shape and ornamented with granules: St. arnellii, St. botrophilum, St. pyramidatum and St. trapezicum. The second one has elliptic semicells with rounded bases, although the more or less flat apex does sometimes give them a somewhat pyramidal shape, and are ornamented with granules: St. muricatum, St. pseudomuricatum Grönblad 1945 (pl. 29 fig. 248) and St. turgescens Notaris 1867 (p. 51 pl. 4 fig. 43, not seen). The third group includes semicells of a shape similar to group two but with short spines instead of granules: St. brebissonii and St. hirsutum. In fact, these are closely related to a whole group of short spined species such as described under St. brebissonii.

TABLE 14

CELL DIMENSIONS AND RADIATION OF ST. MURICATUM
(Clonal cultures; N=see Materials and Methods;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures		L(csp) (µm)				l(csp) (µm)				Is (µm)				L/1	Radiation (%)	
Clone HC	Source	Average	Range	S.D.	C.V.	Average	Range	S.D.	C.V.	Average	Range	S.D.	C.V.		3	4
275	Munday 16-V-80	53	48-58	2.12	4.08	42	38-46	1.89	4.75	17	15-19	0.88	5.30	1.26	97.7	2.3
276	" "	53	50-57	2.41	4.52	42	37-46	2.11	5.01	17	15-17	0.64	3.88	1.26	98.2	1.8
283	" "	53	46-58	2.78	5.29	42	35-50	2.70	6.49	17	15-19	0.98	5.73	1.27	100.0	--
284	" "	54	48-60	3.28	6.08	43	37-51	2.62	6.08	17	14-18	0.98	5.92	1.25	100.0	--
408	Lost 18-VII-80	51	46-55	2.49	4.92	41	37-45	2.16	5.31	17	17-19	0.62	3.57	1.22	100.0	--
409	" "	48	38-52	3.53	7.54	39	36-42	1.77	4.59	18	15-20	0.92	5.25	1.21	100.0	--
410	" "	50	45-53	2.43	4.91	40	35-42	1.89	4.78	17	15-18	0.70	4.21	1.25	100.0	--
411	" "	48	43-51	2.27	4.79	40	37-43	1.91	4.83	17	16-19	0.81	4.71	1.19	100.0	--
414	" "	48	45-53	2.60	5.43	38	33-43	1.76	4.60	18	15-19	0.99	5.61	1.26	100.0	--
415	" "	49	33-55	4.03	8.25	40	35-47	2.33	5.83	17	14-19	0.97	5.72	1.22	100.0	--
417	" "	46	44-51	1.57	3.39	39	37-41	1.08	2.76	17	16-18	0.67	4.01	1.18	100.0	--
418	" "	47	40-54	3.30	7.08	38	32-42	1.94	5.16	17	14-19	1.01	6.06	1.24	100.0	--
492	Lost 20-IX-80	50	43-55	3.32	6.58	41	37-46	2.27	5.55	17	14-18	1.08	6.38	1.23	100.0	--

continued

TABLE 14 (cont'd)

Field material Source	L(csp) (μm)	l(csp) (μm)	Is (μm)	L/l	Radiation 3
Munday 11-X-80	51	42	16	1.29	X
Munday 1-II-81	61	43, 52*	16	1.41, 1.18	X
Munday 13-III-81	49	44, 38*	16	1.13, 1.30	X
" "	55	44, 46*	15	1.26, 1.21	X
" "	53	48	17	1.12	X
" "	51	46, 48*	17	1.13, 1.08	X
Munday 7-IV-81	51	46, 42*	15	1.13, 1.23	X
Munday 27-IV-81	51	42, 40*	15	1.23, 1.29	X
" "	50	42, 44*	13	1.18, 1.13	X
" "	51	44, 42*	15	1.17, 1.23	X
Munday 17-V-81	50	44	13	1.13	X
" "	50	42	15	1.18	X
Munday 9-VI-81	53	48	17	1.12	X
Munday 11-VIII-81	49	40	13	1.23	X

*Dichotypical cells

Plate 4

St. muricatum var. muricatum

SEM photographs

1-5. Clone 414

1, 4. Cells viewed from the front and the apex showing differences in the development of the ornamentation

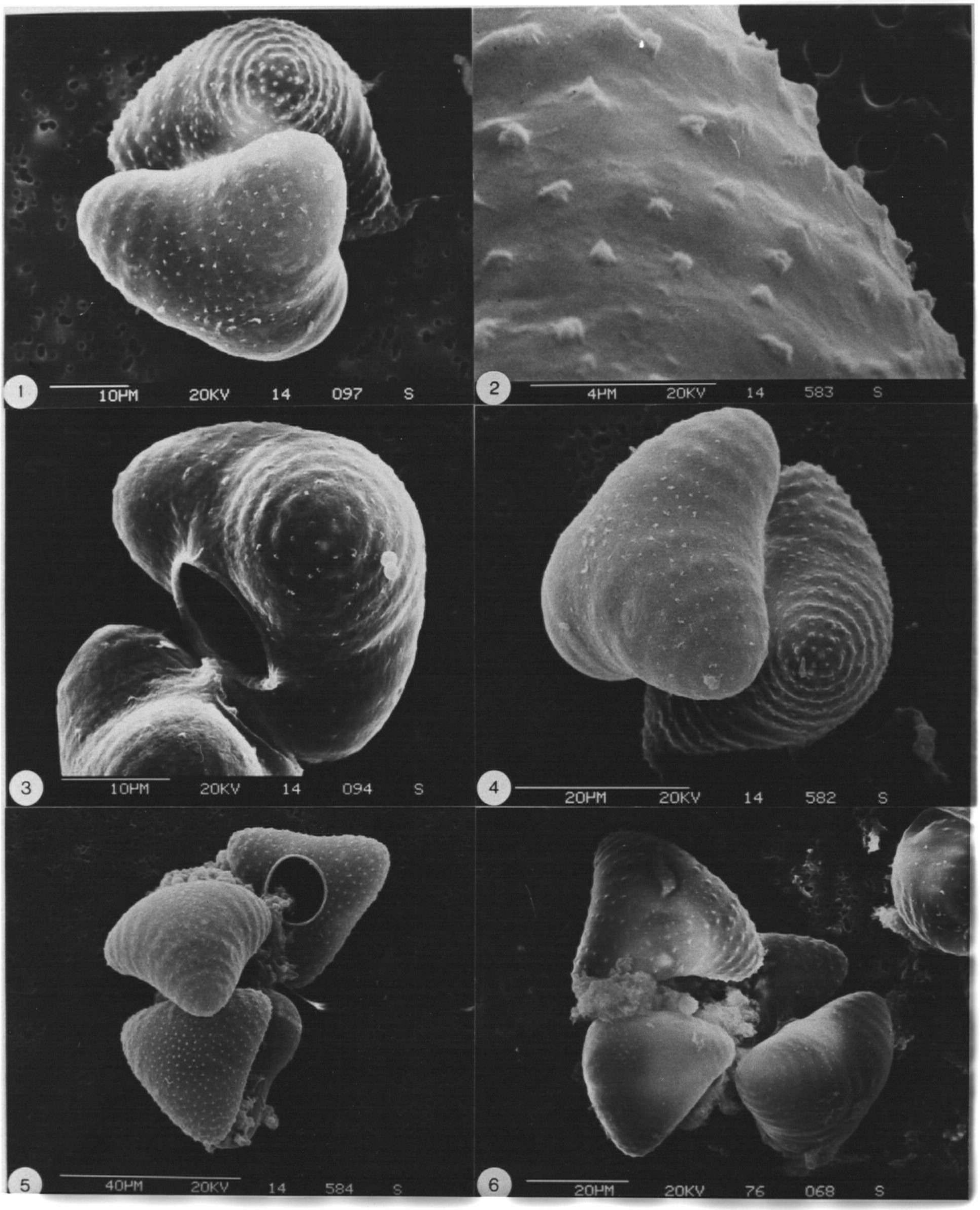
2. Detailed view of the granules

3. Isolated semicell showing the isthmus

5. Group of cells, one semicell in basal view on the right and two cells in vertical view on the left

6. Clone HC 276, group of cells in vertical view showing the apical ormamentation

169A



1
10ΜM 20KV 14 097 S
2
4ΜM 20KV 14 583 S
3
10ΜM 20KV 14 094 S
4
20ΜM 20KV 14 582 S
5
40ΜM 20KV 14 584 S
6
20ΜM 20KV 76 068 S

F. STAURASTRUM AVICULA VAR. AVICULA

St. avicula Brébisson ex Ralfs 1848 (p. 140; pl. 23, fig. 11)

Pl. C Fig. 18:

> "...segments with a forked spine on each side; each angle, in end view, terminated by a mucro-like spine...
>
> "Frond very minute, scarcely rough, the constriction producing wide triangular notches; segments having on each side a spine forked like the tail of a swallow. End view with three slightly inflated angles or lobes, which are tipped by a spine.
>
> "The forked lateral spines of the front view mark the species.
>
> "Length of frond 1/907 of an inch; breadth 1/948; breadth at constriction 1/2403; length of spine 1/4098."

St. avicula was found in abundance on the leaves and stems of Nymphaea odorata and intermingled with other algae, in Como Lake. Stein and Borden (unpublished) note 14 records of the species in British Columbia, including Como Lake. Eight records of St. lunatum var. lunatum are given, including Como Lake and one for its var. planctonicum from Victoria Lake. St. denticulatum was recorded twice but not in the lower Fraser Valley.

Clones examined: HC 12, 20, 22, 24 from Como Lake, 7-VI-79; HC 58, 60 from Como Lake, 28-V-79; HC 325, 331, 354, 369, 383, 386 from Como Lake, 27-VI-80; HC 420, 424 from Como Lake, 18-VII-80 (Table 15).

Thirty-three clones of the species successfully grew in clonal cultures, and 14 of those were observed and measured (Table 15).

The semicells in front view appear elliptic or subtriangular. The apex is either convex or straight and the sides of the semicells are convex. The sinus is acute-angled and forms a small notch which opens widely (Pl. 5 Fig. 1-5; Pl. E Fig. 1-5, 7-9).

The angles are either rounded or more commonly, slightly elongated or prolonged into short processes (Pl. 5 Fig. 1, 5; Pl. E Fig. 1-5, 7-9), which are divergent and tipped with one to three spines. The typical spine arrangement, which according to Ralfs (1848) characterizes the species, is the presence of a forked spine at the angles, the outer spine being longer and divergent, whereas the spine towards the isthmus is shorter and convergent. This pattern is variable and in field material as well as in clonal cultures, cells have one, two or three spines (Pl. E Fig. 1-9). Dichotypical cells with one semicell with one spine and the other with two spines are observed in both culture and field material (Pl. E Fig. 5, 7) and are reported by Croasdale and Grönblad (1964 p. 204; pl. 18, fig. 12). When only one spine is present, a stub or a squared angle usually replaces the second spine (Pl. E Fig. 2). A unique bifurcate spine sometimes replaces the two forked spines (Pl. 5 Fig. 4, 5; Pl. E Fig. 8). This is similar to that shown by Croasdale (1957; pl. 5, fig. 84) for St. avicula forma. The length of the spines varies in field as well as clonal cultures (1.5-7 μm).

The apex and sides of the semicells are either smooth or undulated. When the angles are elongated in short processes, they usually are undulated. Depending on the degree of elongation of the angles, if any, three or four rings of granules surround them. In front or apical view, double verrucae may sometimes be seen on the apex (Pl. 5 Fig. 2). According to Brook (1967), they result from the fusion of apical pairs of granules. These double verrucae were of rare occurrence in material in this study and apical granules were not always present. As Brook (1967) points out, however, apical granulation may often be difficult to see, especially when the ornamentation of the cell is obscured by the cytoplasmic content.

In apical view, the semicell margins are slightly concave, with or without undulated margins (Pl. 5 Fig. 3). When two spines are present at the angles, they often overlap each other so that only one spine is clearly visible (Pl. E Fig. 6).

The cells from field material were all triradiate. In clonal cultures, they were usually triradiate, but tetraradiate and dichotypical cells with one semicell triradiate and the other tetraradiate made up to 4% of the cells counted (Clone HC 354, Table 15).

St. avicula var. avicula is a small species commonly reported in the literature and includes many varieties. Many species are also closely related. Literature reports, as well as observations of clonal cultures and field material in the course of the present study, have shown the species to be very variable.

The cells may have more or less rounded angles (W. West

1899, pl. 369 fig. 10; West _et al._ 1923, pl. 133 fig. 8-10; Wailes 1932, fig. 16; Grönblad 1952, fig. 32, 33; Croasdale 1965, pl. 8 fig. 3, 4; Förster 1970, pl. 27 fig. 5, 6; Coesel 1979, pl. 25 fig. 4) or angles elongated into short processes (Delponte 1877, pl. 12 fig. 22-29; f. Schmidle 1898, pl. 2 fig. 38; Grönblad 1920, fig. 36-38; Lowe 1923, pl. 4 fig. 13; Smith 1924b pl. 68 fig. 8-10; Irénée-Marie 1951, pl. 1 fig. 4; Ruzicka 1973, pl. 16 fig. 3; Thomasson 1972, pl. 1 fig. 8-13). The angles usually bear two spines but, sometimes, they will have only one (Grönblad 1952, fig. 32, 33; Croasdale 1965, pl. 8 fig. 3, 4; Thomasson 1972, pl. 1 fig. 8-13) or occasionally three (Brook 1967, Coesel 1979 pl. 25 fig. 4). The outline of the cell may be smooth (Delponte 1877, pl. 12 fig. 22-29; Schmidle 1898, pl. 2 fig. 38; Irénée-Marie 1951, pl. 1 fig. 4) or more or less denticulated or undulated (G.S. West 1899a, pl. 369 fig. 10; West _et al._ 1923, pl. 13 fig. 8-10; Grönblad 1920, pl. 3 fig. 36-38; 1952, fig. 32, 33; Wailes 1932, fig. 16; Croasdale 1965, pl. 8 fig. 3, 4; Förster 1970, pl. 27 fig. 5, 6; Ruzicka 1973, pl. 16 fig. 3; Thomasson 1972, pl. 1 fig. 8-13; Coesel 1979, pl. 25 fig. 4). The granulation may be limited to the angles (Schmidle 1898, pl. 2 fig. 32; Wailes 1932, fig. 16; Croasdale 1957, fig. 84; Coesel 1979, pl. 25 fig. 4). Apical verrucae are sometimes present (Grönblad 1920, fig. 36-38; Croasdale 1965, pl. 8 fig. 3, 4; Ruzicka 1973, pl. 16 fig. 3). The cells may be entirely covered with granules (G.S. West 1899a, pl. 369 fig. 10; Lowe 1923, pl. 4 fig. 13; Croasdale 1965, pl. 8 fig. 3, 4; Förster 1970, pl. 27 fig. 5, 6).

These different interpretations of the taxon often integrate characteristics of separate species, closely related to *St. avicula*. Such confusion may arise from the great variability of *St. avicula* and the naming of species and varieties on morphological variations that are not significant.

1. Proposed synonyms of *St. avicula* var. *avicula*

   St. avicula var. *brevispinum* Harvey 1892

   St. avicula var. *subarcuatum* (Wolle) W. et G.S. West 1894

   St. avicula var. *subarcuatum* f. *quadrata* Irénée-Marie 1957

   St. avicula var. *verrucosum* W. West 1892a

a) *St. avicula* var. *brevispinum* Harvey 1892 (p. 122; pl. 126, fig. 13) Pl. C Fig. 19:

> "The type of this species was reported in Article I, No. 52, but since then we have found var. *brevispinum* , which differs from the type by being larger (35μd); the spines shorter and thicker, and the sides of the end view concave. None of the type form were found with this..."

Harvey's dimensions expressed as μd(?), probably represent μm. This is very close to the width of 26.7 μm given by Ralfs (1848). Furthermore, all illustrations of *St. avicula* observed have straight or usually concave sides in end view. Ralfs (1848) notes the slightly inflated angles but not inflated sides. Harvey's claim that the concave sides were not seen in the type, disagrees with later illustrations of the type.

Harvey's illustration is totally inadequate; he does not even show an end view of the alga. West and West (1895a) noted that this taxon can not be accepted.

b) St. avicula var. subarcuatum (Wolle) W.et G.S. West 1894 (p. 10)

Basionym: St. subarcuatum Wolle 1880 (p. 46; pl. 5, fig. D) Pl. D Fig. 3:

Syn.: St. avicula var. verrucosum W. West 1892a (p. 174; pl. 23, fig. 2) Pl. C Fig. 20

Wolle's description is:

> "St. mediocre, granulatum, fere tam longum quam latum, medio profunde constrictum, sinu acutangulo ampliato; semi-cellulis a fronte visis ellipticis divergentibus, quasi observe lunatis, granulis in series transversas ordinatis; angulis productis bifidis achrois; dorso papilloso angustato producto, et late truncato; semi-cellulis a vertice visis triangularibus; angulis rotundatis brevi mucrone imposito; lateribus aut rectis, aut leviter concavis, in medio papillis ornatis, nonnumquam productis bifidis. Diam. .0013"-.0015"..."

This taxon was first collected in the United States but has since been found in both Europe and North America. The Wests' interpretation of var. subarcuatum is that:

> "Punctate and finely granulate examples of St. avicula occur more frequently than the glabrous forms. It is to the roughly granulate form that this variety applies..."

Wolle's description of St. subarcuatum did emphazise the presence of subapical or apical "papillae". Furthermore, apical verrucae were occasionally observed in clonal culture. Brook

(1967) notes that in the type species, pairs of granules may join to form double verrucae. Flensburg (1967) combines St. avicula with its var. subarcuatum, because "the systematic validity of the variety appears doubtful".

Many records of var. subarcuatum agree with the Wests' interpretation in that they are coarsely granulate but bear no verrucae (Taylor 1935a, pl. 34 fig. 3; Irénée-Marie 1939, pl. 50 fig. 5, 8; Förster 1970, pl. 27 fig. 7; Taft and Taft 1971, fig. 457). The degree of development of the ornamentation is a variable characteristic which makes a poor taxonomic criterion.

Following Flensburg (1967), it is proposed that var. subarcuatum be made synonymous with St. avicula var. avicula.

c) St. avicula var. subarcuatum forma quadrata Irénée-Marie 1957 (p. 153; pl. 1, fig. 3) Pl. D Fig. 7:

> "L:36-38.6 mμ; l:31-32.4 mμ; Is:11-11.5 mμ; Ep.:3.4-3.6 mμ...
>
> "Forma separata a varietate subarcuatum speciei S. aviculae forma apicali quadrangulari."

Tetraradiate specimens of St. avicula were occasionally observed in clonal culture. Irénée-Marie's forma quadrata would be better termed facies 4, in keeping with Grönblad and Růžička's (1959) recommendations.

d) St. avicula var. verrucosum W. West 1892a (p. 174; pl. 23, fig. 2) Pl. C Fig. 20:

> "Var. membrana distincte verrucosa.

"Long. 22.5-26 μ; lat. 33-37 μ; lat. isthm. 10 μ."

This variety is noted as a synonym of var. subarcuatum in West and West (1894a).

2. Taxa closely related to St. avicula

It is believed that the following taxa belong to St. avicula. However, since the problem is very complex and both species are ubiquitous, it is felt that a more thorough study should be carried out before transferring them to a different taxon.

St. denticulatum (Nägeli) Archer in Pritchard 1861

St. lunatum Ralfs 1848

St. lunatum var. subarmatum W. et G.S. West 1894

St. lunatum var. triangularis Börgesen 1894

St. lunatum var. planctonicum W. et G.S. West 1903

St. lunatum var. ovale Grönblad 1942

St. lunatum var. tvaerminneense Grönblad 1942

a) St. denticulatum (Nägeli) Archer in Pritchard 1861 (p. 738)
Basionym: Phycastrum denticulatum Nägeli 1849 (p. 128; pl. 8C, fig. 3) Pl. D Fig. 9:

Archer's description follows:

"Segments in f.v. subelliptic, inner margin somewhat more turgid than the outer, both undulate or toothed in a scolloped manner with an unequally forked or geminate spine on each side, the upper longer than the lower, the lateral projections having a series of transverse rows of minute granules; e.v. with three subacute angles the spine appearing as a mucro, sides slightly concave at the centre, the margin toothed as mentioned before. "L. 1-70 "'; thickness 1-5 "'."= _Phycastrum denticulatum_ (Näg.)G."

The main difference between _St. avicula_ and _St. denticulatum_ resides in the presence of granulation only around the angles in the latter species. Nägeli, as pointed out by Brook (1967), also shows the apex of the cell to be denticulated, a feature which was not represented by West _et al._ (1923, p. 38; pl. 133, fig. 13-15) nor by West and West (1906, pl. 11 fig. 11), Smith (1924b, pl. 68 fig. 5-7), Messikommer (1938, pl. 9 fig. 103). W. West 1890 (pl. 6, fig. 27) shows a specimen of _St. denticulatum_ with denticulated apex but with the body of the semicell completely covered with granules which are not restricted to the angles of the semicells.

It has been noted earlier that in some published figures of _St. avicula_ as well as the original illustration of _St. subarcuatum_, cells have granules only at the angles. Brook (1967) points out that apical ornamentation is often a difficult feature to distinguish and particularly if cell protoplasm is present. This was certainly true for the present study where some cells did not appear to have any apical ornamentation, whereas others did. In any event, Nägeli's original figure shows apical ornamentation. Because of the divergence between the original and subsequent publications, and the close relationship between _St. avicula_ and _St. denticulatum_, I agree with Brook (1967) that the species _denticulatum_ should be considered only as a form of _St. avicula_.

b) St. lunatum Ralfs 1848 (p. 124; pl. 34, fig. 12) Pl. D Fig. 10:

> "...frond rough with puncta-like granules; segments externally lunate, with an awn at each angle; end view with three inflated awned lobes...
>
> "This species resembles in figure Staurastrum dejectum , but it is larger. Frond deeply constricted at the middle; segments semilunate, the convex margins united, the outer margin rough with minute granules and truncate, each angle tipped by an awn or mucro which is directed obliquely outwards. End view three-lobed, the lobes inflated, obtuse and awned.
>
> "Its rough frond distinguishes Staurastrum lunatum from all the preceeding species, and the inflated awned lobes of its end view from all the following ones.
>
> "Length of frond 1/856 of an inch; breadth 1/686; breadth at constriction 1/2336; length of spine 1/4098."

St. lunatum is a common species which has been reported in many regions of the world. It is another close relative to St. avicula, the main difference between them being the presence of only one spine at each angle in St. lunatum. Croasdale and Grönblad (1964; p. 204) found dichotypical cells with one semicell resembling St. avicula and the other St. lunatum ; another cell of St. lunatum had one angle tipped with two spines with the three other angles bearing only one spine. This phenomenon was observed frequently in HC clones as well as in field material. All combinations were seen. Sometimes the two angles of one semicell each had two spines, whereas the two angles of the corresponding semicell had only one spine each. On other cells, one angle of the semicell bore one spine but the second angle of the same semicell had two spines. Cells with only one angle or with the four angles bearing one spine were also observed.

Based on the variation seen in the drawings presented on Pl. E Fig. 1-9, it seems that there is little differentiation between _St. avicula_ and _St. lunatum_. The number of spines at the angle, does not appear to be a stable taxonomic characteristic. In clonal and field material studied here, the predominant form had two spines at each angle, although the one spine variation was not uncommon. Reports of _St. lunatum_ or of its varieties are usually represented with a single angular spine at each angle. Grönblad (1960, p. 47) states that the main difference between a specimen he named _St. lunatum_ var. _messikommeri_ Grönblad 1948 and _St. avicula_ var. _exornatum_, is the constant presence of one spine at each angle in the former. It still seems that the number of spines at the angles is a feature which is too variable to differentiate between two species; _St. lunatum_ may be better considered as a form of _St. avicula_.

c) Infraspecific taxa of _St. lunatum_

i) _St. lunatum_ var. _subarmatum_ W. et G.S. West 1894 (p. 10; pl. 2, fig. 47) Pl. D Fig. 11:

> "Var. angulis attenuatis in spinam mucronatam.
>
> "Long. 30 μ; lat. c. mucr. 33 μ; lat. isthm. 11.5 μ."

This taxon appears to be rare. The length of the spines, and thus the presence of a mucro instead of a spine, is too variable a feature upon which to base a variety. West and West (1912) consider this taxon as synonymous with St. granulosum (Ehrenberg) Ralfs. It may be better to establish a forma rather than a variety for this minor distinction.

ii) St. lunatum var. triangularis Börgesen 1894 (p. 29; pl. 2, fig. 24) Pl. D Fig. 12:

> "Semicellulae a fronte visae fere triangulares dorso paene recto truncato, aculeis rectis. Cellula minor.
>
> "Long. = 20μ= lat. sin. acul.; lat. isthm.= 9.5μ; long. acul.= 3μ..."

This taxon was first recorded from Greenland. With its very wide open rounded sinus, and triangular shaped semicells with straight apex and sides, it is very different from St. lunatum. In his text, Börgesen uses the nomenclatural rank of variety but in the legend to his plate, he uses forma triangularis instead. This taxon may be better placed in another species.

iii) St. lunatum var. planctonicum W. et G.S. West 1903 (p. 546; pl. 16 fig. 11, 12) Pl. D Fig. 13:

> "Var. paullo major et latior, angulis semicellularum acutioribus, spinis minoribus; semicellulae a vertice visae cum lateribus latissime retusis.
>
> "Long. 40-44 μ; lat. sine spin. 42-50 μ; long. spin. 3-5.5 μ; lat. isthm. 14.5-16 μ..."

This variety was first found in Scotland and has since been reported from both Europe and North America. With its acutely produced diverging angles, it is not unlike some specimens observed in the present study (see Pl. E Fig.5, 7). The Wests indicate that the spines of var. _planctonicum_ are shorter than in the type. A comparison of some measurements may be of interest:

Length of spines:

St. lunatum var. _planctonicum_ in West and West 1903 (p. 546): 3-5.5 µm

St. lunatum in West _et al._ 1923 (p. 30): 3.5-12 µm

St. lunatum in Ralfs 1848 (p. 124): 1/4098" or ca. 6 µm

St. avicula-lunatum Pl. E Fig. 7: 3.5, 5.4 µm.

Thus, the range of variation in the length of the spine is wider in West _et al._ (1923) than in West and West (1903) or Ralfs' original description of _St. lunatum_.

Although Smith's (1924b; pl. 68, fig. 11-13) figures show the elongated diverging angles of the variety _planctonicum_, Irénée-Marie (1939; pl. 50 fig. 6) and Coesel (1979, pl. 25 fig. 1, 2) do not stress this important feature. Grönblad (1960; fig. 208-212) shows different formae of _St. lunatum_, among which there are some algae with almost rounded or slightly pointed angles (fig. 211), and others with one (fig. 208) or two (fig. 210) short divergent spinules or with elongated angles (fig. 212) comparable to var. _planctonicum_ (see Pl. D Fig. 14). His observations and my study emphasize the close affinity between var. _lunatum_ and var. _planctonicum_. It is proposed that var. _planctonicum_ be considered only as a minor variation of _St. lunatum_.

iv) St. lunatum var. ovale Grönblad 1942 (p. 40; pl. 5, fig. 1, 2) Pl. D Fig. 15:

> "Cellulae habitu ut in var. tvaermineense Grönbl. A vertice visae ovales. Massa chlorophyllacea centralis in utraque semicellula nucleis amylaceis singulis et laminis radiantibus. 6. Long. 32 c. spin. lat. 57 s. spin. lat. 31 crass. 18 ist. 9 μ."

Grönblad (1952) expresses the doubt that this variety, first found in the Swedish Lappland, belongs to St. lunatum, and states that it is a temporary arrangement. In his specimens from Greenland (Grönblad 1952), the angles often have two tiny spines at each angle instead of one mucro. The characteristic oval shape of the cell with almost parallel spinules is fairly distinct from St. lunatum which has elliptic or triangular semicells with straight or slightly convex apices and strongly convex sides in front view, the divergent spines being directed upward. In accordance with Grönblad (1952), this variety should be classified in a different species.

v) St. lunatum var. tvaerminneense Grönblad 1942 (p. 42).

> "Syn. St. lunatum Ralfs forma Grönbl., Tvärminne p. 266 Fig. 43-44 (long. 23 lat. 30 ist. 9 μ). Differt a typo granulis in seriebus paucioribus, numero 8, dispositis. Sinu introrsum lineari extrorsum dilatata, angulis basalibus semicellularum valde rotundatis."

No figure was provided in Grönblad (1942) and the figure referred to on the first line of the description was not available. No record of the variety was found in later publications, and the description does not stress any feature which would make this variety obviously different from St. lunatum.

3. Other infraspecific taxa of St. avicula

The following taxa have characteristics which have not been observed in this study and no conclusions can be drawn. Some have been placed as synonyms of other taxa by different authors.

St. avicula var. aciculiferum W. West 1889

St. avicula var. inerme Irénée-Marie 1949

a) St. avicula var. aciculiferum W. West 1889 (p. 293; pl. 291, fig. 12) Pl. D Fig. 4

Syn.: St. aciculiferum (W. West) Andersson 1890 (p. 11; pl. 1, fig. 4).

This rare variety is considered a separate species, St. aciculiferum, by Andersson. At least two new varieties of St. aciculiferum have been named, var. pulchrum (W. et G.S. West) Förster 1970 (p. 332; pl. 27, fig. 21) and var. burkartii Tell 1980 (p. 146 pl. 1 fig. 10)

The elongated processes and subapical spines illustrated by W. West were not seen in the material observed in this study. Andersson's interpretation of this taxon as a distinct species, appears to have been endorsed by modern authors who named new varieties of the species and I agree with their interpretation.

b) St. avicula var. inerme Irénée-Marie 1949a (p. 102; pl. 1, fig. 1) Pl. C Fig. 17:

> "...Planta minutissima cujus corpus simillinum typicae speciei, sed dimidio minor et cujus anguli in inermis processibus producunt. Optimum est religare hanc varietatem ad speciem Aviculam tanquam varietas inermis."

With its small size and the lack of spines at its angles, this variety, first reported in the area around Trois-Rivières (Québec, Canada), is easily distinguished from St. avicula var. avicula. It appears to have been reported only from the Trois-Rivières area (Irénée-Marie 1949a, 1957).

4. Uncertain varieties of St. avicula

The original publications of the following taxa were not available and no conclusions can be drawn.

St. avicula var. rotundatum W. et G.S. West 1907

St. avicula var. exornatum Messikommer 1929

a) St. avicula var. rotundatum W. et G.S. West 1907 (p. 214; pl. 15, fig.25) Pl. D Fig.5:

This alga was first collected in Burma. It appears to be rare. The rounded angles, open sinus and granules covering most of the cell, seem to be the most important feature of this alga. All of these characteristics were seen in published reports of St. avicula (see for example the very similar alga illustrated by Wailes 1932, fig. 16, and which differs mostly by the more convex apex, straighter sides of the semicell and granules grouped around the angles). Cells with rounded angles were found in clonal cultures (Pl. E Fig. 4, 8). This may be a synonym of St. avicula but no conclusion can be drawn without consulting the original publication.

b) St. avicula var. exornatum Messikommer 1929 (pl. 1, fig. 15)

The original publication of this variety, which seems to be rare, was not available; a figure given by Coesel (1979, pl. 25 fig. 5, 6) is shown on Pl. D Fig. 6. According to Grönblad 1948 (p. 417), this variety may be a synonym of St. avicula var. subarcuatum (Wolle) W. et G.S. West, but consultation of the original description is necessary before any conclusion can be made.

5. Related species to St. avicula

The following species are similar to St. avicula var. avicula

St. caronense Irénée-Marie 1949a

St. granulosum (Ehrenberg) Ralfs 1848

a) St. caronense Irénée-Marie 1949a (p. 103; pl.1, fig. 3) Pl.D Fig. 8:

> "... L.(sp): 27.3-27.5; (cp): 35.4-36.5; l.(sp): 25.5-25.8; (cp): 35.4-36.2; Is.: 10.8-11... Cellula parva constrictione profunda, sinibus apertissimis et acutis ad apicem. Semicellulae fere semi-circulares arcu ad isthmum verso, diametris apices efficientibus. Laterales anguli in longis processibus leviter granulosis producti et in 2 vel 3 divergentibus validis spinis desiti. Ab spicale visa stella cum 4 processibus 3 vel 4 granulorum annulis ornatis, cujus leviter capitati apices 2 spinis terminantur prominentibus altera super alteram (saepissime 3

triangulatim dispositis). Margines leviter undulatae praeter in mediis qui retusi sunt. Quaeque semicellula 4 parie alibus chloroplastibus ornata, reliquentes vacuum inter se in centro, ab polo ad polum visum ut licidum punctum a vertice visum."

This taxon was first reported from the Trois-Rivières area (Quebec, Canada), but has not been recorded since. This small species has much in common with St. avicula. It is similar in shape, the angles are produced and tipped with two or three spines and the sinus is acute and widely open; it is tetraradiate with a straight apex and granulation restricted to the angles. All these characteristics have been observed in published illustrations or clonal cultures of St. avicula. It is not clear why Irénée-Marie did not stress the resemblance between his species and St. avicula. The description of St. caronense does not state any strong feature which justifies the creation of a new species but its constant tetraradiation seems to distinguish it from the mostly triradiate St. avicula var. avicula. Observation of the material from the type locality would be advised before placing this taxon as an infraspecific taxon or synonym of St. avicula var. avicula.

b) St. granulosum (Ehrenberg 1839; p. 51, 56 pl. 1 fig. 12) Ralfs 1848 (p. 217)

Syn.: St. lunatum var. subarmatum W. et G.S. West 1894

St. granulosum is a small punctate alga of shape similar to St. avicula but with angles having only " a mucro (or very minute spine)" (West and West 1912; p. 189, pl. 128 fig. 10-12). West and West (1912) see St. lunatum var. subarmatum as a synonym of this species. This alga was first described by Ehrenberg (1839) under the name Desmidium granulosum. Ralfs 1848 (p. 217) transferred it to the genus Staurastrum but did not give any description or figure, noting only that " this species is known to me only by name."

Ehrenberg's publication was not available. From other illustrations of the species, it appears to be closely related to St. avicula. One very interesting record is by Taft and Taft (1971, fig. 468) where the four angles each bear two minute spines instead of one. The Taft and Taft record would be better identified as St. avicula, because of the presence of two spines and since the spines have been shown to vary in length in St. avicula. Before drawing any conclusion about St. denticulatum, a more thorough investigation and observation of the original publication is necessary.

6. Conclusion

In conclusion, the group St. avicula-denticulatum-lunatum-granulosum comprises many species and varieties, among which intermediate forms are known. The number of spines at the angles, the ornamentation or the shape of the angles have proved to be variable in the Como Lake populations and in clonal cultures and justifies the need for a very thorough and critical reevaluation of the whole taxonomic complex.

TABLE 15

CELL DIMENSIONS AND RADIATION OF ST. AVICULA
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(csp) (μm) Average	Range	S.D.	C.V.	l(csp) (μm) Average	Range	S.D.	C.V.	Is (μm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3		
12	Como 7-VI-79	25	22-28	1.35	5.54	28	24-34	2.31	8.40	10	8-11	0.79	8.25	0.89	98.8	--	1.2
20	" "	24	23-27	1.27	5.23	25	22-29	1.82	7.76	10	9-12	0.65	6.56	0.88	100.0	--	--
22	" "	25	20-28	2.04	8.27	27	22-32	2.68	9.99	10	9-12	0.89	8.63	0.92	98.4	1.6	--
24	" "	23	19-27	1.95	8.49	26	19-30	2.81	10.90	9	6-12	1.40	15.19	0.89	98.4	1.6	--
58	Como 28-V-79	25	22-30	1.78	7.21	26	22-33	2.87	10.88	10	7-12	1.00	9.96	0.93	98.4	1.6	--
60	" "	24	21-27	1.84	7.74	26	21-31	3.13	12.12	11	9-12	0.79	7.34	0.92	100.0	--	--
325	Como 27-VI-80	25	22-31	1.87	7.37	26	22-32	2.37	8.08	11	9-14	0.88	8.38	0.97	97.7	--	2.3
331	" "	25	22-33	2.31	9.32	28	22-41	3.85	13.92	10	8-16	1.61	14.79	0.87	98.6	1.4	--
354	" "	24	22-27	1.80	7.53	25	22-31	2.55	10.12	10	7-13	0.96	9.32	0.85	95.9	0.7	3.4
369	" "	26	23-28	1.48	7.80	28	24-32	2.11	7.60	11	10-12	0.83	7.35	0.81	99.5	--	0.5
383	" "	25	22-29	1.83	7.64	27	23-32	3.17	11.87	11	9-12	0.87	8.10	0.86	98.2	1.8	--
386	" "	27	24-31	1.71	6.36	28	23-34	2.66	8.42	12	10-15	1.03	8.48	0.86	98.3	1.7	--
420	Como 18-VI-80	25	22-28	1.84	7.34	28	23-34	3.05	11.05	10	8-11	0.74	7.36	0.81	98.6	0.5	0.9
424	" "	25	23-29	1.30	5.17	27	22-34	2.61	9.82	11	9-13	0.96	8.95	0.95	98.0	--	2.0

continued

TABLE 15 (cont'd)

Field material

Source	L(csp) (µm)	L(ssp) (µm)	l(csp) (µm)	l(ssp) (µm)	Is (µm)	Sp	L/l	Radiation 3
Como 16-V-79	28	21	24	--	5	--	1.15	X
" "	21	--	28	--	7	--	0.74	X
" "	17	--	28, 27*	--	7	--	0.61, 0.63	X
Como 28-V-79	21	--	25	23	9	--	0.82	X
Como 7-VI-79	26	--	30	--	--	--	0.88	X
" "	26	--	29	--	--	--	0.89	X
" "	26	19	30	--	5	--	0.88	X
" "	18	--	28, 32*	--	6	--	0.64, 0.57	X
" "	20	--	30	--	7	--	0.67	X
" "	24	21	30, 25*	--	6	3, 4, 2, 5, 6, 4, 5.	0.84, 0.96	X
" "	23	--	29	--	6	--	0.78	X
Como 14-VI-79	25	20	32, 32*	--	7	--	0.78, 0.80	X
Como 28-VI-79	27	--	27	--	8	--	1.00	X
Como 6-VII-79	18	--	26	--	8	--	0.69	X
Como 26-VIII-79	28	20	32	--	7	--	0.90	X
Como 1-VIII-79	23	--	32	--	7	--	0.71	X
" "	20	17	23	11	6	--	0.88	X
Como 15-VIII-79	21	--	34	--	7	--	0.62	X

*Dichotypical cells

continued

TABLE 15 (cont'd)

Field material

Source	L(csp) (μm)	L(ssp) (μm)	l(csp) (μm)	l(ssp) (μm)	Is (μm)	L/l	Radiation 3
Como 23-II-80	27	--	36	--	10	0.74	X
Como 27-VI-80	22	19	31	--	8	0.70	X
" "	24	20	31	--	9	0.77	X
Como 18-VII-80	27	21	32	25	9	0.84	X
" "	25	21	31	--	8	0.80	X
" "	25	19	29, 30*	--	7	0.86, 0.82	X
Como 8-VIII-80	21, 23	19	28, 31*	--	7	0.74, 0.73	X
" "	21	19	28, 32*	--	8	0.74, 0.65	X
" "	23	20	25	21	8	0.91	X
Como 1-XI-80	26	23	31	25	8	0.83	X
Como 7-IV-81	32	26	38	28	9	0.83	X
Como 28-VIII-81	24	21	29	--	7	0.82	X
" "	23	21	29	--	7	0.79	X
" "	22	--	27	--	8	0.81	X
" "	26	22	30	--	8	0.86	X

*Dichotypical cells

Plate 5

<u>St.</u> <u>avicula</u> var. <u>avicula</u>

SEM photographs

1. Clone HC 24, cell in front view

2, 3. Clone HC 22

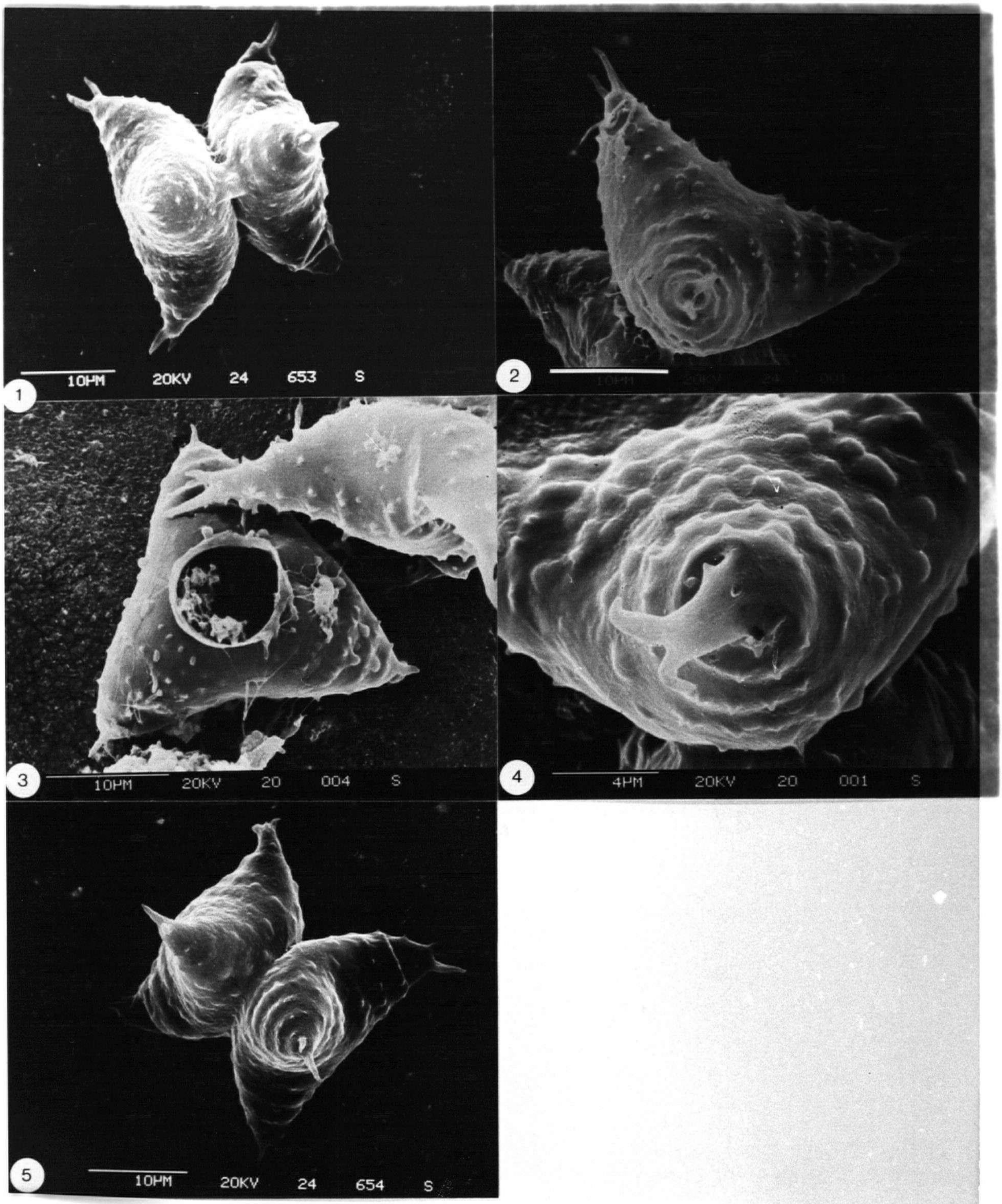
2. Cell viewed from the front and the apex showing the double apical verrucae

3. Isolated semicell in basal view.

4. Clone HC 20, detail of a cell in front view showing a bifurcate spine

5. Clone HC 24, cell in front view showing a bifurcate spine (upper right angle) and a forked spine (lower right angle)

192A



1
10PM 20KV 24 653 S
2
3
10PM 20KV 20 004 S
4
4PM 20KV 20 001 S
5
10PM 20KV 24 654 S

G. STAURASTRUM PROBOSCIDEUM FORMA MINOR INCLUDING ST. PROBOSCIDEUM VAR. PROBOSCIDEUM

St. proboscideum (Ralfs) Archer f. *minor* (Schmidle 1898, p. 60 pl. 3 fig. 16) Prescott, Bicudo et Vinyard 1982 (p. 285; pl. 439, fig. 4)

Basionym: *St. borgeanum* Schmidle f. *minor* Schmidle 1898 (p. 60; pl. 3, fig. 16) Pl. E Fig. 10:

> "Cellulae minores, 20 μ longae et latae, aut 37-32 μ latae, 32-29 μ longae eadem granulatione (supra isthmum interdum binis seriebus granulorum), e vertice plerumque vix contortae...
>
> "Die Exemplare der forma *minor* nähern sich dem *St. polymorphum*."

There are only two records of *St. proboscideum* var. *proboscideum* in British Columbia, both from the Peace River area (Stein and Borden, unpublished). The similar species, *St. borgeanum*, has never been recorded. However, the variable and closely related *St. polymorphum* var. *polymorphum* has been reported 38 times, including from Lost, Munday and Como Lakes. The similarity between the three taxa will be discussed later.

Clones examined: HC 2, 4, 6, 62 from Como Lake, 28-V-79; HC 242 from Como Lake 26-IV-80; HC 278 from Como Lake, 16-V-80; HC 333, 334, 362, 363, 370, 378, 381, 388, 389 from Como Lake, 27-VI-80; HC 422 from Como Lake, 18-VII-80; HC 293, 295, 301 from Munday Lake, 7-VI-80; HC 433 from the VanDusen Garden, 28-VII-80 (Table 16).

Fifty-five of the clones isolated grew successfully and 20 were measured and observed, 17 from Como Lake, three from Munday

Lake and one from the VanDusen Botanical Garden.

In front view, the cell has a cup-shaped acute-angled sinus which opens widely. The base of the semicell usually has a ring of supraisthmial granules. The cells are slightly wider than long and the L/l ratio in field specimens is usually slightly lower than in clonal cultures (Table 16), indicating possibly shorter processes in cultures.

The apex is convex and usually bears more or less prominent double verrucae or granules (Pl. 6 Fig. 2, 3, 5-7). Granules are seen on the front face of the semicell (Pl. 6 Fig. 1). The angles are extended into processes of varying length (Pl. 6 Fig. 1-4) which are usually tipped with four minute spines. The processes, which are either parallel or convergent, are ornamented by concentric rings of small conical granules.

In apical view, the sides of the semicell are slightly concave and lined with small conical granules (Pl. 6 Fig. 5-7). The centre of the apex is free of ornamentation but lined by double verrucae (Pl. 6 Fig. 5, 7). On some cells, double verrucae are absent and replaced by simple granules (Pl. 6 Fig. 6). Conical granules run down on the front of the semicell from the most central verrucae or granules (Pl. 6 Fig. 5-7).

One dichotypical specimen was observed in field material whereas in clonal cultures as much as 5.0% of the cells counted were tri-tetraradiate (clone HC 278). Only tri- and tetraradiate semicells were observed in field material. In clonal cultures, tri-, tetra- or pentaradiate specimens were present (Table 16).

St. proboscideum f. minor is considerably smaller than St. borgeanum (L = 45; l = 53 μm) or St. proboscideum (L = 46; l = 41; Is = 11 μm). The size variation in field material from the present study is L = 21-31, l(cp) = 22-41 μm. In clonal culture it is, L = 19-34, l(cp) = 20-37 μm. Since this range differs largely from either St. borgeanum var. borgeanum or St. proboscideum var. proboscideum, forma minor is retained as a good forma. The transfer of St. borgeanum to St. proboscideum will be discussed later. Prescott et al. (1982) changed the name of the infraspecific epithet from minor to minus. This does not appear warranted since minor is the comparative of parvus and an adjectival form. Thus, the original epithet is kept in the present study.

1. Proposed synonym of St. proboscideum f. minor

   St. borgeanum var. parvum Messikommer 1949

St. borgeanum var. parvum Messikommer 1949 (p. 247; pl. 1, fig. 17) Pl. F Fig. 7:

"Lge. 30 μ, Br. 37 μ, Isthm. 12 μ."

This taxon was created after forma minor, but it also represents small forms of St. borgeanum. Messikommer may simply not have been aware of the existence of forma minor Schmidle 1898.

St. proboscideum (Brébisson ex Ralfs 1848) Archer in Pritchard 1861 (p. 742)

Basionym: St. asperum var. proboscideum de Brébisson ex Ralfs 1848 (p. 139; pl. 22, fig. 6, pl. 23 fig. 12) Pl. E Fig. 12:

Ralfs description follows:

" S. asperum (Bréb.); segments elliptic or somewhat cuneiform, rough with minute spines, which on the outer margin are usually dilated at the end or forked.

"α . Angles in end view rounded.

"β . proboscideum, Bréb.; angles in end view prolonged into short rays terminated by minute spines...

"Frond comparatively large, rough with minute acute granules or spines; segments slightly tapering on the inner side, so that their figure is somewhat cuneate, and the constriction forms a wide notch on each side. The outer margin is flattened, and its spines are usually more evident than the rest, and are also in general slightly forked. In α . the lateral margins are broadly rounded, but in β . they extend into a process about as long as broad and tipped with a few acute spines, which are larger than those on the segment itself. The end view, in which the sides are nearly straight, has the angles in α . rounded, but in β . terminated by short rays.

"The sporangia, which I have gathered at Penzance, are orbicular, and their spines are twice branched at the apex.

"The form of the segments distinguishes Staurastrum asperum from all states of S. muricatum. S. punctulatum is smaller, and its granules are more like puncta than spines. In S. rugulosum the segments in the front view are elliptic, not tapering at the junction, and its spine-like granules are confined to the angles.

"Length of frond 1/555 of an inch; breadth 1/615; breadth at constriction 1/2403; diameter of sporangium 1/519; length of spines 1/2040..."

The first valid publication of St. proboscideum was by Ralfs 1848 under the name St. asperum var. proboscideum.

Unfortunately as is true for many of Ralfs' illustrations, the figures are very poor and do not stress the distinctive features of the species. Archer (in Pritchard 1861) later gave the name St. proboscideum to this taxon. St. asperum var. asperum has been recorded only a few times and its validity is uncertain.

2. Synonyms of St. proboscideum var. proboscideum

St. borgeanum Schmidle 1898

St. proboscideum var. productum Messikommer 1942

a) St. borgeanum Schmidle 1898 (p. 60; pl. 3, fig. 7) Pl. E Fig. 11:

> "Cellulae submagnae, 45 µ longae, 53 µ latae profunde constrictae, constrictura ampla, intus rotunda, extus ampliata; semicellulae e fronte subcuneatae, lateribus valde divergentibus, concavis et in processus 2 granulatos, apice truncatos et granulato-dentatos exeuntibus, apice late rotundato. Membrana apicis glabra, area glabra undique serie processuum bifurcatorum parvorum circumdata, latera et basis processuum (e fronte) in series rectas verticales granulatae (granula processus bifurcatos apicis non nisi ad extremos angulos attingentia), supra isthmum series horizontalis granulorum. Cellulae e vertice quadrangulares, raro triangulares, lateribus concavis, acute granulatis, medio in apice glabrae, radiis subcontortis...
>
> "Unsere Algae steht zwischen St. hexacerum und cyrtocerum ; zu ihr gehört wohl als einfachere Form St. hexacerum var. ornatum Borge, l.c. Sie steht ausserdem dem St. basidentatum Borge nahe, unterscheidet sich aber durch die Granulation und Grösse. St. dubium West und St. proboscideum Archer sind ebenfalls nahe stehende Arten."

St. borgeanum is considered synonymous with St. proboscideum by Nordstedt 1908 (p. 32) and West et al. 1923 (p. 129-31).

Grönblad (1926) later rejected this synonymy and recognized *St. borgeanum* as a good species. Cedergren (1932) did suggest establishing a variety *borgeanum* of *St. proboscideum* for it.

Ralfs' drawings are too sketchy to be used as type species as stressed by Thomasson (1957). The figure in West *et al.* (1923; pl 143, fig. 9) proposed by Grönblad as the type figure for *St. proboscideum* does not resemble Ralfs' description. However, reading Grönblad's text, it appears obvious that he was referring to *St. cyrtocerum* (*sensu* West *et al.* 1923, pl. 149 fig. 9). Thomasson rectified Grönblad's error. Plate 143 fig. 9 is identified as *St. crenulatum* and has very short processes not tipped with spines. The cell illustrated on plate 149 fig. 9 has converging processes contrary to Ralfs' illustration. It also differs in dimensions:

St. cyrtocerum (West *et al.* 1923):
L: 23-29; l(cp): 33-60; Is: 8-11 µm.
St. asperum (Ralfs 1848):
L:45.8; l:41.3; Is: 10.6 µm.

These dimensions and the comparison between length and width show that West *et al.*'s taxon is not as long as but is wider, than Ralfs'. However, while describing two distinct taxa, that is *St. asperum* with rounded angles and its var. *proboscideum* with short processes, Ralfs gave only one set of dimensions. These dimensions, which point to a plant almost equal in length and width, may be misleading. I think that they refer to the specimen with rounded angles, that is *St. asperum*, rather than to var. *proboscideum*. Furthermore, Ralfs' illustrations are very sketchy and the front view gives no details of the cell ornamentation. Grönblad's decision to pair pl. 149 fig. 9 of West *et al.* (1923) with Ralfs' (1848) pl. 123 fig. 12 b and c, appears mostly based on the resemblance between the vertical views of those two cells. I feel that this decision is based on very poor information and is too subjective. The ICBN (1978, p. 75) states that the choice made by the original author is final (see *St. polymorphum*).

While noting that he recognizes *St. borgeanum* as a good species that differs from *St. proboscideum*, Grönblad (1926) does not state those differences. Thomasson (1957) thoroughly discusses *St. borgeanum* and related species although he witholds his conclusion on *St. proboscideum*.

Prescott *et al.* (1982) propose that *St. borgeanum* be reduced to synonymy with *St. proboscideum* and I agree with them. This is based on the variation observed among HC clones, particularly in the length and the stoutness of the processes (Pl. 6 Fig. 1-4), degree of development of the ornamentation, including the often indistinguishable supraisthmial ring of granules (represented in Schmidle 1898 for *St. borgeanum*) and lack of unmistakable illustration of *St. proboscideum*. *St. proboscideum* encompasses species with short stout processes intermediate between its var. *compactum* Grönblad 1927 (p. 26 fig. 89-90), discussed later, and the type species. The name *St. proboscideum* has to be chosen because of article 11.3 of the ICBN (1978). Ralfs' description being inadequate, I further suggest that it be emended to include Schmidle's description of St. borgeanum.

A remark is in order about the spelling of the species name. West et al. (1923; p. 29) used the name St. proboscidium instead of proboscideum as a few other authors have done (Wolle 1882, Messikommer 1942, Thomasson 1952). Why this happened is uncertain, as W. West (1890) used the correct name St. proboscideum. Without any doubt, the name proboscideum was used both by Ralfs (1848; p. 139) and Archer (in Pritchard 1861; p. 742).

b) St. proboscideum var. productum Messikommer 1942 (p. 165; pl. 17 fig. 3) Pl. F Fig. 1:

> "Die neue Varietät besitzt einerseits Ahnlichkeit mit St. proboscidium (Bréb.) Arch., anderseits mit St. Borgeanum Schmidle. Zum letzteren kann unsere Form nicht gezogen werden, weil ihre Zellarme gegen das Ende zu zu schlank sind und am Scheitel nur 3 gleichzeitig sichtbare, aber gut entwickelte Stachelchen tragen. Gegenüber St. proboscidium bedeutet dieses Moment kennen Widerspruch. Da nach der Auffassung von Grönblad (1926) pag. 26 St. borgeanum nicht mit St. proboscidium identifiziert werden kann, wie dies in West (1904-1923) pag. 129 (V) geschieht, so kommt für unsere Anschlussbestrebungen einzig St. proboscidium in Frage. Unsere Form unterscheidet sich aber von diesem neben anderen kleineren Abweichungen hauptsächlich durch ihre länger ausgezogenen und gegen das Ende zu mehr allmählich verschmälerten Zellarme.
>
> "Forma nostra a forma typica praecipue differt processibus longioribus apicem versus graduatim attenuatis. - "Long. 32 1/2 -33 μ, lat. (cum process. sed sine acul.) 33-38 1/2 μ, isthm. 12 1/2 μ."

This variety is distinguished by the processes which are gradually attenuated towards the extremity and tipped with three spines. The number of spines at the end of the processes is a feature which has been shown to vary considerably in both the present study and the literature. It is not a good taxonomical characteristic.

Variety productum is cited as a synonym of the species St. borgeanum by Thomasson (1957); however, the cells he studied are wider than Messikommer's, L = 36-45; l(csp.) = 52.5-60 μm. Otherwise the descriptions are in agreement.

3. Species related to St. proboscideum f. minor

The following species is closely related to St. proboscideum forma minor. Since its name has been widely used a more thorough investigation is suggested before drawing any conclusions.

St. polymorphum Brébisson ex Ralfs 1848 (p. 135; pl. 22, fig. 9, pl. 34 fig. 6) Pl. F Fig. 8:

> "...segments rough with minute granules, having on each side a short process tipped with spines; end view three- to six-rayed.
>
> Frond much smaller than that of Staurastrum gracile, deeply constricted at the middle; segments irregular in form, but generally broader than long. Each side terminates in a short truncate projection or process, which is scarcely longer than broad, and tipped by three or four distinct, diverging spines; frequently there are also a few inconspicuous scattered spines on the segment itself. The number of the angles or rays in an end view varies from three to six, but the four-rayed form is the most abundant. The size of the frond is proportionate to the number of these rays.
>
> "The sporangia which I have gathered at Dolgelley, are

orbicular; their spines are few and forked at the apex. I have seen three-rayed fronds coupled with four-rayed ones."

Some clonal and field material observed in the present study has similar dimensions to those of St. polymorphum. Ralfs (1848) states that it is "smaller and less spinous than St. asperum ", that is, after conversion of Ralfs' figures to µm, ca. 25 µm long, 22 µm wide and with an isthmus of 10 µm wide.

Some literature reports of St. polymorphum also closely resemble the material observed in the present study (Grönblad 1920, pl. 3 fig. 81-83; Taylor 1935a, pl. 34 fig. 4; Messikommer 1957, pl. 2 fig. 26; Förster 1965, pl. 8 fig. 27, 28; Coesel 1979, pl. 30 fig. 1-3). Field and clonal specimens which do not possess apical double verrucae (Pl. 6 Fig. 6) are closely allied to St. polymorphum.

St. polymorphum is often cited as being variable and Ralfs also noted this. It is also quoted as a species needing thorough revision (Florin 1957, Grönblad 1960), and has become a "rubbish box" type species for similar forms, as is St. paradoxum. All reports of St. polymorphum without a figure should be treated with caution.

Without the thorough study of the variability of the material observed here, isolated specimens with reduced ornamentation could well be considered as St. polymorphum. In the identification of the material of this study, much importance has been attached to the presence of double apical verrucae on most cells.

Grönblad (1960) suggests that either the type specimen of St. polymorphum should be that of Wittrock and Nordstedt exsicc. Nr. 71 or to simply reject the species. This exsicatta is not easily available. Furthermore, in article 7 of the ICBN (1978), a neotype is defined as "a specimen or other element selected to serve as nomenclatural type as long as all the material on which the name of the taxon was based is missing." Since the original publication of Ralfs is available, the rejection of the name St. polymorphum seems the best solution.

4. Other infraspecific taxa of St. proboscideum

The taxonomic features of the following taxa were not observed in the present study.

St. proboscideum var. americanum Wolle 1882

St. proboscideum var. altum Boldt 1885

St. proboscideum var. brasiliense Börgesen 1890

St. proboscideum var. subglabrum W. West 1890

St. proboscideum var. compactum (Grönblad) Prescott, Bicudo et Vinyard 1982

a) St. proboscideum var. americanum Wolle 1882 (p. 29; pl. 13, fig. 10) Pl. F Fig. 2:

> "This plant was collected in Crystal Bay, St. Lawrence River, Canada, by J. M. Adams. It bears some similarity to a variety of St. asperum, described by Brébisson, and also to a form, Javanica, described by Nordstedt; but it differs in the arrangement of the granules and in the shape of the rays (proboscidii), which are longer and more

cylindrical."

Wolle gives only a poor illustration of a vertical view of his plant. I suggest that the name be rejected as it is impossible to assign it to any taxon with the information provided. Prescott _et al._ (1982; p. 353) list it as a _Var. Inquir._

b) _St. proboscideum_ var. _altum_ Boldt 1885 (p. 117; pl. 6, fig. 34) Pl. F Fig. 3:

"Var. major tam longa quam lata. Semicellulae a fronte visae ventre valde inflato, dorso alte convexo, in medio truncato, margine dorsali aculeis firmis 2-3-fidis armato, radiis apice 3-5-cuspidatis, paullum incurvis, seriebus granulorum transversalibus ornatis; a vertice visae triangulares, lateribus subrectis vel paullulo convexis, intra margines laterales spinis trifidis 4 in seriebus simplicibus, lateribus parallelis, dispositis.

"Long. 76,8 μ; lat. = long.; lat. isthm. 16,8 μ."

The strong ornamentation of this variety and the presence of subapical spines suggest a stronger link with the _St. sebaldi-manfeldtii_ group (which will be examined later with _St. manfeldtii_ Delponte var. _parvum_ Messikommer) than with _St. proboscideum_.

c) _St. proboscideum_ var. _brasiliense_ Börgesen 1890 (p. 46; pl. 5, fig. 49) Pl. F Fig. 4:

"Forma major brachiis longioribus; semicellulae a vertice visae, margine in lateribus medio laevi, ad angulos versus undique 8 dentibus ornatae, intra marginem seriebus spinarum acutarum medio bifidarum praeditae.

"Long. 39 μ, lat. 70 μ, lat. isthm. 13 μ.

"Cfr. Ralfs Brit. Desm. pag. 139 tab. 23, fig. 12."

This variety is much wider and shorter than stated by Ralfs 1848 for var. proboscideum. It may also be better placed in the St. sebaldi-manfeldtii group.

d) St. proboscideum var. subglabrum W. West 1890 (p. 295; pl. 6, fig. 35) Pl. F Fig. 5:

"Var. margine undulato nec spinis truncatis vestitis, radii apicibus integris.

"This differs from the type in being undulately rough and not adorned with truncate spines, as well as in the entire apices of the processes."

West et al. (1923) state this variety has never been recorded since its description and is poorly represented. They consider it a doubtful form. The form represented on Pl. F Fig. 5 has very irregular features and does not show much relation to St. proboscideum. W. West may have observed an abnormal cell of an unknown taxon. Rejection of the name is proposed.

e) St. proboscideum var. compactum (Grönblad) Prescott, Bicudo et Vinyard 1982 (p. 286; pl. 439, fig. 6)

Basionym: St. borgeanum var. compactum Grönblad 1927 (p. 26; fig. 89, 90) Pl. F Fig. 6:

"Habitus plus compactus radiis brevioribus crassioribusque, membrana granulata etiam in apicibus radiorum, verrucis apicalibus valde depressis. Long. 34-37, lat. 28, isthm. 9,5-12 μ - Ist dem S. proboscideum in W & W, Mngr. V. Pl. 143, Fig. 14

> sehr ähnlich, nur mit etwas dickeren und stumpferen Fortsätzen. Ubrigens entspricht nach Dr Borges Ansicht diese kaum dem wirklichen Typus, und ich glaube, dass diese auch gut zu <u>S.</u> <u>Borgeanum</u> v. <u>compactum</u> gerechnet werden kann."

This variety vaguely resembles some forms with shorter processes seen in this study (Pl. 6 Fig. 2-4), but has a more elongated sinus and shorter and more compact processes. Croasdale's (1962, fig. 145) figure of this variety has a short sinus. This resembles specimens observed in the present study.

5. Uncertain infraspecific taxon of <u>St.</u> <u>proboscideum</u>

The original publication of the following taxon was not available

<u>St.</u> <u>proboscideum</u> forma <u>javanica</u> Nordstedt 1880 (p. 11; pl. 1, fig. 19)

Unfortunately, the illustration published by Nordstedt was not available, but Wolle (1882) states it resembles his var. <u>americanum</u>.

TABLE 16

CELL DIMENSIONS AND RADIATION OF ST. PROBOSCIDEUM F. MINOR
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (µm) Average	Range	S.D.	C.V.	l(cp) (µm) Average	Range	S.D.	C.V.	Is (µm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3	4	5	3-4	4-5
2	Como 28-V-79	24	19-26	1.66	6.95	30	24-35	3.02	10.10	10	7-11	1.06	11.02	0.79	11.6	97.3	1.1	---	---
4	" "	27	24-32	1.72	6.26	29	21.37	3.82	13.25	11	9-14	1.16	10.6	0.95	3.8	92.2	3.7	0.5	0.9
6	" "	24	19-26	1.66	6.95	30	24-35	3.02	10.08	10	7-11	1.06	11.02	0.79	0.7	94.0	5.2	0.1	---
62	" "	27	21-31	2.43	8.02	30	23-37	3.90	13.26	11	10-13	0.80	7.32	0.84	7.0	91.6	1.4	---	---
242	Como 26-IV-80	28	25-32	1.90	6.74	28	23-36	3.33	11.94	11	9-13	0.85	7.96	1.01	---	92.7	4.2	0.5	2.6
278	Como 16-V-80	27	24-32	1.78	6.58	32	25-35	2.28	7.22	11	10-12	0.68	6.38	0.85	---	93.5	3.5	5.0	2.5
333	Como 27-VI-80	28	25-32	2.13	7.69	30	24-37	3.92	13.04	10	9-12	0.56	5.39	0.92	1.6	98.4	---	---	---
334	" "	27	25-31	1.67	6.17	30	24-36	3.69	12.19	10	9-11	0.63	6.13	0.89	100.0	---	---	---	---
362	" "	29	24-34	2.57	8.82	30	21-36	3.52	11.90	11	9-13	1.16	10.63	0.98	2.0	95.9	2.0	---	---
363	" "	28	25-30	1.34	4.86	26	21-32	2.67	10.31	11	9-12	0.87	8.18	1.07	---	95.1	4.9	---	---
370	" "	28	26-32	1.41	4.89	31	24-37	2.88	8.67	11	9-13	0.69	6.63	0.92	2.3	93.1	4.6	---	---
378	" "	27	26-32	1.23	4.14	27	23-35	2.61	8.65	10	9-11	0.61	6.86	1.00	0.4	97.8	1.8	---	---
381	" "	28	25-32	1.75	6.32	30	25-41	3.68	11.88	11	9-12	0.82	8.08	0.91	---	84.2	10.5	0.9	4.4
388	" "	27	24-29	1.22	4.56	32	25-37	2.36	7.38	10	9-11	0.55	5.33	0.84	---	87.4	6.9	---	5.7
389	" "	27	24-29	1.31	4.84	31	27-35	2.82	9.06	10	10-11	0.44	4.39	0.87	---	84.6	10.4	---	5.0
422	Como 18-VII-80	25	23-28	1.59	6.41	27	23-33	3.19	11.78	10	9-12	0.67	6.59	0.92	---	96.4	1.5	2.2	---
293	Munday 7-VI-80	24	22-29	1.93	8.07	28	23-33	2.89	10.32	9	8-12	0.97	10.63	0.85	1.3	89.4	6.0	1.3	3.3

continued

TABLE 16 (cont'd)

Clonal cultures

Clone HC	Source	L(cp) (µm) Average	Range	S.D.	C.V.	l(cp) (µm) Average	Range	S.D.	C.V.	Is (µm) Average	Range	S.D.	C.V.	L/1	Radiation (%) 3	4	5	3-4	4-5
295	Munday 7-VI-80	24	20-30	2.66	10.96	26	20-34	3.43	13.17	9	7-12	1.09	11.76	0.93	---	81.1	11.9	2.1	4.9
301	" "	25	21-29	2.01	8.21	27	21-37	4.15	15.29	9	7-10	0.91	9.85	0.90	4.7	87.3	9.4	2.2	1.1
433	VanDusen Garden 28-VII-80	27	23-31	2.06	7.60	32	27-39	3.76	11.77	9	8-10	0.60	6.61	0.85	1.0	82.9	6.8	0.5	8.8

Field material

Source	L(cp) (µm)	l(cp) (µm)	l(sp) (µm)	Is (µm)	L/1	Radiation 3	4	3-4
Como 28-V-79	29	46	25	10	0.63			X
" "	21	35	--	--	0.61		X	
" "	27	34	--	11	0.78		X	
" "	25	34	--	8	0.74		X	
" "	25	33	--	7	0.76		X	
" "	21	22, 24*	--	6	0.80, 0.85		X	
" "	26	39	--	--	0.67		X	
Como 28-V-79	24	33	--	9	0.73		X	
Como 25-I-80	33	37, 41*	--	10	0.89, 0.80		X	
" "	31	41, 30*	--	11	0.75, 1.03		X	
Como 7-VI-80	27	38	--	8	0.70		X	
Como 27-VI-80	26	32, 37*	--	8	0.78. 0.70.		X	

*Dichotypical cells

continued

TABLE 16 (cont'd)

Field material

Source	L(cp) (µm)	l(cp) (µm)	Is (µm)	L/l	Radiation 3	4	3-4
Como 20-IX-80	24	27	7	0.88		X	
Como 1-XI-80	23	34	7	0.67		X	
Como 16-V-80	27	33	9	0.81		X	
Como 22-II-81	31	35, 38*	9	0.88, 0.81		X	
Como 7-VI-79	25	32, 31*	9	0.80, 0.82		X	

*Dichotypical cells

Plate 6

<u>St.</u> <u>proboscideum</u> f. <u>minor</u>

SEM photographs

(marker= 10 μm unless indicated otherwise)

1, 2. Clone HC 2

1. Cell in front view with long processes

2. Cell viewed from the front and the apex

3. Clone HC 6, cell viewed from the front and the apex; arrow indicates the supraisthmial ring of granules

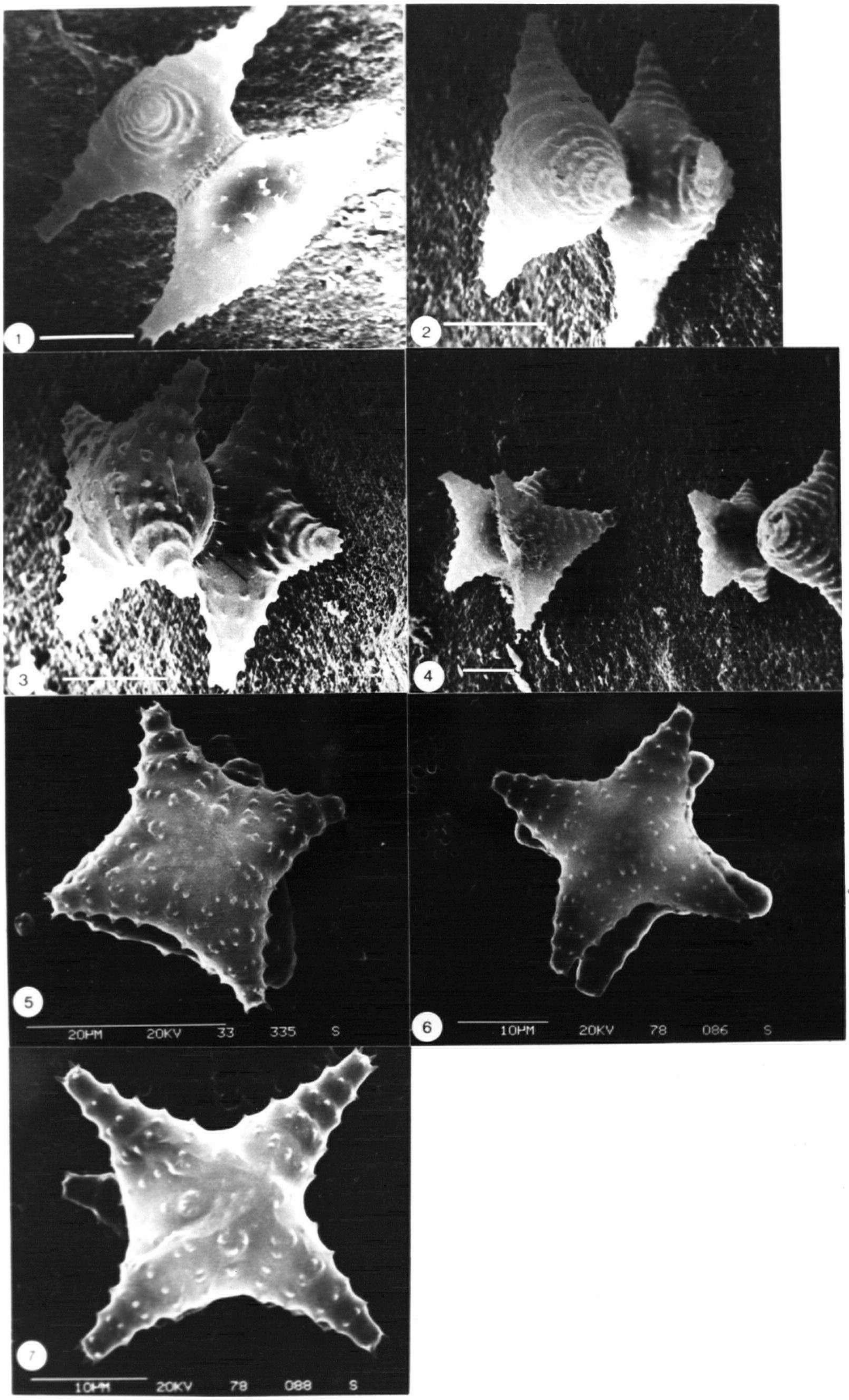
4. Clone HC 2, two dichotypical cells viewed in a tilted position.

5. Clone HC 433, cell in vertical view with apical double verrucae

6, 7. Clone HC 378

6. Cell in vertical view without apical double verrucae

7. Cell in vertical view with apical double verrucae


1
2
3
4
5
20µM 20KV 33 335 S
6
10µM 20KV 78 086 S
7
10µM 20KV 78 088 S

H. STAURASTRUM SEXCOSTATUM VAR. PRODUCTUM INCLUDING ST. SEXCOSTATUM VAR. SEXCOSTATUM

St. sexcostatum var. productum W. West 1892b (p. 733; pl. 9, fig. 34) Pl. F Fig. 14:

> "S. circiter tam longum quam latum (cum processibus); semicellulae processibus brevibus sex (non lobis), cum apicibus processuum truncatis et sexdentatis, cum annulo granulorum aculeatorum ad basem semi-cellularum; apices verrucis emarginatis irregulariter dispersis ornati; a vertice sexradiatis, radiis semi-cellulae utriusque alternantibus.
>
> "Long. 40-43 μ; lat. 43 μ; lat. isthm. 16-17 μ."

St. sexcostatum Brébisson ex Ralfs 1848 (p. 129; pl. 23, fig. 5) Pl. F Fig. 9:

> "...segments in the front view with a toothed angle at each side; end view circular, with five or six broad, short, toothed lobes...
>
> "Frond large, rough with conic granules which give a dentate appearance to the outline; segments about as broad as long, produced into a toothed angle on each side, where also a triangular sinus is formed between the angles. The end view is circular and elevated in the centre, and has five or six broad, short, toothed, marginal lobes. The transverse view has a large central opening surrounded by a row of large granules.
>
> "I refer this plant to Brébisson's Staurastrum sexcostatum, on his own authority, but a drawing sent by him of S. sexcostatum represents a smaller state.
>
> "Length of frond 1/661 of an inch; breadth from 1/833 to 1/694; breadth at constriction 1/1597."

St. sexcostatum var. productum was found in Jacobs Lake among plants of Utricularia during the summer months. Stein and Borden (unpublished) list only one record of St. sexcostatum var. sexcostatum in British Columbia and two records for St.

sexcostatum var. productum.

Clones examined: HC 427, 430, 469 from Jacobs Lake, 8-VIII-80 (Table 17).

Semicells of Staurastrum sexcostatum var. productum are subtriangular in shape with a convex apex and a cup-shaped sinus forming an acute notch in the middle of the semicell (Pl. 7 Fig. 1). In clonal culture, the cells are about as long as wide or slightly longer. The cells are slightly wider than long in field material (Table 17). The base of the semicell has a supraisthmial row of granules (Pl. 7 Fig. 1-3, 6) but this row is not always distinguishable with the light microscope. This may be due to the variation in the size of the granules and to the cell content which obscure their presence.

The apex is ornamented with double verrucae. The degree of development of the apical ornamentation varies, the apical verrucae being sometimes very reduced or missing (Pl. 7 Fig. 9). The centre of the apex and the rest of the body of the semicell (except the processes) are free of ornamentation, but pore openings may be seen (Pl. 7 Fig. 3, 7-9).

The semicells bear four to six processes of varying length, but always stout and fairly short. The processes are parallel or slightly divergent and bear three or four concentric rings of conical single or double granules (Pl. 7 Fig. 4, 5). The processes are tipped with four, five or more of the same kind of conical granules ornamenting the processes (Pl. 7 Fig. 4).

In apical view, the apex is ornamented with double verrucae disposed somewhat in the shape of a star (Pl. G Fig. 1, 2). The centre of the apex is free of ornamentation. Rings of granules are seen on the processes.

Pentaradiate cells were predominant in all three clones with 20.0-26.8% of tetraradiate cells. Occasional hexaradiate cells were observed in two cultures. Field specimens were either tetra- or pentaradiate (Table 19).

From Ralfs' measurements, the L/l ratio of St. sexcostatum is calculated as 1.04-1.25. This ratio is intermediate between var. truncatum (L/l = 1.25) which is discussed later, and var. productum (L/l = 0.93-1.00). In HC clones, the L/l ratio is 0.95-1.06, whereas it is 0.77-0.92 in field material, thus in better agreement with var. productum.

In his description of the species, Ralfs notes the presence of an elevated apex in apical view, although there is no mention of any ornamentation pattern or presence of double verrucae as in var. productum. However, the mention of an elevated apex seems to imply the presence of double verrucae which Ralfs may not have been able to distinguish with the microscope available to him.

Nordstedt (1896, 1908) notes a few records of St. sexcostatum var. sexcostatum, most without illustrations. In modern literature its varieties are more commonly reported than the type species, which seems very rare. St. sexcostatum fits between var. truncatum and var. productum on a scale of decreasing L/l ratio and seems to be only an intermediate form. It seems more logical to have St. sexcostatum var. sexcostatum as a variation of var. productum rather than the reverse, but unfortunately this is not the case since var. _sexcostatum_ was named first. I propose to unite var. _sexcostatum_ and var. _truncatum_ (which will be discussed later) to accommodate taxa with short processes.

1. Synonym of _St._ _sexcostatum_ var. _productum_ :
   _St._ _aculeatum_ var. _ornatum_ forma _simplex_ Boldt 1888

_St._ _aculeatum_ var. _ornatum_ forma _simplex_ Boldt 1888 (p. 38; pl. 2, fig. 49) Pl. F Fig. 13:

> "Forma a vertice visa 4-gona, aculeis simplicibus, non bifidis, lateribus late concavis.
>
> "Long. 38 μ; lat. 40,8 μ; lat. isthmi 15 μ..."

This taxon, which is distinguished from _St._ _aculeatum_ var. _ornatum_ by its reduced ornamentation, is considered by West _et al._ 1923 (p. 148) as a synonym of _St._ _sexcostatum_ var. _productum_.

Croasdale (1965) observes a triradiate form of _St._ _aculeatum_ var. _ornatum_ forma _simplex_. She believes that Boldt's form, which is tetraradiate and broader than long, should not be synonymous with _St._ _sexcostatum_ var. _productum_ as proposed by West _et al._ (1923).

Both de Brébisson's (in Meneghini 1840) description of _St._ _sexcostatum_ and W. West's description of _St._ _sexcostatum_ var. _productum_ note an hexaradiate vertical view. However Ralfs (1848) mentions five or six marginal lobes for _St._ _sexcostatum_.

The clones in the present study were tetra-, penta- and hexaradiate. Thus, Boldt's specimen may be considered to belong to St. sexcostatum var. productum. Furthermore, the dimensions of Boldt's specimen (38 μm long x 40 μm wide), give a L/l ratio of 0.95 which is in the range observed for my clones (Table 19).

Observations of all three clones agree with the inclusion by West et al. of St. aculeatum var. ornatum forma simplex Boldt in St. sexcostatum var. productum. Due to the absence of any triradiate specimens in HC clones, no conclusion can be made on Croasdale's (1965) specimens. It is interesting to note, that St. aculeatum var. ornatum f. spinosissima Wille 1879 (pl. 13, fig. 67-68) was found in the tri-, tetra- and pentaradiate state.

2. Proposed synonym of St. sexcostatum var. sexcostatum

St. sexcostatum var. truncatum Raciborski 1885

St. sexcostatum var. truncatum Raciborski 1885 (p. 85; pl. 121, fig. 14) Pl. F Fig. 10:

> "A vertice visum hexagonum, angulis truncatis, verrucosis, lateribus (non profunde) concavis, verrucis binis ornatis.
>
> "Long. cellular. =31-33 μ
>
> "Latit. cellular. =25-26 μ.
>
> "Latit. apic. = 15 μ.
>
> "Latit. isthm. = 13-15 μ..."

This variety described from Poland was also reported by Grönblad

(1942) from Swedish Lappland. It is distinguished by its very short processes. Variation in the length of the processes has been observed commonly throughout this investigation. The range of variation in width in all three clones (Table 19) shows such a phenomenon. Dichotypical cells in which the two semicells were of different width were found both in field and clonal material. Cells with such short and truncated processes as observed for var. truncatum were not seen. The L/l ratio for var. truncatum is ca. 1.25. Thus it appears that the proportions of var. truncatum are in the range of St. sexcostatum (L/l = 1.04-1.25). Consequently, there is no need to establish a variety based on the length of the processes.

3. An additional infraspecific taxon of St. sexcostatum

St. sexcostatum var. ornatum (Nordstedt) Förster 1963 (p. 55)
Basionym: St. aculeatum var. ornatum Nordstedt 1872 (p. 40; pl. 7, fig. 27) Pl. F Fig. 12:

Nordstedt's description is:

"Semicellulae ad basim serie transversali aculeorum ornatae, prominentiis radiorum simplicibus subulatis, ceteris, fere omnibus, fissis. Forma tri- et tetragona.

"Long. 0,0018-19" = 45-48 μ. Lat. 0,0014" = 35 μ. Lat. isthmi 0,00055" = 14 μ...

"Ad St. Cerastem Lundell (Desm. p. 69, t. IV, f. 6) accedens, imprimis differt semicellulis introrsum nunus ventricosis, radiis crassioribus."

The alga illustrated by Förster 1965 (p. 157; pl. 9, fig. 10;

Pl. F Fig. 11) is a pentaradiate specimen, while *St. aculeatum* var. *ornatum* is described as tri- or tetraradiate. Förster's vertical view shows a central row of double verrucae and lateral double verrucae. Although this is not clear in the vertical view of var. *productum*, the front view shows the presence of apical and subapical double verrucae (Pl. F Fig. 14). The specimens described by Förster seem more strongly ornamented and bigger (L = 51-54; l = 46-48 μm), than var. *productum*. They are also longer than wide as are the specimens identified as *St. aculeatum* var. *ornatum* by Nordstedt (1872). Because of those differences, *St. sexcostatum* var. *ornatum* is recognized as a valid variety.

Förster also includes as a synonym of *St. sexcostatum* var. *ornatum*, the *St. sexcostatum* var. *productum* of Borge (1923; pl. 2 fig. 29). Borge's specimen shows two subapical spines between each process in apical view but no subapical double verrucae. Borge's material seems to correspond better to *St. aculeatum* var. *ornatum* forma *simplex* and thus to *St. sexcostatum* var. *productum*.

4. Uncertain taxon of *St. sexcostatum*

St. sexcostatum var. *depauperatum* Gutwinski 1896 (p. 60; pl. 7, fig. 70)

Mention of the variety was found in Nordstedt (1908), but no figures or descriptions were available. No further record of the taxon was found in a literature search.

TABLE 17

CELL DIMENSIONS AND RADIATION OF ST. SEXCOSTATUM VAR. PRODUCTUM
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (μm) Average	Range	S.D.	C.V.	l(cp) (μm) Average	Range	S.D.	C.V.	Is (μm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 4	5	6	4-5
427	Jacobs 8-VIII-80	37	33-41	2.11	5.76	39	34-45	2.65	6.84	14	12-16	1.47	10.39	0.95	26.6	73.4	---	---
430	" "	38	32-43	6.51	17.04	37	31-44	3.55	9.63	15	13-17	1.23	8.46	1.06	26.8	70.2	1.0	7.1
469	" "	38	35-41	1.55	4.04	38	35-41	1.62	4.28	14	13-16	1.20	8.39	1.02	20.0	78.0	2.0	---

Field material

Source	L(cp) (μm)	l(cp) (μm)	Is (μm)	L/l	Radiation 4	5
Jacobs 8-VIII-81	34	37, 44*	13	0.92, 0.77		X
Jacobs 9-VI-81	38	42	16	0.90	X	

*Dichotypical cells

Plate 7

_St._ _sexcostatum_ var. _productum_

SEM photographs

1-9. Clone HC 427

1. Cell viewed in a tilted position showing the shape of the cell

2. Semicell in front view showing the ornamentation

3. Isolated semicell showing the ornamentation and the pores; the arrow indicates a pore

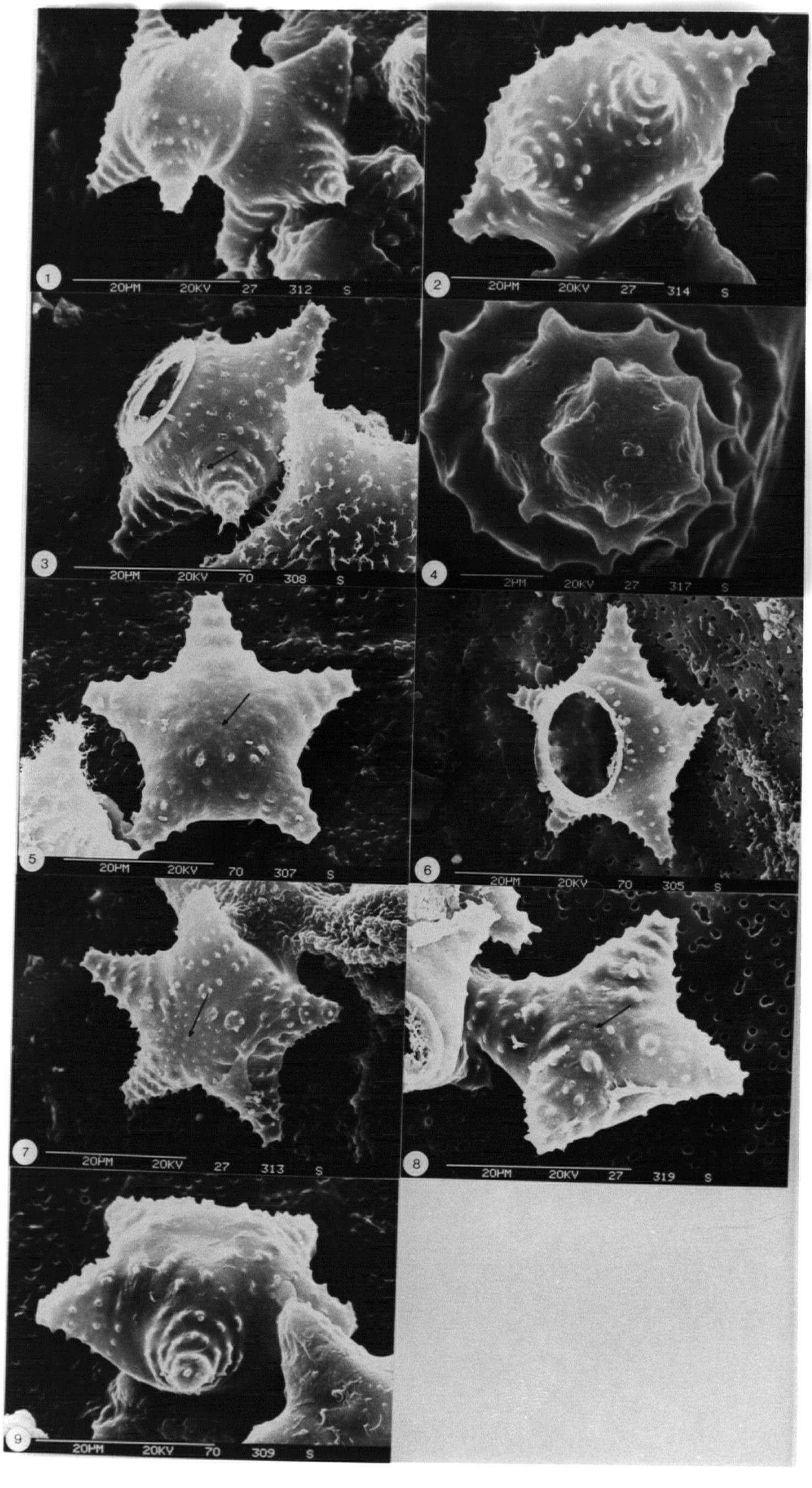
4. Detail of the extremity of one process

5, 7, 8. Cells in vertical view; the arrows indicate the pores

6. Isolated semicell showing the supraisthmial granules

9. Cell viewed from the front and the apex, note the reduced double verrucae

220A



1 20µm 20KV 27 312 S
2 20µm 20KV 27 314 S
3 20µm 20KV 70 308 S
4 2µm 20KV 27 317 S
5 20µm 20KV 70 307 S
6 20µm 20KV 70 305 S
7 20µm 20KV 27 313 S
8 20µm 20KV 27 319 S
9 20µm 20KV 70 309 S

I. STAURASTRUM CRENULATUM VAR. CRENULATUM

St. crenulatum (Nägeli) Delponte 1877 (p. 68; pl. 12, fig. 1-11)

Basionym: Phycastrum crenulatum Nägeli 1849 (p. 129; pl. 8B)

Pl. G Fig. 3:

Nägeli's original description is:

"Querprofil drei- bis sechseckig; Ecken vorgezogen, am Ende schmal -gestutzt oder gespalten.

"Die beiden Zellenhälften sind im Längenprofil querspindelförmig, häufig ziemlich deutlich in ein Mittelstück und in die Strahlen geschieden, welche bald kurz und dick, bald lang und sehr dünn sind; der äussere Rand ist gerade, oder convex, oder concav. Die Seiten des Querprofils sind concav. Die Strahlen sind gleich dick oder von innen nach aussen verschmälert, am Ende gerade-abgestutzt, oder 2 bis 4spaltig; ihr Querprofil ist kreisförmig. Die Membran ist glatt, oder warzenförmig-gekerbt, oder warzig, oder stachelig. Die Warzen umgeben die Strahlen ringförmig, so dass die letztern dadurch wie gegliedert erscheinen (Fig. h-p); ein verschmälerter Strahl, welcher oben angesehen wird, zeigt daher eine Zahl concentrischer Ringe (fig. o). Ein gleicher Ring von Warzen oder Punkten zeigt sich zuweilen auch an der Endfläche, mit einigen Punkten im Centrum (fig. p)...

"Länge 1/90 bis 1/66"', Dicke 1 bis 1 1/2 Mal so gross; das Längenprofil der Hälfte quer-spindelförmig, gerade; das Querprofil 3, 4, 5strahlig; Strahlen nach dem schmalgestutzten Ende allmälig verdünnt, der Länge nach gekerbt und durch die ringförmig verlaufenden Kerben scheinbar gegliedert, am Ende mit zwei (zuweilen undeutlichen) kleinen Stacheln..."

Stein and Borden (unpublished) list four records of St. crenulatum var. crenulatum for British Columbia, including Jacobs Lake. The alga was not observed in field material.

Clone examined: HC 435 from the VanDusen Botanical Garden, 28-VII-80 (Table 18).

Clone HC 435 has semicells with the angles extended into processes of varying length which are either parallel or slightly divergent. The cells are slightly longer than wide (Table 18, L/l=0.79). The base of the semicell above the isthmus is cylindrical (Pl. 8 Fig. 1-3), and short spines or granules may often be seen on the cylindrical swelling (Pl. 8 Fig. 2), or may be absent (Pl. 8 Fig. 1). The isthmus is wide open and forms an acute notch in the middle of the semicell.

The apex of the cell is ornamented with double verrucae. These verrucae run along the process but are usually reduced to single spines at the extremity of the processes (Pl. 8 Fig. 1-3). The size of the verrucae varies.

The processes are tipped with three or usually four spines. The processes have deep undulations which are usually tipped with one spine (Pl. 8 Fig. 1, 4). Sometimes a cell has two of the apical verrucae tipped with two groups of two spines (Pl. 8 Fig. 3). At the junction of the processes with the body of the semicell, three small granules are often seen just underneath the processes (Pl. 8 Fig. 2). The remainder of the semicell body is free of ornamentation.

In vertical view, apical verrucae are seen on each side of the semicell (Pl. 8 Fig. 5). The sides of the semicells are straight and prolonged into processes of varying length. Short spines are arranged in concentric rows around the processes. No subapical ornamentation was ever seen in apical view. Laterally, the processes are not as deeply incised as they are ventrally and dorsally, as is shown by the smaller and shallower undulations of the processes in vertical view (Pl. 8 Fig. 5).

Most of the specimens were triradiate (96.2%) or tetraradiate. The published dimensions of St. crenulatum agree fairly well with clone HC 435 (Table 18). The sinus is usually more cup-shaped than in this study (Krieger 1932, pl. 17 fig. 8, pl. 19 fig. 10; Irénée-Marie 1939, pl. 49, fig. 17; Schumacher 1969, fig. 103; Coesel 1979, pl. 29, fig. 11-15). Published records show different degrees of development of the undulations. Few of the published figures consulted show the presence of spines or granules on the basal part of the semicell or of the three granules at the point of junction of the processes with the body of the semicell (see Pl. 8 Fig. 2 and Grönblad 1920, pl. 3 fig. 62). Some light granulation is shown by Coesel 1979 (pl. 9, fig. 13-15) below the processes on the front of the semicell, which suggests the presence of such granules.

A morpha described by Croasdale and Grönblad (1964; pl. 20 fig. 8) has only slight undulations of the short processes, a cup-shaped sinus and a stouter cell. This seems related only distantly to St. crenulatum.

Nägeli's first figures of St. crenulatum represented strongly undulated processes but without any apical verrucae. Most further publications of the species show the presence of apical ornamentation at least in apical view (West et al. 1923, pl. 143 fig. 12; Grönblad 1920, pl. 3 fig. 63; Krieger 1932, pl. 17 fig. 8, pl. 19 fig. 10; Irénée -Marie 1939, pl. 49 fig. 17; Scott and Prescott 1961, pl. 59 fig. 10; Schumacher

1969, fig. 103; Tell 1980, pl. 10 fig. 1).

Since both Nägeli and Delponte failed to present good and unequivocal illustrations of the species, it is difficult to establish what the entity St. crenulatum represents. Efforts by later investigators to clarify the species concept will be described later. In deciding on this species for clone HC 435, the strong undulations represented in Nägeli (1849) and the discussion and illustrations given by Brook (1959a; p. 601-2, pl. 17, 18) were predominant. There is some difference between clone HC 435 and the illustrations of St. crenulatum by Brook. For example spines are present on the basal part of the semicell in St. pingue sensu Brook (1959a; pl. 17 fig. 8, 11, pl. 18 fig. 9, 11) as in clone HC 435, but not in his front view of St. crenulatum. However, Brook (pl. 18 fig. 1) represents supraisthmial spines below each process of St. crenulatum in basal view.

St. crenulatum has been found in many areas of the world. There have been few varieties described and the information available on those was limited. St. crenulatum is strongly related to St. pingue Teiling but St. crenulatum is smaller. According to Brook (1959a) St. crenulatum, St. pingue and St. planctonicum Teiling form a continuous series of increasing size with intermediate specimens. The original descriptions of St. pingue and St. planctonicum are:

St. pingue Teiling 1942 (p. 66; fig. 3-5) Pl. G Fig. 4:

"Semicellulae, a fronte visae, subquadratae, angulis inferioribus rotundatae vel retuse angularibus, angulis superioribus in processus longas, divergentes extensis, in apice tri- vel quadricuspidatos, marginibus granulatis. Semicellulae sub brachiis aliquantum expandutur, e vertice visae, triangulares. Apex semicellulae inter bases processium 6 verrucis bicuspidatis ornatae.

"Long. cell. 28-30 μ, lat. cell. (sub brachiis) 10-13 μ, lat. isthmi 5-6 μ, long. brach. 22-27 μ..."

St. planctonicum Teiling 1946 (p. 77; fig. 30, 32) Pl. G Fig. 5:

"Cellula duplo longius quam lata (sine processibus), profunde constricta, sinu incisa; semicellula tripyramidalis, elongata, apice plano vel leviter convexo, in marginibus tumores duos, humiles, bigranulatos praebente; angulis in processus longos, subcylindricos, aculeatos divergentes promucronibus processuum trispinatis.- Dim.: long. cell. 44 μ (40-49 μ), lat. cell. ad sinus 14,7 μ (13,3-17 μ), lat. isthm. 10,7 μ (9,5-11,7 μ), long. brach. 29 μ (22-38 μ).-Verbreitung: In mässig eutrophen Seen nicht selten."

1. Uncertain infraspecific taxa of St. crenulatum

Only two varieties of St. crenulatum have been described but the original publication was not available

St. crenulatum var. continentale Messikommer 1927

St. crenulatum var. britannicum Messikommer 1927

a) St. crenulatum var. continentale Messikommer 1927 (p. 107)

From a discussion in Cedercreutz and Grönblad (1936), it seems that Messikommer described this variety in an effort to clarify the taxonomy of St. crenulatum. Cedercreutz and Grönblad state that Delponte's (1877) and Nägeli's (1849) figures represent two species. Figures h, l, m of Delponte and figures 6, 7 of Nägeli represent a form corresponding to var. *continentale*. Grönblad (1960) argues that this is contrary to the ICBN (1956) and that the proper name for this variety should be var. *crenulatum* and not var. *continentale*. Since the original description was not consulted, it is impossible to know if Messikommer split the genus into two varieties, var. *crenulatum* and var. *continentale* or described only var. *continentale*. Only in the second case would this move be contrary to the ICBN.

b) *St. crenulatum* var. *britannicum* Messikommer 1927 (p. 107; pl. 5, fig. 8, pl. 6, fig. 1, 2)

Grönblad (1960) notes that this variety is a synonym of *St. crenulatum sensu* West *et al.* (1923; pl. 143. fig. 9-13) and to *St. gracile* Ralfs var. *coronulatum* Boldt 1885. Based on records in the literature, this variety appears as common as the type species and very similar to clone HC 435.

Nygaard (1949; p. 86-89) thoroughly discussed two unnamed formae of var. *britannicum*. In forma 1, the two long verrucae at the base of each process (seen in front view) seem characteristic of var. *britannicum*; however, these may be replaced by two long spines. In basal view, three pairs of two supraisthmial spines are seen alternating with each process. Scott and Grönblad (1957; pl. 30 fig. 11-13) compare their specimens of var. *britannicum* to Nygaard's forma 1. Their specimens differ by the arrangement of the supraisthmial spines which are below the processes and do not alternate with them. Scott and Grönblad's alga is also similar to var. continentale f. mammiferum from which it differs by the presence of double verrucae. This taxon appears as a good variety, closely related to clone HC 435.

2. An additional infraspecific taxon of St. crenulatum

The following appears distinct from St. crenulatum

St. crenulatum var. continentale forma mammiferum Prescott et Scott 1952 (p. 66; pl. 5, fig. 3) Pl. F Fig. 15:

> "A form differing from the typical variety by having a spine-tipped mammilla on each side at the base of the semicell, producing a slightly narrower crown and transverse rows of granules on the arms. L. 23; W. 30; I. 6. Happy Reservoir, B50. Messikommer, E., 1927, p. 107.
>
> "Forma a planta typica differens possessione mammillae spina minutae utroque in latere ad basim semicellulae, sinum paululo angustiorem efficientis; cellula a vertice visa triangularis, oridnationem triangularem granulorum binorum ad coronam necnon ordines transversos granulorum, in brachiis habens. Long. 23; lat. 30; isthm 6."

The main characteristic of this forma, the spine tipped mamilla at the base of each process, was observed in some cells of clone HC 435 (Pl. 8 Fig. 2). The dimensions of clone HC 435 also correspond to var. continentale f. mammiferum. Prescott and Scott show paired granules instead of the strong double verrucae observed in clone HC 435, thus the two taxa appear distinct.

TABLE 18

CELL DIMENSIONS AND RADIATION OF *ST. CRENULATUM*

(Clonal cultures; N=see Materials and Methods; S.D.= Standard deviation; C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (µm) Average	L(cp) (µm) Range	L(cp) S.D.	L(cp) C.V.	l(cp) (µm) Average	l(cp) (µm) Range	l(cp) S.D.	l(cp) C.V.	Is (µm) Average	Is (µm) Range	Is S.D.	Is C.V.	L/l	Radiation (%) 3	Radiation (%) 4
435	VanDusen Garden 28-VI-80	22	19-24	1.32	5.97	27.9	23-35	3.35	12.02	7	6-9	0.75	10.55	0.79	96.2	3.8

Plate 8

St. crenulatum

SEM photographs

1-5. Clone HC 435

1. Cell in front view, the two semicells have processes of different length

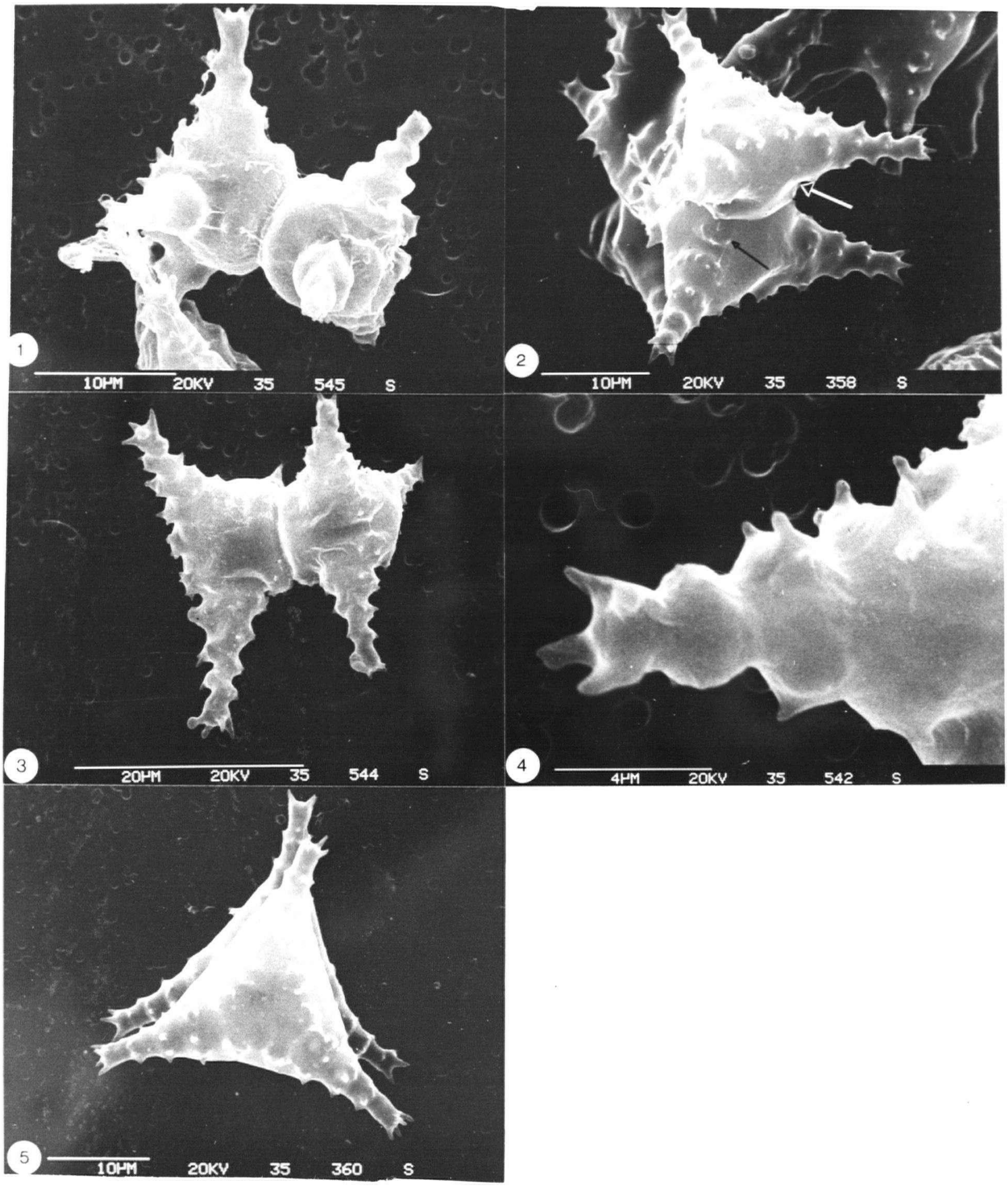
2. Cell in a tilted position; arrows indicate the presence of three granules at the base of the processes

3. Cell in front view, the central apical verrucae are tipped with two groups of two spines

4. Detailed view of the extremity of one process

5. Cell in vertical view showing the apical ornamentation

229A


1
10µM 20KV 35 545 S
2
10µM 20KV 35 358 S
3
20µM 20KV 35 544 S
4
4µM 20KV 35 542 S
5
10µM 20KV 35 360 S

J. *STAURASTRUM MANFELDTII* VAR. *PARVUM* INCLUDING *ST. MANFELDTII* VAR. *MANFELDTII*

St. manfeldtii Delponte var. *parvum* Messikommer 1942 (p. 173; pl. 19, fig. 1):

Messikommer's original publication was not available, but Růžička (1973, p. 219) gives details of the taxon. Messikommer based this variety on the smaller size of his tetraradiate specimens with slightly divergent processes, that is, "32 x 52 µm". This variety has been recorded from different regions of the world. Růžička (1973, p. 219; pl. 15, fig. 10-18) studied the variability of a population of *St. manfeldtii* var. *parvum*. He observed variation in the length of the processes and the degree of constriction of the swelling above the isthmus, and found that in apical view there may be either two, rarely four, subapical spines. These observations correspond very well to the variation seen in clones HC 45 and 67.

Stein and Borden (unpublished) report six collections of *St. manfeldtii* var. *manfeldtii* for British Columbia, including Munday Lake and one from var. *annulatum*. *St. sebaldi* var. *sebaldi* counts two records and var. *ornatum*, one.

Clones examined: HC 45, 67 from Jacobs Lake, 14-VI-79 (Table 19).

The semicells are cup-shaped and slightly wider than long. The basal part of the semicell above the isthmus is slightly swollen (Pl. 9 Fig. 1). The degree of swelling varies (Pl. 9 Fig. 1-7). The sinus is more or less open. At the isthmus, the two semicells overlap forming a fringed lip (Pl. 9 Fig. 1, 3, 4) as observed with the SEM. As far as could be seen, this characteristic is present only in clone HC 45 and not in clone HC 67. The basal swelling is sometimes ornamented with two strong granules or short spines (Pl. 9 Fig. 1, 6, 7).

The processes are either parallel or slightly divergent, and show considerable variation in length (Pl. 9 Fig. 1, 4, 5). The ornamentation is quite strong with apical double verrucae continuing down the length of the processes. These double verrucae often change to single spines toward the extremity of the processes which are tipped with two, three or four spines. Double verrucae or single spines are present below the processes, down to the level of the basal swelling. Granules form concentric rows around the processes. The front of the semicell also bears granulation (Pl. 9 Fig. 4).

In vertical view, the sides of the semicell are straight and prolonged into processes of different length (Pl. 9 Fig. 3). One row of apical double verrucae is present. The dorsal sides of the processes are ornamented with either double or single verrucae. Subapically, that is on the margin of the semicells, short spines can be seen (Pl. 9 Fig. 3). There are often only two such spines, at the base of the processes, but they may also cover the whole margin or be wanting.

The vast majority of the cells in culture were triradiate (over 94.4%) with a few tetraradiate cells or dichotypical cells (with one semicell triradiate and the other tetraradiate). The one specimen from the field was triradiate. No biradiate specimens were seen during measurements and counts of radiation but one biradiate cell was observed with the SEM (Pl. 9 Fig. 6). The second semicell of this specimen is stunted but the biradiate part has fairly long processes.

St. manfeldtii Delponte 1877 (p. 64; pl. 13, fig. 6-19) Pl. H Fig. 1:

> "Lorica tuberculata dentato-spinulosa, tertia parte magis lata quam longa profunde constricta: e dorso triradiata, radiis praelongis sensim attenuatis tuberculato-spinulosis, apice tricuspicatis e latere oblongo linearibus complanato subrotundatis subincurvis, basi veluti in istmum productis. Tuberculis dorsalibus uniseriatis aliis (uno scilicet pro unoquoque angulo) teretibus, aliis cuneato bifidis, reliquiis dentato spinulosis..."

Delponte's dimensions of the species are, L:0.0576 l:0.1008. Although no units are recorded, it is assumed that they represent mm, so that the actual measurements in μm would be, L:57.6 μm, l:100.8 μm. West et al. (1923; p. 115) dimensions are, L = 42-57; l(cp) = 55-100.8 μm.

1. Taxa related to St. manfeldtii

St. manfeldtii is closely related to St. sebaldi Reinsch but particularly to variety ornatum. Much confusion exists in the literature between these taxa, which are described and discussed here.

St. sebaldi Reinsch 1867b (p. 133; pl. 24D I, fig. 1-3) Pl. H Fig. 2:

"Plantae corpus a fronte visum in medio utrimque semielliptice emarginatum, corporis dimidia a fronte visa in ambitu truncato-obconica usque fere trapezica, anguli exteriores sensim angustati et paulo producti, breviter truncati, tri-quadridentati, margo terminalis in medio subconvexus utrimque subdeclinatus, angulorum exteriorum distantia corporis dimidii inferioris partis latitudinis duae quintae, margines laterales et margo terminalis et dimidiorum superficies aculeis firmis armati, anguli exteriores verrucis in seriebus transversis parallelis dispositis exasperati, marginis terminalis spinae bi-tridentatae, superficiei et marginum lateralium integerrimae; corporis dimidia e vertice visa trigona, lineae laterales rectae, spinis integerrimis armatae, anguli subito angustati et in processum breviter truncatum verrucis in seriebus transversis parallelis dispositis exasperatum prolongati, marginum lateralium spinae bi-tridentatae in seriebus binis (interdum singula) lineis lateralibus parallelis dispositae; articuli conjunctivi latitudo corporis diametri transversalis (angulorum exteriorum distantiae) triens et paulo minor; corporis diameter transversalis diametro longitudinali aequalis et paulo longior; spinarum longitudo diametri transversalis 10a-12a pars.

"Longit. 0,076 -0,073 mm; 0,0349-0,0337 "' rhen.
"Latit. 0,076 -0,069 mm; 0,0349-0,0322 "' rhen.
"Spinarum longit. 0,006 mm; 0,0029"' rhen.
"In fossis humidis sylvae Sebaldianae per sylvas ductis pr. Puckenhof in Franconia; Bischoffsee."

St. sebaldi var. ornatum Nordstedt 1873 (p. 34; pl. 1, fig. 15) Pl. H Fig. 3:

"Semicellulae ad basin utrimque granulis nonnulis ornatae, radiis gracilioribus et longioribus.

"Long. c. rad. 0,0032"= 81 μ; Lat. c. rad. 0,0052"= 132 μ; Lat. isthmi 0,00072"= 22 μ."

St. manfeldtii belongs to a group of species whose limits are not always clear, with specimens sometimes presenting characteristics of different species. This fact is supported by observations and discussions of different authors (Bourrelly, 1957; Florin, 1957; Lind and Croasdale, 1966; Coesel, 1979) but most notably by Teiling (1947). Teiling established the shape of the sinus as the predominant characteristic differentiating St. manfeldtii and the closely related St. sebaldi; it is narrow and cylindrical in the former species but open and conical-cup shaped in the second.

The arrangement and development of the spines and verrucae have been shown in this study to be fairly variable, and Delponte's figures are themselves fairly variable in that respect. On the other hand, the difference in sinus shape emphasized by Teiling for the two taxa is actually supported by the original illustrations of St. sebaldi Reinsch (see Pl. H Fig. 2), and partly by those of Delponte (see Pl. H Fig. 1; fig. 11 and 15 show a more open slightly slanted sinus). The shape of the sinus has been adopted as an important factor in differentiating the two species in the present study, but since this characteristic varies, it cannot form a clear-cut separation between the species, as I will show later.

It is difficult to apply strictly Teiling's interpretation of St. manfeldtii and St. sebaldi, since the specimens of the present study possess a cylindrical sinus, which Teiling (1947) attributes to St. manfeldtii, coupled with an open sinus which points towards St. sebaldi. Variation of these features was observed in the present study and the literature. The degree of opening of the sinus varies, but it is never as closed as in Delponte's figures 10 and 12 (Pl. H Fig. 1). The basal swelling above the isthmus is more or less pronounced, but most cells can be said to have a cylindrical shape, the sinus forming a notch in the middle of the semicell.

Coesel (1979) also discussed the same problem and referred to intermediate forms found in the literature (Nygaard 1945, fig. 79; Skuja 1964, pl. 55 fig. 3, 4). In observing illustrations of St. manfeldtii by different authors, it becomes obvious that most algae reported under this name have an open sinus (Boldt 1885, pl. 6 fig. 32; West and West 1902b, pl. 1 fig. 29, 1905a pl. 2 fig. 26; West et al. 1923, pl. 148 fig. 2; Irénée-Marie 1939, pl. 48 fig. 4; Flensburg 1967, pl. 7 fig. p; Gruendling and Mathieson 1969, fig. 29; Grönblad and Croasdale 1971, pl. 9 fig. 125).

Since the original illustrations of St. manfeldtii have either a slightly open or closed sinus, this reinforces the idea that algae with an open sinus can belong to St. manfeldtii.

The typical St. sebaldi, as described by Reinsch has a wide open cup-shaped sinus and can be easily differentiated from St. manfeldtii. The major problem arises when the very common variety St. sebaldi var. ornatum Nordstedt is considered. As represented by Nordstedt (Pl. H Fig. 3), this variety has an open sinus which forms a distinct notch in the middle of the semicell. The basal part of the semicell is slightly slanted but it does approach the cylindrical shape. That shape represents a transition between St. sebaldi and St. manfeldtii but probably comes closer to St. manfeldtii.

The decision to name an alga St. manfeldtii or St. sebaldi var. ornatum may be very subjective and subsequent illustrations of the second species support this view. The basal part of the semicell often shows a swelling or is cylindrical without slanted sides as in the cup-shaped St. sebaldi, but a few authors represent a definitely cup-shaped sinus or a form close to Nordstedt's illustration of St. sebaldi var. ornatum. Thomasson (1957, fig. 4) points out that his specimens of St. sebaldi var. ornatum do not have the supraisthmial granules under the processes shown by Nordstedt. Neither Irénée-Marie (1939) nor Tell (1980) who represent a cup-shaped sinus show these granules. Similarly, cells with a conical shape above the isthmus also lack the granules (Rich 1932, fig. 15; Messikommer 1957, pl. 2 fig. 5, 6; Förster 1964a, pl. 31 fig. 9-11; Taft and Taft 1971, fig. 477).

A further examination of reports of St. manfeldtii shows that some of them do possess the granules on the basal part of the semicell (Grönblad and Croasdale 1971, pl. 9 fig. 125; Coesel 1979, pl. 28 fig. 5, 6). A feature of St. manfeldtii which should also be noted is the increased length of the apical verrucae on each side of the apex in front view of fig. 10, 12, 14 and 15 of Delponte. As far as is known, this characteristic has not been observed by any subsequent authors.

This discussion of St. manfeldtii and St. sebaldi var. ornatum shows that the distinction between the two algae may be very subjective and that there is no feature which can unambiguously tell them apart. As Lind and Croasdale (1966) point out, " Staurastrum sebaldi var. ornatum is a widespread and very variable desmid, which seems often to have been confused with St. manfeldtii Delponte and sometimes with other species." I feel that the two taxa may better be grouped under the same species, leaving the name St. sebaldi to the specimens having a definite cup-shaped semicell, rather than a swelling or cylindrical part at the base of the semicell. However the St. manfeldtii - sebaldi group is too complex and variable and includes too many varieties and species to consider settling the problem here. St. sebaldi var. ornatum f. minor which is closely related but distinct from St. sebaldi var. ornatum will be discussed.

1. Infraspecific taxon of St. sebaldi

St. sebaldi var. ornatum f. minor Bourrelly 1957 (p. 1087; pl. 16, fig. 141) Pl. G Fig. 6:

> "Cette petite forme: 33 μ x 55-60 μ, isthme 8-10 μ, est par son sinus, la base peu bulbeuse de l'hémisomate et son ornementation, très proche de St. Sebaldi var. ornatum. Mais ses dimensions sont beaucoup plus faibles et ses bras sont parallèles ou légèrement convergents. L'ornementation est très vigoureuse: en vue apicale on observe une couronne de 6 verrues tri- ou quadrifurquées; à la naissance de chaque bras se trouvent 2 verrues bifides suivies d'épines simples. Autour de l'isthme il y a 3 groupes de 4 à 5 petits granules. Les bras se terminent par 2 ou 3 épines.
>
> "La belle mise au point de Teiling (1947) permet de placer cette forme parmi St. Sebaldi. Elle rappelle pourtant beaucoup le St. Manfeldtii v. parvum Messikommer (1942) et aussi St. cyclacanthum v. nonincurvatum Rich (1935)."

The shape of the semicell, as pointed out by Bourrelly, warrants the classification of this taxon as St. sebaldi. Although some specimens of clone HC 45 and 67 are similar to this taxon, based on the shape of the basal part of the semicell, most have a cylindrical and even swollen basal part and are thus distinct from St. sebaldi var. ornatum f. minor.

2. Other infraspecific taxa of St. manfeldtii

The taxonomic characteristics of the following taxa have not been observed in clonal cultures and there is no reason to reject them, although some taxa appear doubtful. Further study is necessary before any conclusions are made.

St. manfeldtii var. bispinatum Turner 1892

St. manfeldtii var. pinnatum Turner 1892

St. manfeldtii f. spinulosa Lutkemüller 1900

St. manfeldtii var. annulatum W. et G.S. West 1902b

a) St. manfeldtii var. bispinatum Turner 1892 (p. 128; pl. 16, fig. 11, 12) Pl. G Fig. 7:

> "Apud angulos spinis vel pinnis truncato-emarginatis binis munitum.
>
> "Long. 48-50, lat. 58-64, lat. isth. 13-14 μ...
> "Ad fig. Delpontii 13 (semic. infer.) accedens."

This variety was first found in East India and no further records were found in the literature. As pointed by Turner (1892), this variety is very similar to Delponte's fig. 13 of St. manfeldtii, the double verrucae on each side of the apex being larger than the central ones. However, the two spines in front of the semicell are not shown by Delponte.

b) St. manfeldtii var. pinnatum Turner 1892 (p. 128; pl. 16, fig. 10) Pl. G Fig. 8:

> "Dorso inflatum, serie prominentiis pinnato-emarginatis circ. 7 ornatum.
>
> "Long. 50, lat. 60, lat. isth. 10 μ.
> "Fig. 11 f. Delpontii proximum.
>
> "The latter is so different from the other forms figured by the Italian author that it might reasonably claim to rank as a species."

This variety was first recorded in East India and no further records were found in the literature. It appears more strongly ornamented than on Delponte's drawings of St. manfeldtii and its apex is more convex. It seems unwarranted to establish a new species based on the strength of the ornamentation as suggested by Turner.

c) St. manfeldtii forma spinulosa Lutkemüller 1900b (p. 123; pl. 6, fig. 32-33) Pl. G Fig. 9:

> "Zeigt in Scheitelansicht an jedem Rande mehrere einfache Stacheln. Dieselben, an jeder Seite höchstens sechs, sind meist kürzer als bei dem abgebildeten Exemplare. Delponte's Fig. 8 scheint sich auf die gleiche Form zu beziehen. Die Species ist überhaupt in der Gestalt der Zellen, der Länge der Radien und der Entwicklung der Bestachelung sehr variabel, und es stellt die Abbildung nur eine extreme Form dar."

This variety was first found in Central China and appears rare. The presence of lateral and apical spines, in addition to the apical double verrucae, was illustrated in Delponte's St. manfeldtii (fig. 8) and this feature has been found to be variable in HC clones. Lutkemüller notes that his taxon is very variable, especially in the development of the spines, and that his figures represent an extreme form. The lateral spines link f. spinulosa to St. pseudobaldi Wille 1880, although the problem is too complex to be discussed here.

d) St. manfeldtii var. annulatum W. et G.S. West 1902b (p. 56; pl. 1, fig. 30-31) Pl. G Fig. 10:

> "Var. processibus paullo gracilioribus, verrucis emarginatis ad apicem semicellularum paullo reductis, cum annulis granulorum binis circa basin semicellularum.
>
> "Long. 46-49 μ; lat. cum proc. 63-70 μ; lat. isthm. 10.5 μ...
>
> "The double ring of granules round the base of the semicells and the slight reduction of the apical emarginate warts are characters which at once distinguish this variety. It bears a certain resemblance to S. Pseudosebaldi Wille, but the body of the plant is relatively larger and the verrucation is different. In the vertical view the sides are quite smooth, all the verrucations being within the margins as in typical S. Manfeldtii."

This variety was first found in the North of Ireland and has since been recorded in many areas of the world. The presence of the double row of supraisthmial granules seems to be a reliable characteristic.

3. Uncertain infraspecific taxa of St. mandfeldtii

St. manfeldtii var. planctonicum Lutkemüller ?

St. manfeldtii var. fluminense Schumacher et Whitford 1961

a) St. manfeldtii var. planctonicum Lutkemüller

The original publication of the variety was not available. It is recorded as a synonym of St. luetkemuelleri Donat by Grönblad (1942; p. 42) and as St. sebaldi var. ornatum f. planctonicum (Lutkemüller) Teiling 1947 by Prescott et al. (1982, p. 307).

b) St. manfeldtii var. fluminense Schumacher et Whitford 1961 (p. 275; fig. 1-3)

This variety is cited in Thomasson (1974b) and Prescott et al. (1982; P. 248). The original publication was not available.

TABLE 19

CELL DIMENSIONS AND RADIATION OF <u>ST</u>. <u>MANFELDTII</u> VAR. <u>PARVUM</u>
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (µm) Average	L(cp) (µm) Range	L(cp) S.D.	L(cp) C.V.	l(cp) (µm) Average	l(cp) (µm) Range	l(cp) S.D.	l(cp) C.V.	Is (µm) Average	Is (µm) Range	Is S.D.	Is C.V.	L/l	Radiation (%) 3	Radiation (%) 4	Radiation (%) 3-4
45	Jacobs 14-VI-79	37	34-42	2.13	5.72	39	34-49	3.93	9.98	11	9-13	0.86	8.06	0.95	94.4	0.7	4.9
67	" "	39	34-43	2.32	5.97	43	34-52	4.62	10.82	11	10-14	0.87	8.61	0.91	97.4	0.5	2.0

Field material

Source	L(cp) (µm)	l(cp) (µm)	l (above Is)	Is (µm)	L/l	Radiation 3
Jacobs 14-VI-79	32	49	13	9	0.66	X

Plate 9

St. manfeldtii var. *parvum*

SEM photographs

(marker= 10 µm unless indicated otherwise)

1-7. Clone HC 45

1, 2. Cells in front view

3. Group of cells in front and vertical view

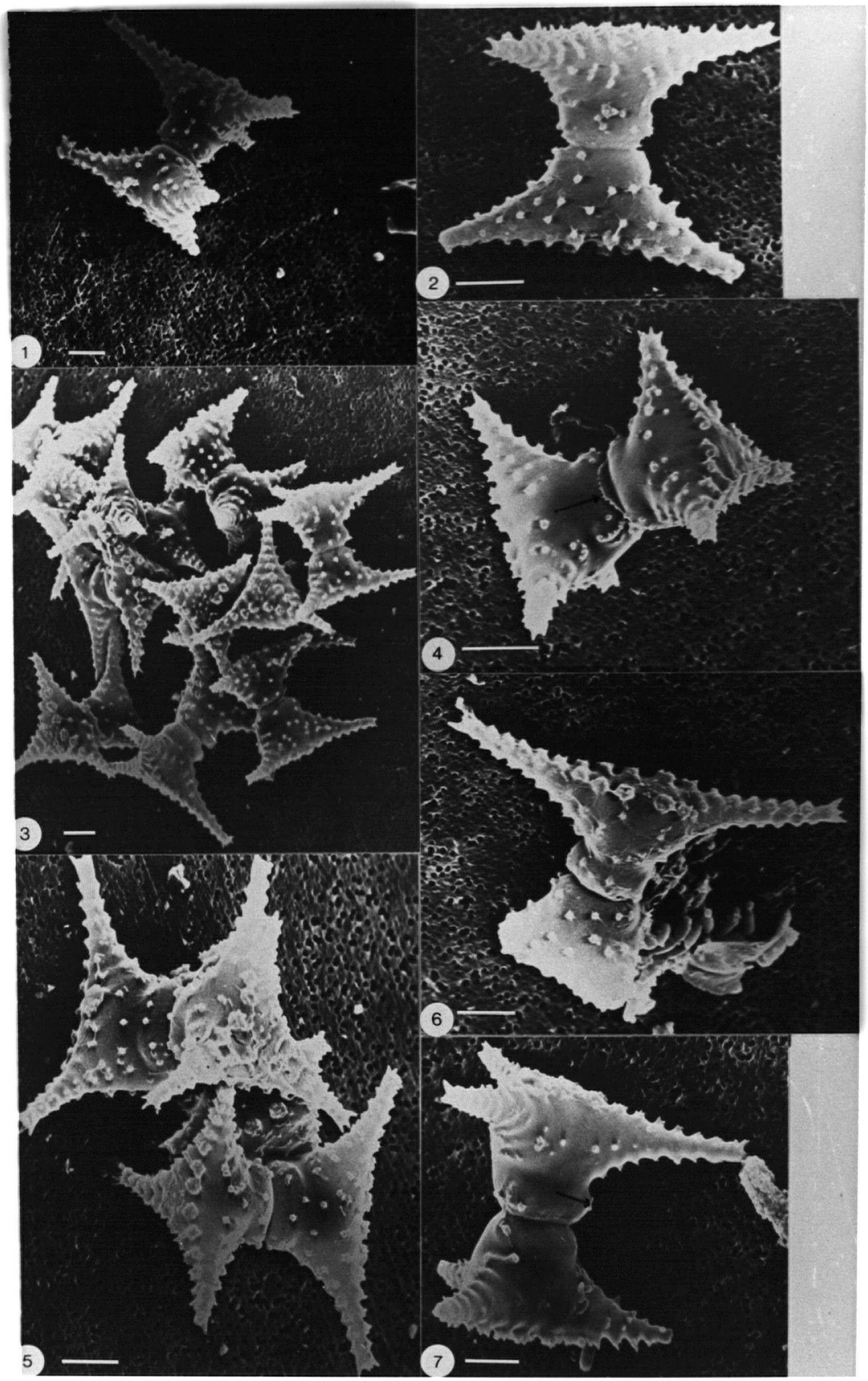
4. Cell viewed from the front and the apex; arrow indicates the fringed lip at the isthmus

5. Two cells, one in front view with the processes of different length (lower right) and one viewed from the front and the apex (upper left)

6. Biradiate cell, the lower semicell has stunted processes

7. Cell in front view showing the processes of different length; the arrow indicates the granules on the basal swelling

243A



K. STAURASTRUM VESTITUM VAR. VESTITUM

St. vestitum Ralfs 1848 (p. 143; pl. 23, fig. 1) Pl. H Fig. 4:

> "...frond rough with minute emarginate spines; segments fusiform; end view triradiate, each side having two spines, short, slender, and often accompanied by other smaller ones.
>
> "Frond broader than long, about as large as that of Staurastrum gracile, deeply constricted at the middle, the constriction forming a triangular notch on each side; segments somewhat fusiform, turgid on the inner margin, tapering at each side into a short process which is tipped by three or four minute spines; outer margin fringed with minute emarginate spines or tubercles. End view triradiate, showing also two slender forked spines at the middle of each side, whilst the margin is often fringed with other spines, which are smaller and either simple or notched. The rays are elongate, rough with minute granules, and terminated by minute subulate spines.
>
> "In the end view Staurastrum vestitum resembles S. gracile in figure, but that species is not spinous. The rays in the end view are more slender than those of S. aculeatum or S. controversum : but the most distinctive character of this species is the presence of a pair of slender forked spines at the middle of each margin.
>
> "Length of frond 1/625 of an inch; breadth 1/384; breadth at constriction 1/3205."

Stein and Borden (unpublished) report 14 collections of St. vestitum var. vestitum in British Columbia, including Munday Lake.

Clones examined: HC 49, 66 from Jacobs Lake, 14-VI-79; HC 151, 153, 154, 226 from Jacobs Lake, 29-VIII-79; HC 210 from Jacobs Lake, 26-IV-80; HC 271, 272 from Jacobs Lake, 29-VIII-79; HC 311 from Jacobs Lake, 7-VI-80; HC 468 from Jacobs Lake, 8-VIII-80; HC 479 from Placid Lake, 8-VIII-80 (Table 20).

Of the 20 clones of St. vestitum isolated from Jacobs and

Placid Lakes which grew successfully in culture, 13 were measured. The seven remaining clones were discarded because of the considerable number of deformed cells. The remaining clones grew well.

St. vestitum has semicells of subfusiform shape with processes slightly divergent to subparallel or most commonly convergent (Pl. 10 Fig. 1-5) of variable length. The cells are wider than long as shown by the L/l ratio (Table 20). The processes are denticulate and bear concentric rings of single or double spines or verrucae (Pl. 10 Fig. 1). They are tipped with three or four spines.

The apex is slightly convex and in front view, shows a row of double or single verrucae diminishing in size from the centre to the processes. The front of the cell usually bears two double verrucae which are sometimes reduced to single spines (Pl. 10 Fig. 4, 5) or which are lined on each side by one smaller verruca or spine (Pl. 10 Fig. 3). These are the marginal verrucae so obvious in vertical view and which are the main characteristic of St. vestitum (Pl. 10 Fig. 2-6).

The sides of the semicell may be smooth or ornamented with single or double verrucae about three-fourths of the way down the sides (Pl. 10 Fig. 1). The sinus is widely open and slightly rounded. It is definitely less constricted (Is = 13-18 µm in culture, 11-12 µm in the field) than suggested by West et al. 1923 (ca. 9 µm) or Ralfs 1848 (ca. 7.9 µm).

In apical view, the sides are straight or slightly concave and are extended into processes of varying length. The processes are occasionally slightly curved in the same direction as in var. tortum which will be discussed later. Double apical verrucae line the sides of the semicell (Pl. J Fig. 5, 6). The two double verrucae or spines seen in front view are visible subapically. The degree of development of the verrucae varies (Pl. 10 Fig. 2, 3, 6; Pl. J Fig. 5, 6). The subapical verrucae or spines also vary in number with usually only two central ones, or occasionally three (Pl. 10 Fig. 6). Sometimes two central spines are lined on each side by smaller verrucae or spines (Pl. 10 Fig. 3).

The L/l ratio and dimensions given in Table 20 are similar for clonal (0.62-0.80) and field (0.56-0.97) material. The slightly smaller ratio observed in field material may indicate longer processes in the field. It is well documented that Staurastrum will often have shorter processes in culture (Mix, 1965; Förster, 1967; Naef et al. 1978; Brook, 1982; present study).

Most cells are triradiate but tetraradiate cells were seen in field material as well as in clonal cultures. In clone HC 47, a clone with many deformed or dead cells which was eventually discarded, there were as high as 30% tetraradiate cells. Dichotypical cells, with one semicell triradiate and the other tetraradiate, were also seen in culture. There were up to 17.6% tetraradiate and tri- tetraradiate cells (clone HC 479) in healthy clones. Also, one pentaradiate isolated semicell was found in clone HC 479 from Placid Lake. A dichotypical cell with one semicell triradiate and the other pentaradiate occurred in clone HC 153. Cells from field material were triradiate, except for one tetraradiate cell seen only in vertical view and thus not included in Table 20.

1. Synonym of St. vestitum var. vestitum

In his revision of the St. anatinum-group, Brook (1959a) reclassified St. vestitum as forma vestitum of St. anatinum. Brook's study was very much needed as the taxonomy of the group involved is very confused. However, Brook's classification is not currently accepted as discussed here. Prescott et al. (1982; p. 342) also kept the name St. vestitum.

St. anatinum f. vestitum (Ralfs) Brook 1959a (p. 597; pl. 5, fig. 6, pl. 7, fig. 1-5; pl. 8, fig. 2-5) Pl. I Fig. 2-5.

St. anatinum Cooke et Wills in Cooke 1881 (p. 92; pl. 139, fig. 6) Pl. I Fig.1:

Cooke and Wills' description is:

> "Segments in front view broadly fusiform; rough with prominent granules, which are truncate on the outer margin; processes elongate, rough, terminated with minute spines. End view triradiate, processes elongate, rough, slightly and gradually concave, nodules at the centre truncate.
>
> "Length .05 mm. Breadth, including the processes, .1 mm. Breadth at the sinus, .02 mm. Length of the processes, .025 mm.
>
> "Allied to S. Sebaldi, but differs in the front view in the broadly fusiform segments, and the upward, rather than downward, direction of the processes, hence, the third process is usually visible on one or both segments in the front view."

As illustrated and described by Cooke and Wills, St. anatinum possesses divergent processes. St. vestitum as seen on Ralfs' illustration (Pl. H Fig. 4), has convergent processes. West et al. (1923) state that St. anatinum has divergent processes (p. 142) whereas St. vestitum (p. 158) has "nearly horizontal or slightly converging" processes. This statement for St. vestitum basically agrees with the findings of the present study, although the processes sometimes appeared subparallel or slightly divergent. Brook (1959a; pl. 7 fig. 1, 5; Pl. I Fig. 4, 5) illustrates St. anatinum f. pelagicum-glabrum-vestitum and f. longiradiatum-denticulatum-vestitum with cells having strongly divergent processes. Other figures (pl. 8, fig. 2-5; Pl. I, Fig. 2, 3) show cells with subparallel to convergent processes. Brook himself describes St. anatinum has having processes "subparallel to divergent."

In the literature some cells with divergent processes but possessing the two bifurcate lateral spines characteristic of St. vestitum have been classified as St. vestitum (Grönblad 1926 forma, fig. 117-8; Croasdale 1957, pl. 8 fig. 118). However, St. vestitum var. subanatinum was created for an alga with strongly divergent processes as St. anatinum but also possessing the two subapical verrucae of St. vestitum. The presence of the two prominent bifurcate, or sometimes single, lateral spines has thus became the main feature for the identification of St. vestitum.

Brook's study does contribute to the understanding of this group of Staurastrum, although his scheme is not complete; the description of *St. anatinum* would have to be emended to accept taxa with convergent processes. Brook suggested the transfer of *St. vestitum* as forma *vestitum* of the species *anatinum* but he did not review the fate of the already described infraspecific taxa of *St. vestitum*. Until further clarification and more complete restructuring of the group is undertaken, the use of *St. vestitum* var. *vestitum* is preferred.

2. Proposed synonyms of *St. vestitum* var. *vestitum* :

St. vestitum var. *splendidum* Grönblad 1920

St. vestitum var. *cedercreutzii* Croasdale in Croasdale and Grönblad 1964

a) *St. vestitum* var. *splendidum* Grönblad 1920 (p. 81; pl. 3, fig. 100-102) Pl. J Fig. 2:

> "Semicellulae a fronte visae subtrapetziformes, dorso altiore recto, angulis superioribus in processus apice tricuspidatos divergentes productis, sinu latius aperto; a vertice visae quadrangulatae undique in marginibus spinis acutis medioque spinis bifurcatis, intra margines seriebus verrucarum 4-dentatarum cum marginibus congruentibus ornatae; a ventre visae in radiis seriebus granulorum transverse dispositis ornatae. Cum proc. long. 53, lat. 68, isthm. 17 μ.
>
> "A vertice visa forma nostra maxime ad *S. vestitum* Ralfs l. c. fig. 1 d accedit. Cfr. etiam *S. concinnum* West, Journ. Linn. Soc. Bot. 33 t. 18 f. 17 (synon.= *S. forficulatum* Wolle, non Lundell), quod quidem a vertice visum marginibus in parte centrali glabris et a fronte visum forma cellularum haud parum differt."

This variety was first found in Finland and was later recorded in the United States. It differs very little from *St. vestitum* var. vestitum. As represented by Grönblad (1920; Pl. J Fig. 2), the processes are very slightly divergent or subparallel. Smaller spines or verrucae on each side of the two central ones were seen in the present study and are also represented by Ralfs (1848, fig. 1d). Tetraradiate specimens of St. vestitum were not uncommon both in field and clonal cultures. There seems to be very little ground for the separation of var. splendidum from the type species. Prescott et al. keep it as a valid taxon.

b) St. vestitum var. cedercreutzii Croasdale in Croasdale et Grönblad 1964 (p. 207; pl. 20, fig. 14, pl. 21, fig. 1-4) Pl. J Fig. 4:

> "Cellulae 20-35 μ x 25-49 μ, isth. 8.5-11 μ lat. Semicellulae fusiformes, tres vel quattuor processus horizontales breves, in quattuor (raro quinque) spinas breves abeuntes, habentes. Haec varietas differt cellulis spinas simplices irregulares in margine et per superficiem semicellulae, ut in S. aculeato, habentibus, verrucis apicalibus paucioribus. A vertice visae duae spinae mediae furcatae in specie typica, ad spinas simplices saepe reductae, interdum marginales, interdum intramarginales.
>
> "Semicells fusiform with three or four short horizontal processes ending in four (rarely five) short spines. The variety differs in the cells having simple irregular spines on the margin and across the face of the semicell as in S. aculeatum, and in having fewer apical verrucae. In vertical view the two median furcate spines typical of the species are often reduced to simple spines, marginal or intramarginal. HC first called this a var. of S. aculeatum, but RG pointed out that " S. aculeatum has much more numerous spines-always"; he suggested S. Suchlandtianum Messikommer (1942, p.163, XVIII:4) (which, however, has no simple marginal spines), or a new var. of S. vestitum. A new variety seems best, and it is appropriate to name it after Dr. Carl Cedercreutz who has made the first and major

contribution to our knowledge of Labrador desmids. The variety was abundant and variable. (Fig.1 on Pl. XXI is RG's)."

This variety seems to be based on a very variable population of *Staurastrum* and refers to characteristics which are known to be very unstable, e.g., number of verrucae or spines, and degree of development of ornamentation (spines or verrucae). Variation in the number of subapical verrucae as well as in their degree of development (spines or double verrucae) was seen in my clonal cultures. It would thus seem better to consider these specimens as extreme variations of a population of *St. vestitum* without naming a separate taxon. This variety is described by Croasdale and Grönblad as being very variable. Prescott *et al.* (1982; p. 342) accept it as a valid taxon.

3. Other infraspecific taxa of *St. vestitum*

The main characteristics of the following taxa were not found in clonal cultures or field material and no conclusions can be drawn. Some taxa have been previously placed as synonyms of other taxa by different authors and their conclusions are accepted at the present time.

St. vestitum var. *diplacanthum* Rabenhorst 1868

St. vestitum var. *distortum* Wolle 1883

St. vestitum var. *denudatum* Nordstedt 1869

St. vestitum var. *ornatum* Istvanffi 1887

St. vestitum var. *semivestitum* W. West 1892b

St. vestitum var. *subanatinum* W. et G.S. West 1902b

St. vestitum var. *gymnocephalum* Scott et Prescott 1961

a) St. vestitum var. diplacanthum Rabenhorst 1868 (p. 219): Basionym: St. diplacanthum De Notaris 1867 (p. 49; pl. 4, fig. 38)

> "(Staurastr. diplacanthum De Ntris Element. p. 49. N. 37. T. IV. F. 38.), semicellulis et a fronte et a vertice radiis minus productis, prominentiis marginalibus singulis elevatis.
>
> "Hab. in fossis, fodinis turfosis totius Europae, passim."

Rabenhorst referred to De Notaris' figure of St. diplacanthum without providing an illustration of his new taxon. The publication of De Notaris was not available. West et al. (1923; p. 186) recognize St. diplacanthum as a good species.

b) St. vestitum var. distortum Wolle 1883 (p. 20; pl. 27, fig. 15) Pl. I Fig. 7:

> "Separated from the typical plant by its unsymmetrical form, irregularly arranged vesture, and deeply notched margins.
>
> "Collected in the vicinity of Minneapolis, Minn."

Wolle's figure and description are not very detailed. In fig. 15a, the alga is presented in a tilted position and this should permit a view of the apical verrucae lining the sides of the cell (see Pl. J Fig. 6); however, they are not visible. It is difficult to know what taxon this represents. No further records were found in the literature.

c) St. vestitum var. denudatum Nordstedt 1869 (p. 230; pl. 4, fig. 40) Pl. I Fig. 8:

> "Minor, semicellulae in dorso nudae, ventre valde inflatae.
>
> "Long. 0,00075-90" = 19-23 μ. Lat. 0,0014-17" = 36-43 μ."

Only one further record of this variety was found in the literature. The figures presented by Nordstedt are very poor but his description states that this taxon is smaller than the type species and without apical verrucae. All cells observed in the present study had apical verrucae.

d) St. vestitum var. ornatum Istvanffi 1887 (p. 240):

> "Semicellulis dorso mucronibus bidentatis ornatis.
> "Diameter 50 μ.
> "In turfosis Cserna, Razsahegy in lacunis prope fl. Vag."

No further records of this variety were found in the literature. Istvanffi did not include any illustration or reference to a previous illustration of his new taxon. His short description does not stress any important feature which could distinguish var. ornatum from var. vestitum. West et al. (1923; p. 158) consider var. ornatum as a synonym of the type species.

e) St. vestitum var. semivestitum W. West 1892b (p. 732; pl. 9, fig. 38) Pl. I Fig. 9:

Syn.: St. anatinum f. semivestitum (W. West) Brook 1959a (p. 597):

> "S. minor quam forma typica; semicellulae apicibus subrectis; a vertice visae triradiatae processibus curvatis trifurcatis (ut in _S. cyrtocero_), cum spina furcata una ad basem lateris convexi processus uniuscujusque.
>
> "Long. c. spin. 21-28 μ; lat. 34.5-42 μ; lat. isthm. 4.5-8 μ."

This variety was first found in the English Lake district (England) and has since been found in the United States. The bent processes in apical view and the presence of only one lateral double verruca at the base of each process, characteristic of this variety, were never observed in the present study. Brook (1959a) considers it as a forma of _St. anatinum_, but as discussed previously for _St. vestitum_ var. _vestitum_, the parallel processes of var. _semivestitum_ do not agree with the strongly divergent processes of _St. anatinum_.

f) _St. vestitum_ var. _subanatinum_ W. et G.S. West 1902b (p. 54; pl. 1, fig. 28) Pl. J Fig. 1:

> "Var. processibus longis et subdivergentibus, verrucis ut in _S. anatino_ similibus.
>
> "Long. sine proc. 35 μ; lat. cum proc. 86-102 μ; lat. isthm. 13.5 μ...
>
> "This variety, which we have also seen in abundance from Arderry Lough, Co. Galway, bears a striking resemblance in the outwardly diverging processes and in the general verrucation to _S. anatinum_ Cke. & Wills."

This variety was first found in the North of Ireland and has since been reported for North America. Brook 1959a (p. 595) suggests that:

> "Varieties such as _curtum_, _longibrachiatum_ and _denticulatum_ (and also the species _S. vestitum_ and its var. _subanatinum_) which are based on such variable characters as length of processes and the extent of various decorations of the cell body should, it is believed, be reduced in rank to the status of forms."

Brook does not describe a forma _subanatinum_ and it is assumed that he integrated it with forma _vestitum_. This move would be unwarranted, as the HC clones always have convergent, subparallel or slightly divergent processes, but never the strongly divergent processes observed in variety _subanatinum_ (see Pl. J Fig. 1). This later feature, combined with the presence of two double apical verrucae, was observed in one clone from Jacobs Lake (HC 236). However, this clone was growing very poorly, and was eventually discarded. The following measurements were averaged from two cells, L:35 μm; l: 48 μm; Is:12 μm. Thus, the presence of strongly diverging processes seems to be stable enough to warrant recognition of a separate taxon. If Brook's scheme is followed, _St. vestitum_ var. _subanatinum_ would become _St. anatinum_ f. _subanatinum_, but since _St. vestitum_ is considered as a good species, the taxonomic position of var. _subanatinum_ is not changed.

g) _St. vestitum_ var. _gymnocephalum_ Scott et Prescott 1961 (p. 118; pl. 58, fig. 9) Pl. J Fig. 3:

> "Varietas a specie differens quod minor quodque processus breviores atque nullas verrucas apicales habet. Aliae proprietates quasi eadem atque in specie.

"Size smaller than in the species, and with shorter processes. Differs in the absence of all apical verrucae, the other characteristics about the same as in the species. L 21; W cpr 32; I 7."

The features and the dimensions stated by Scott and Prescott link this variety from Java to var. denudatum Nordstedt. This variety does not appear common. No cells without apical verrucae were observed in field or clonal material.

3. Uncertain infraspecific taxa of St. vestitum

St. vestitum var. tortum W. et G.S. West 1898b

St. vestitum f. minor Schmidle 1898

a) St. vestitum var. tortum W. et G.S. West 1898b (p. 317; pl. 18, fig. 16):

This variety was first found in the United States. It does not appear to be common. West and West (1898b) and Irénée-Marie (1939) illustrate the apical view with the processes bent in one direction. This characteristic was observed occasionally on cells of clonal cultures, although the degree of the curvature was much less pronounced than in Irénée-Marie (1939, pl. 56 fig. 4, 5) or West and West (1898b; pl. 18, fig. 16b). Because of this difference, var. tortum is not placed as a synonym of var. vestitum.

Brook (1959a; p. 597, pl. 4, fig. 5) Pl. I Fig. 6 (= f. denticulatum-tortum) described a forma tortum of St. anatinum :

"Processi in vertice visi pari modo earundem partium S. cyrtocero Bréb. contorti.

> "Processes in vertical view bent round in one direction as in S. cyrtocerum Bréb.
>
> "Forms differing considerably in the character of their body ornament and length of processes may possess this character."

Brook did not mention var. tortum described by West and West, although the new forma does seem to correspond to var. tortum as illustrated by West and West (1898b).

b) St. vestitum forma minor Schmidle 1898 (p. 63).

The original publication of this forma was not available. Fritsch and Rich (1937; p. 214) record St. vestitum f. minor :

> "Long. cell., 26-28 μ; lat. cum proc. 30-52 μ; isthm. 4-7 μ..."

This is smaller than any of the field or clonal material studied, especially for the length. Some cells from field material and clones HC 151 and 226 were 32-33 μm long, approaching f. minor. Since these cells were not common, their occurrence does not seem to justify the inclusion of f. minor as a synonym of var. vestitum at the present time.

TABLE 20

CELL DIMENSIONS AND RADIATION OF *ST. VESTITUM*
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (µm) Average	Range	S.D.	C.V.	l(cp) (µm) Average	Range	S.D.	C.V.	Is (µm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3	4	3-4	3-5
49	Jacobs 14-VI-79	38	34-41	1.72	4.51	48	41-56	4.18	8.65	15	14-16	0.78	5.17	0.79	100.0	---	---	---
66	" "	38	32-41	2.33	6.24	48	39-56	3.95	8.24	14	12-15	0.84	6.14	0.74	97.0	---	3.0	---
151	Jacobs 29-VIII-79	33	29-36	1.60	4.93	43	33-58	5.91	13.67	16	14-17	1.01	6.40	0.75	85.4	5.6	7.0	
153	" "	37	33-40	1.61	4.42	47	35-52	4.06	8.67	15	13-16	0.87	5.98	0.78	95.2	---	4.2	0.6
154	" "	36	32-38	1.33	3.77	45	36-58	3.94	8.81	13	12-14	0.72	5.59	0.78	100.0	---	---	---
226	" "	33	29-36	2.83	8.46	48	39-56	4.05	8.48	17	16-20	1.17	6.77	0.70	100.0	---	---	---
210	Jacobs 26-IV-80	37	34-40	1.88	6.31	51	43-57	3.68	7.24	14	13-16	0.83	6.88	0.73	100.0	---	---	---
271	Jacobs 29-VIII-79	35	31-39	2.05	5.86	44	35-51	4.40	10.07	14	12-16	0.99	6.96	0.80	97.2	0.5	2.3	---
272	" "	37	32-41	1.76	4.80	50	43-60	3.62	7.22	14	13-15	0.69	4.87	0.71	96.1	---	3.9	---
311	Jacobs 7-VI-80	37	33-43	2.32	6.36	49	39-61	5.56	11.3	14	12-16	2.39	17.36	0.74	94.6	4.4	1.0	---
468	Jacobs 8-VIII-80	35	31-45	2.42	6.92	56	31-55	4.73	8.41	14	14-15	0.67	4.72	0.62	98.1	0.8	1.1	---
479	Placid 8-VIII-80	44	39-50	2.67	6.77	55	46-66	5.58	10.07	18	16-20	1.13	6.34	0.80	82.4	14.6	3.0	---

Field material

Source	L(cp) (µm)	l(cp) (µm)	Is (µm)	L/l	Radiation 3
Jacobs 7-VI-80	33	38, 52*	11	0.86, 0.64	X
Jacobs 26-VII-79	33	59	12	0.56	X
Jacobs 26-IV-80	33	34, 43*	11	0.97, 0.76	X

*Dichotypical cells

Plate 10

St. vestitum var. *vestitum*

1. Clone HC 122, SEM photograph; cell in front view

2. Clone HC 40, SEM photograph; cell in basal view

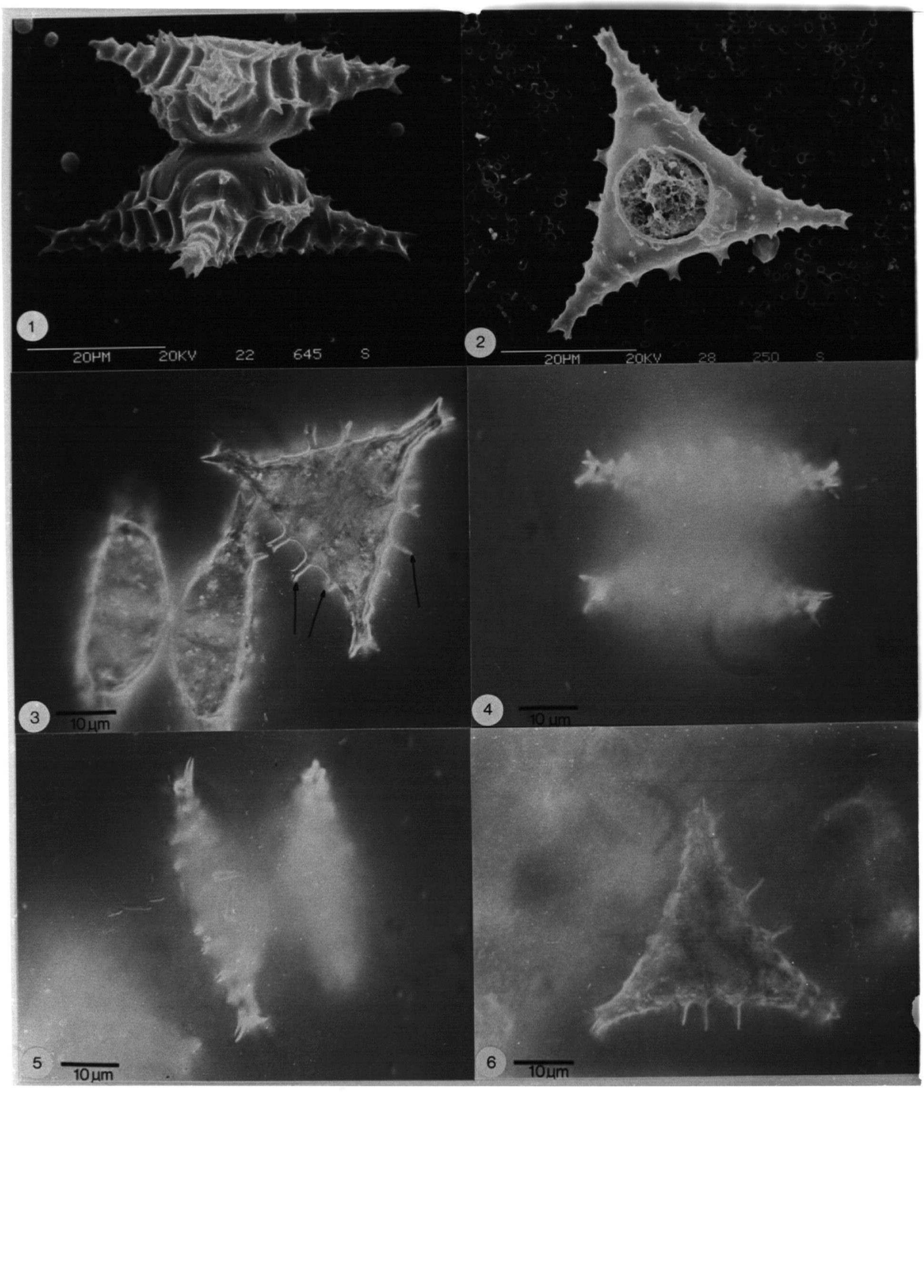
3. Clone HC 47, light microscope photograph; lower cell in front view, upper cell in vertical view. The arrow indicates the subapical verrucae and spines

4. Clone HC 40, light microscope photograph; cell in front view showing the subapical spines

5. Clone HC 66, light microscope photograph; cell in front view showing the subapical spines

6. Clone HC 49, light microscope photograph; cell in apical view showing three subapical spines on one side and two on another side

259A



1
20PM 20KV 22 645 S
2
20PM 20KV 28 250 S
3
10 µm
4
10 µm
5
10 µm
6
10 µm

L. STAURASTRUM INFLEXUM VAR. INFLEXUM

St. inflexum Brébisson 1856 (p. 140; pl. 1, fig. 25) Pl. J Fig. 7:

> "S. parvulum, granulosum; hemisomatiis ovoïdeis, radiatis, e dorso convexis prominulis nudis, radiis leviter inflexis.
>
> "St-Pierre-sur-Dives. Eaux courantes.
>
> "Ce *Staurastrum* a de grands rapports avec les deux espèces précédentes, mais le dos des hémisomates est convexe saillant, nu, sans papilles ou poils. Les rayons, au nombre de trois ou quatre, sont presque droits, à peine fléchis en dedans."

St. inflexum is a common species which was first recorded from Normandy (France), but has since been found in Africa, Europe and North America. It is very common in Como Lake and is found with *St. proboscideum* f. *minor* on the stems and under the leaf blades of *Nymphaea odorata*. It was also found in Munday Lake among *Sphagnum* populations. Stein and Borden (unpublished) report seven collections of *St. inflexum* in British Columbia, including Lost and Jacobs Lakes. *St. brachycerum* was found on Bald Mountain and *St. cyrtocerum* was recorded six times, including collections from Mike and Jacobs Lakes.

Clones examined: HC 18 from Como Lake, 7-VI-79; HC 68 from Como Lake, 26-VII-79; HC 437 from Como Lake, 16-V-80; HC 490 from Como Lake, 20-IX-80; HC 347, 355, 403 from Como Lake, 27-VI-80; HC 294, 296, 297, 302 from Munday Lake, 7-VI-80 (Table 21).

Cells of *St. inflexum* are cup-shaped with a slightly rounded or acute sinus forming a notch in the middle of the semicell. The sides of the semicell are straight or slightly convex, while the apex is markedly convex (Pl. 11 Fig. 1, 3).

The angles are extended into processes tipped with three or four short spines. Concentric rows of conical granules or short spines, ornament the processes which are subparallel to convergent. The stoutness and the length of the processes vary.

A row of supraisthmial granules often surrounds the isthmus, although it is sometimes missing or indistinguishable (Pl. 11 Fig. 3, 7). Granules also ornament the cell between the processes. They run about halfway down the sides of the semicell, leaving an area free of ornamentation between the supraisthmial row of granules and the level of the processes (Pl. 11 Fig. 3). The cells are characteristically twisted at the isthmus so that the two semicells alternate with one another (Pl. 11 Fig. 2).

In apical view, the sides are straight or slightly concave. Rows of granules or short spines and sometimes small double verrucae surround a central area free of ornamentation that often has a rosette composed of six to nine pore openings (Pl. 11 Fig. 4, 6).

In culture, the cells were mostly triradiate but tetraradiate cells or dichotypical cells with one semicell triradiate and the other tetraradiate form up to 22% of the cells counted (clone HC 68). In field material, only triradiate cells were seen. The L/l ratio is generally smaller in the field (0.59-0.96) than in culture (0.82-0.90) and probably indicates longer processes in the field. On plate 11 Fig. 7 an isolated semicell from Como Lake appears to belong to St. inflexum, although the whole cell would be needed for positive identification.

Because of the occasional presence of apical double verrucae in field and culture material, St. inflexum shows a resemblance to St. proboscideum f. minor (which was previously discussed and with which St. inflexum grows). However, St inflexum is distinguished by its smaller size, slender and converging processes, twisting of the cells at the isthmus and predominantly triradiate form.

1. Proposed synonyms of St. inflexum var. inflexum :

St. brachycerum Brébisson 1856

St. cyrtocerum Brébisson ex Ralfs 1848 sensu Croasdale 1957, 1965, 1973

a) St. brachycerum Brébisson 1856 (p. 139; pl. 1, fig. 24) Pl. J Fig. 8:

> "S. parvulum granulosum; hemisomatiis ovato-lunatis, radiatis, e dorse convexis asperis, radiis brevibus inflexis.
> "Falaise. Rare.
>
> "Cette espèce est plus petite que la précédente et le dos des hémisomates (le disque, la partie opposée à la suture), est convexe et très légèrement hispide, tandis que dans le S. cyrtocerum , cette partie est plane et présente des papilles terminées par deux très courtes épines. Les angles se prolongent en courts rayons denticulés, courbés en dedans."

West et al. (1923; p. 137) note that this species is not at all common. In fact, apart from its original description, it has been reported only five times (Archer in Pritchard 1861, p. 42; Roy and Bisset 1894, p. 180 as St. polymorphum var. brachycerum ; Rabenhorst 1868, p. 210; Borge 1899, p. 764; Comère 1901, p. 157, pl. 11 fig. 4). In later publications, Beck-Mannagetta (1931) lists the species whereas Messikommer (1949) mentions a var. destitutum Messikommer and a forma reductum Messikommer, without giving the original reference of these taxa.

West et al. (1923, p. 109, 137) note the similar size of St. inflexum and St. brachycerum, but distinguish St. inflexum from St. brachycerum,

> "by its (St. inflexum) longer and more slender processes, which are not so strongly incurved. The "body" of the cell is also relatively smaller, and not as broad in proportion with the length of cell."

Brook (1959d) places material collected and identified by de Brébisson as St. paradoxum var. incurvum with St. brachycerum (Pl. K Fig. 1A). Brook also notes that previous reports of St. inflexum (Brook 1958, fig. 60; Round and Brook, 1959; see Pl. K Fig. 1B) really is St. brachycerum, since the apical and isthmial ornamentation agree with de Brébisson's material. The slender processes of St. brachycerum sensu Brook do not agree with West et al.'s (1923) interpretation of St. brachycerum and St. inflexum. It appears from de Brébisson's description that St. brachycerum is distinguished mainly from St. inflexum by its more incurved processes and slightly hispid apex (with minute spines).

The two features of curvature of the processes and development of ornamentation have often been shown to vary. The clonal and field material of St. inflexum in this study confirm this. For example, on Pl. 11 Fig. 1, the processes are strongly incurved but not on Fig. 3. On Pl. 11 Fig. 6, the isthmial ornamentation is represented by spines, whereas granules are seen on Fig. 3. Furthermore, Fig. 5, 7 show the presence of apical double verrucae but not Fig. 3 or 4.

Such variable features can not be used to distinguish clearly between the two species and I would propose that St. brachycerum be considered at this time as a synonym of the more common St. inflexum. Prescott et al. (1982; p. 147) accept St. brachycerum as a valid taxon.

b) St. cyrtocerum Brébisson ex Ralfs 1848 sensu Croasdale 1957, 1965, 1973

Croasdale (1957; p. 143) describes a form of St. cyrtocerum that is similar to St. inflexum of the present study. Croasdale's St. cyrtocerum forma resembles St. proboscideum (discussed in F.) and she notes:

> "This form approaches S. proboscidium (Bréb.) Arch. and S. Borgeanum Schmidle, but differs from both in its smaller size, strongly converging processes, its more obscure apical verrucae, and from the latter also in its triradiate form and its lack of supraisthmial ornamentation."

Croasdale's specimens from Alaska are slightly bigger (24-33.5 x 30 x 33 μm) than those studied here and lack supraisthmial granules. Her algae differ significantly (especially in width), from those described in Ralfs (1848, p. 139) as St. cyrtocerum:

	L (μm)	l(cp) (μm)	Is (μm)	L/l
Ralfs	32	51	9	0.62
Croasdale	24-33.5	30-33	---	0.8-1.02
HC Clones (average)	20	23	8	0.87

Croasdale (1965, 1973), shows forms of St. cyrtocerum with a ring of supraisthmial granules. It is thought that drawings by Croasdale (1957, pl. 6 fig. 102, 103; 1965, pl. 8, fig. 11, 12; 1973, pl. 18 fig. 17, 18) of St. cyrtocerum correspond to the material observed in this study and should be classified as St. inflexum, emended to include forms with apical verrucae. Croasdale's specimens have either straight or slightly bent processes in vertical view.

2. Taxon related to St. inflexum

St. cyrtocerum Brébisson ex Ralfs 1848 (p. 139; pl. 22, fig. 10) Pl. K Fig. 2:

> "...frond rough with minute granules; segments in the front view somewhat triangular with short incurved processes.
>
> "Frond rather larger than that of Staurastrum tricorne , deeply constricted at the middle, rough with minute spine-like granules, which on the processes are arranged in transverse lines. The segments are truncate and taper towards their junction, so that the constriction forms a broad notch on each side. The spines on the outer margin are larger than those on the rest of the segment, and frequently are obscurely notched. The end view has three blunt angles, much like those of Staurastrum tricorne, and usually a little curved.
>
> "The sporangia are orbicular and their spines slightly

forked at the apex.

" *Staurastrum* *cyrtocerum* is smaller than *S.* *aculeatum* and *S.* *controversum*, and its spines are far less conspicuous. It is best distinguished by is converging processes.

"Length of frond 1/800 of an inch; breadth 1/500; breadth at constriction 1/2747."

This species is a close ally of *St.* *inflexum*, but differs mainly by its larger size. West *et al.* (1923; p. 136) also note as distinguishing feature, "...the row of tiny emarginate granules on the apex of the semicell" and "Its (*St.* *cyrtocerum*) short, stout, converging processes, frequently seen in the vertical view to be bent abruptly in one direction.".

Ralfs 1848 (pl. 22, fig. 10; see Pl. K Fig. 2) shows several rows of granules lining the sides of the semicell in apical view, but not one row of emarginate granules. In apical view, he represents the processes as curved in one direction but not abruptly bent.

Ralfs' dimensions for *St.* *cyrtocerum* converted to μm are L:32 l:51 Is:9. Cells found in the present study were not classified as *St.* *cyrtocerum*, because of their smaller size and the fact that in vertical view no processes bent in one direction were seen.

St. *inflexum* and *St.* *cyrtocerum* appear as two different but closely related taxa. Ralfs and de Brébisson's descriptions are sketchy and have lead to different interpretations of the two taxa. A thorough reevaluation of *St.* *inflexum* and *St.* *cyrtocerum*, their respective features and the variation involved, would help in understanding each taxon.

TABLE 21

CELL DIMENSIONS AND RADIATION OF ST. INFLEXUM
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (μm) Average	Range	S.D.	C.V.	l(cp) (μm) Average	Range	S.D.	C.V.	Is (μm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3	4	3-4
18	Como 7-VI-79	21	19-23	1.02	4.77	25	19-28	1.88	7.69	8	7-9	0.55	6.81	0.86	88.0	4.7	7.3
68	Como 26-VII-79	19	16-21	1.14	6.14	22	17-24	1.88	8.61	7	6-8	0.66	9.19	0.85	77.4	9.7	12.9
437	Como 16-V-80	20	17-23	1.33	6.74	24	20-31	1.96	8.20	9	8-10	0.61	6.98	0.83	85.6	10.0	4.5
490	Como 20-IX-80	18	15-21	1.37	7.43	22	16-27	2.33	10.78	7	6-8	0.62	8.87	0.85	91.2	8.8	---
347	Como 27-VI-80	22	19-24	1.19	5.55	26	23-32	2.17	8.37	8	7-8	0.64	8.42	0.82	99.3	0.7	---
355	" "	21	19-24	1.00	4.78	24	19-28	2.22	9.44	8	6-8	0.70	9.18	0.89	96.6	3.4	---
403	" "	21	19-23	1.52	7.27	24	20-30	1.95	8.08	9	7-10	0.83	9.69	0.87	86.0	14.0	---
294	Munday 7-VI-80	20	13-29	2.56	12.97	23	18-27	2.10	9.27	7	6-10	0.97	13.40	0.90	94.5	2.2	3.3
296	" "	18	16-20	1.09	6.28	20	14-26	2.39	11.89	7	6-7	0.41	6.29	0.87	98.7	1.3	---
297	" "	18	17-21	0.88	4.79	23	18-28	1.87	8.82	7	6-8	0.66	8.09	0.84	90.2	1.2	8.6
302	" "	21	19-25	1.38	6.60	25	20-28	2.39	9.71	8	7-8	0.48	6.12	0.85	86.0	8.3	5.8

Field material

Source	L(cp) (μm)	l(cp) (μm)	Is (μm)	L/l	Radiation 3
Como 16-V-79	18	31, 25*	6	0.59, 0.70	X
Como 28-V-79	21	22, 24*	6	0.96, 0.85	X
" "	22	27	7	0.80	X

*Dichotypical cells

continued

TABLE 21 (cont'd)

Field material

Source	L(cp) (μm)	l(cp) (μm)	Is (μm)	L/l	Radiation 3
Como 28-V-79	22	29	7	0.75	X
Como 7-VI-79	16	26	6	0.62	X
" "	19	28	6	0.68	X
Como 25-I-80	21	29	6	0.72	X
" "	22	31	6	0.70	X
Como 7-VI-80	20	31	7	0.63	X
Como 27-VI-80	21	29	6	0.72	X
" "	21	32	7	0.65	X
Como 18-VII-80	20	28, 24*	6	0.71, 0.83	X
Como 8-VIII-80	21	28	6	0.74	X
Como 11-X-80	20	30	6	0.66	X
Como 22-XI-80	19	30	6	0.62	X
Como 22-II-81	21	30	6	0.69	X
Como 28-VIII-81	21	33	6	0.61	X
" "	20	32	6	0.61	X
" "	20	33	6	0.59	X

*Dichotypical cell

Plate 11

St. inflexum var. inflexum

SEM photographs

(marker= 10 μm unless indicated otherwise)

1, 2. Clone HC 68

1. Cell in front view with strongly convergent porcesses

2. Cell in vertical view showing the alternate semicells

3, 4. Clone HC 18

3. Cell in front view; the arrow indicates the supraisthmial row of granules

4. Cell in vertical view showing the apical ornamentation

5, 6, 8. Clone HC 25

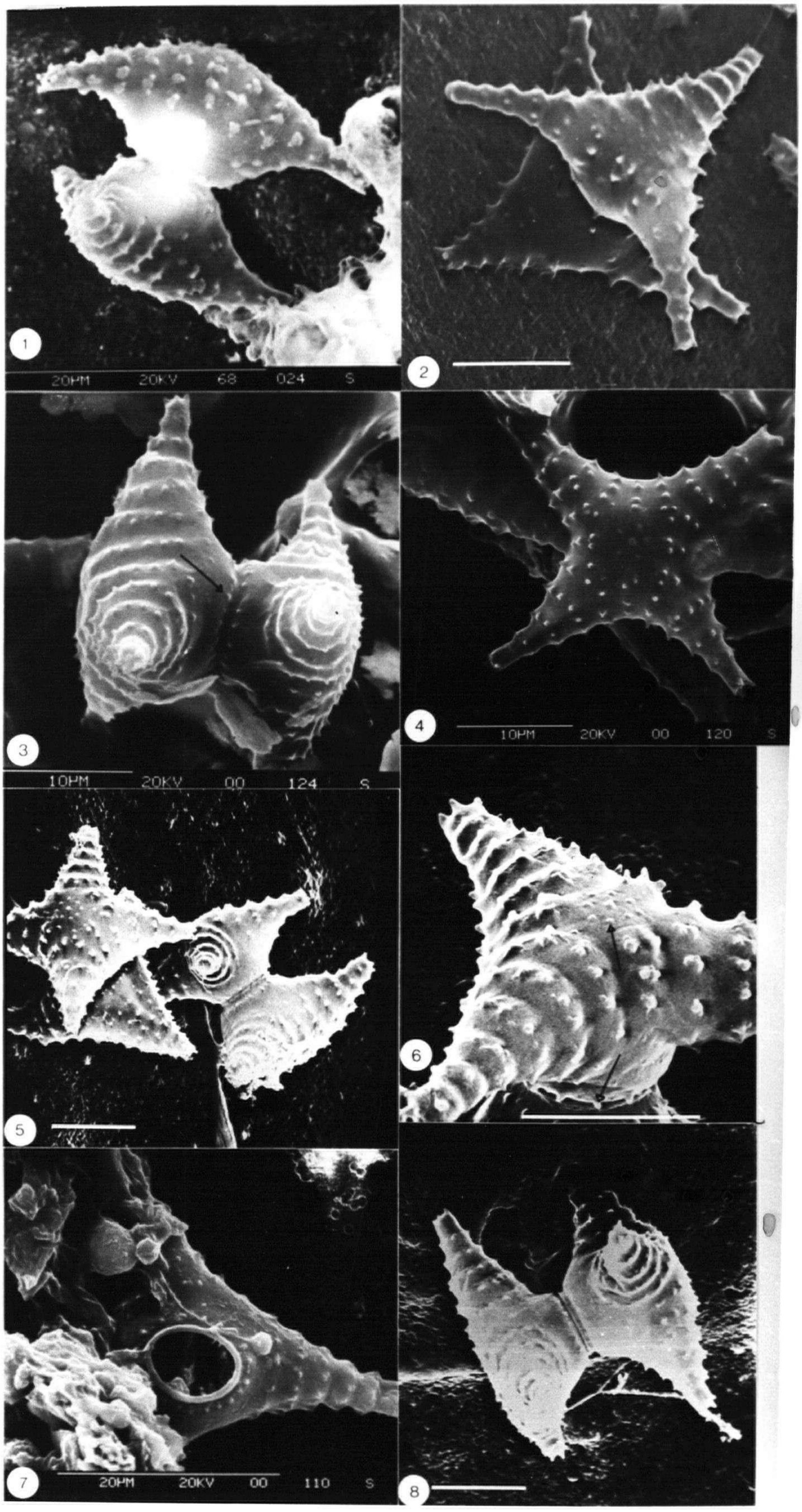
5. Cells in front or vertical view

6. Semicell viewed from the front and the apex; arrows indicate the rosette of pores in the centre of the apex and the supraisthmial spines

8. Cell in front view

7. Como 28-V-79, isolated semicell in basal view

270A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8

M. STAURASTRUM TETRACERUM VAR. TETRACERUM

St. tetracerum (Kützing) Ralfs 1848 (p. 136; pl. 23, fig. 7)

Pl. K Fig. 3:

> "...frond rough; front view with four slender diverging processes which are entire at the apex; end view compressed, with a process at each extremity...
>
> "Frond very minute; front view nearly square, the angles elongated into straight, slender processes which diverge from each other; frequently however a segment may be so twisted, that one of its processes is situated behind its companion, and is not seen unless carefully looked for; in this case the frond seems to have only three processes in a front view. The end view is much compressed and terminated both ways by an elongated process. The frond is rough with minute puncta-like granules, which form transverse lines on the processes and give them a jointed appearance. The colouring matter is very pale.
>
> "Ehrenberg and Meneghini unite the Micrasterias tetracera of Kützing to the Staurastrum paradoxum, Meyen; but whilst the latter plant has four processes at each end, this has only two, which, if I am correct in my view of the following species, differ also by having entire extremities.
>
> Length of frond 1/2703 of an inch; length of process 1/3030; breadth of frond 1/1785."

St. tetracerum was originally described by Kützing 1833 as Micrasterias tetracera and was first transferred by Ralfs to the genus Staurastrum (Ralfs 1845). Ralfs published basically the same description in 1848 as in 1845. He indicated (1845) that the species has two processes (=biradiate), yet fig. 1b illustrates a triradiate end view.

St. tetracerum is a common species which was found in five of the lakes studied: Munday, Como, Jacobs, Mike and J.K. Henry. Stein and Borden (unpublished) list 18 reports of the species in British Columbia, including Mike, Munday and Como Lakes. They also report St. tetracerum forma trigona and var. validum in Mike Lake; these taxa are discussed later.

Clones examined: HC 292 from Munday Lake, 7-VI-80; HC 368 from Como Lake, 27-VI-80 (Table 22).

This species was easy to isolate and grow in culture. The cells are subtriangular in shape with a smooth concave or straight apex (Pl. 12 Fig. 1). On each side of this smooth area the ornamentation of the processes begins and this often looks like protuberances tipped with a spine (Pl. 12 Fig. 1, 2).

The sinus is widely open and rounded. Small spines, while visible above the isthmus (Pl. 12 Fig. 2, 4), do not form a supraisthmial ring of granules as seen in taxa such as St. proboscideum f. minor (see Pl. 7 Fig. 3).

The processes are strongly divergent and vary greatly in length (ca. 3-12 um; Pl. 12 Fig. 3, 8). They are strongly denticulated, the denticulations being tipped with a single or occasionally a double spine. Generally, concentric rows of granules or short spines surround the processes, although they are not always regular and may be missing (Pl. 12 Fig. 2, 3, 5). The cells are often twisted at the isthmus (Pl. 12 Fig. 7). The front of the semicell may bear more or less pronounced protuberances or be mostly smooth (Pl. 12 Fig. 4-7). This characteristic links St. tetracerum to St. irregulare W. et G.S. West or other related species which differ mainly by the presence of a ventral protuberance bearing two to four spines (see Brook, 1982).

In apical view, the cells are predominantly biradiate but triradiate cells or dichotypical cells with one semicell biradiate and the other triradiate were also seen (up to 2.7% in clonal material). In field material, only two cells were triradiate, the others were biradiate. The two clones cultivated varied mostly in size, the Como Lake clone being on the average slightly smaller.

The clones in culture tend to be wider than long on the average (L/l= 0.92, 0.94; Table 22), whereas the field specimens are usually longer than wide (L/l=0.93-1.22; Table 22). Generally, field material has longer processes than cultured material as previously indicated for other taxa. Comparison of the length of the cells with and without processes, shows that the processes are longer in field material and the cells in clonal culture have a larger body. The wider isthmus of the cells in culture also support the observation that the cells are stouter in culture.

Brook (1982) studied *St. tetracerum*, *St. irregulare* W. *et* G.S. West, *St. bibrachiatum* Reinsch and *St. pseudotetracerum* (Nordstedt) W. et G.S. West. He believes that Ralfs is incorrect in stating that in *St. tetracerum* "minute puncta-like granules,...form transverse lines on the processes and give them a jointed appearance." Brook says that although the processes appear denticulate in front view, they do not show "rings of granules forming transverse lines" and that, instead, the disposition of the granules down the processes is alternate (Brook 1982, p. 261, fig. 1a-f). He states that "acceptable, subsequent publications" do not show the transverse lines described by Ralfs.

<u>St.</u> <u>tetracerum</u> is a small species and, as such, it is often difficult to distinguish the tiny granules and spines on the body of the cells in light microscopy. In field material, cells often contain some protoplasm which compounds the difficulty in distinguishing the pattern of ornamentation. Brook uses methyl violet to show the tiny granules and spines of <u>St.</u> <u>tetracerum</u>. He also studies culture material and has probably observed more empty cells. I do not agree with Brook that "<u>all</u> acceptable, subsequent publications (of <u>St.</u> <u>tetracerum</u>) show no ring of granules on the processes", and that arrangement of the granules along the processes is alternate. At least two "acceptable" reports show rings of granules on the processes (Taft 1945, pl. 5 fig. 17; Croasdale 1957, pl. 6 fig. 95). SEM work permitted observation of the minute ornamentation and clearly show that rings are sometimes present, although the number of granules forming the rings may vary, or the granules may be completely lacking (Pl. 12 Fig.1-8). They are never regularly alternate.

Brook (1982; fig. 1 d-e) also emphazises the usual presence of a central apical granule, a feature which was not pointed out by Ralfs. In some cases, one minuscule apical granule was seen (Pl. 12 Fig. 2) in clonal cultures.

1. Proposed synonyms of <u>St.</u> <u>tetracerum</u> var. <u>tetracerum</u>

   <u>St.</u> <u>tetracerum</u> f. <u>biradiata</u> Borge 1925

   <u>St.</u> <u>tetracerum</u> forma Borge 1936

St. tetracerum f. trigonum Lundell 1871

a) St. tetracerum forma biradiata Borge 1925 (pl. 1, fig. 23) Pl. K Fig. 8:

> "...sinu aperto intimo rotundato, radiis apice tridentatis margine utrinque denticulis 2 ornatis, angulis inferioribus semicellularum denticulis singulis ornatis. Long. cum rad. 21-22 μ, sine rad. 10 μ; lat. cum rad. 21 μ, supra isthm. 8-9 μ; lat. isthm. 3,5 μ..."

Forma biradiata would be better named St. tetracerum facies 2 in accordance with Grönblad and Růžička's (1959) recommendations. Förster (1970) reported specimens of facies 2 or 3 and dichotypical cells bearing two and three processes respectively, on each semicell. This was also observed in clonal cultures and both bi- and triradiate cells were seen in field material.

b) St. tetracerum forma Borge 1936 (p. 46; pl. 3, fig. 57) PL. K Fig. 9:

> "...forma brachiis margine 6-10 undulatis, apice bifidis, semicellulis e vertice visis bi-vel tri-radiatis. Long. sine brach. = lat. 7-7.5 μ; long. cum brach.= lat. 28,5 μ; lat. isthm. 4-4,5 μ..."

Borge's illustration shows a specimen with long, slender and less denticulated processes than forma biradiata published 11 years earlier. Similarly, the sinus is not as deep and there are no spines on each side of the isthmus. This resembles St. tetracerum in Grönblad 1960 (fig. 179) and Förster 1970 (pl. 29, fig. 7-12), and therefore it should probably be treated as var. _tetracerum_.

c) _St. tetracerum_ forma _trigonum_ Lundell 1871 (p. 69)

The original publication was not available, but according to West _et al._ 1923 (p. 120), this is just a triradiate form of _St. tetracerum_. Thus it would be better to refer to it as facies 3 in accordance with Grönblad and Růžička's (1959) recommendations. Prescott _et al._ (1982; p. 331) consider it as a distinct taxon.

2. Other infraspecific taxa of _St. tetracerum_

Some of the following taxa have been placed in synonymy by other authors, whereas in others more thorough study is needed before any conclusions are made about the validity of the taxa.

St. tetracerum var. _undulatum_ W. et G.S. West 1895b

St. tetracerum var. _validum_ W. et G.S. West 1897c

St. tetracerum var. _evolutum_ W. et G.S. West 1905a

St. tetracerum var. _evolutum_ f. _minor_ Irénée-Marie 1957

St. tetracerum var. _trigranulatum_ W. et G.S. West 1907

St. tetracerum var. _cameloides_ Florin 1957

St. tetracerum var. _maximum_ Messikommer 1966

a) _St. tetracerum_ var. _undulatum_ W. et G.S. West 1895b (p. 80; pl. 9, fig. 6) Pl. K Fig. 4:

"Var. processibus distincte undulatis et apicibus processuum emarginatis.

"Long. sine proc. 11 μ, cum proc. 27 μ; lat. cum proc. 27 μ; lat. isthm. 5 μ; crass. 6 μ."

This variety was first recorded from Madagascar and no further records were found. Ralfs (1845, 1848) did not indicate if spines were present at the tip of the processes of St. tetracerum and this may be the reason why West and West created var. undulatum. In West et al. (1923, p. 119) however, it was included as a synonym of St. tetracerum and this conclusion is accepted.

b) St. tetracerum var. validum W. et G.S. West 1897d (p. 495; pl. 6, fig. 25) Pl. K Fig. 5:

"Var. corpore longiori, processibus validioribus non attenuatis et 5-nodulosis.

"Long. s. proc. 18 μ, c. proc. 42 μ; lat. s. proc. 13 μ, c. proc. 37 μ; lat. isthm. 5 μ."

This variety was first found in the South of England and later reported in North America. Its original illustration shows a slightly convex apex contrary to the type species which usually has a straight or concave apex. The sides of the semicell in front view are straight and the sinus is widely open and acute, whereas in most illustrations of St. tetracerum, the sides of the semicells are slightly convex and the sinus forms a small notch in the middle of the semicell. Variety validum is also longer with stouter processes. It is very distinctive from var. tetracerum.

c) St. tetracerum var. evolutum W. et G.W. West 1905a (p. 25; pl. 2, fig. 31) Pl. K Fig. 6:

> "Var. processibus cellularum longioribus; semicellulis a vertice visis triangularibus, lateribus convexis, angulis in processus longos productis."

This variety was first found in the Orkneys and Shetland Islands (England) and later in North America. It was transferred to St. paradoxum by West et al. (1923; p. 107, pl. 145 fig. 7, 8). Smith (1924b; p. 97, pl. 76 fig. 11-14) retained it as a variety of St. tetracerum, but he may not have been aware of West et al.'s work. Variety evolutum is triradiate and it has much longer processes than var. tetracerum. The transfer to a different species, although not St. paradoxum, appears warranted; Brook (1959a) suggests that St. paradoxum be considered as nominum inquirendum and I agree with him.

d) St. tetracerum var. evolutum forma minor Irénée-Marie 1955 (p. 200; fig. 24) Pl. K Fig. 11:

> "L: 38.4-41.6 mμ; (sp): 19-19.5 mμ; l.: 24-38 mμ; (sp): 12.9-13 mμ; Is.: 4.5-6 mμ...
>
> "Forma propioris varietati evolutum. Appendices minus longae, et minus latae."

This forma was only recorded from the Trois-Rivières area (Québec, Canada). The dimensions given by Irénée-Marie rank between those of Smith (1924b) for var. evolutum and those for St. tetracerum var. tetracerum (Ralfs 1848). Irénée-Marie's dimensions suggest a cell which is longer than wide.

Calculation of the ratio L/l for both extreme values gives L/l = 38.4/24 = 1.6; L/l = 41.6/38 = 1.09. Direct measurements of Irénée-Marie's fig. 24 show that the L/l ratio would be around 0.81. Irénée-Marie's record could belong to St. pseudotetracerum W. et G.S. West. Comparison of the dimensions by West and West (1895b; p. 79) for St. pseudotetracerum with Irénée-Marie's dimensions show that only the L(cp) parameter differs significantly, that is 38.4-41.6 µm in Irénée-Marie, and 23-26 µm in West and West. All other measurements and features seem to agree with St. pseudotetracerum.

e) St. tetracerum var. trigranulatum W. and G.S. West 1907 (p. 217; pl. 15, fig. 19) Pl. K Fig. 7:

This variety was first found in Burma and does not appear to have been reported since. The original description was not available but, according to the original figure, this variety is distinguished by the presence of six subapical granules as seen in end view. This feature was not noted in the present study. However, subapical granules were observed in clonal cultures (Pl. 12 Fig. 6)

f) St. tetracerum var. cameloides Florin 1957 (p. 130; pl. 29, fig. 5-8) Pl. L Fig. 1:

Basionym: St. paradoxum Meyen var. osceolense Wolle 1885 forma biradiata Georgewitsch 1910 (p. 245, fig. 6) Pl. K Fig. 13

Syn.: St. osceolense (Georgewitsch) Grönblad 1945 (p. 26; fig. 214)

St. osceolense var. fennicum Grönblad 1948 (p. 422; fig. 35-38).

Georgewitsch's description and discussion are:

> " St. paradoxum Meyen var. osceolense Wolle forma biradiata n. f. Icon. nostr. 6.
>
> "Long. cum proc. 27 μ, sine proc. 15 μ, lat. cum proc. 32 μ, sine proc. 12 μ, lat. isth. 5 μ.
>
> "Diese Form unterscheidet sich vom Typus dadurch, dass sie in vertikaler Ansicht nur zwei Radien aufweist."

Florin's (1957) Latin description for the new variety is:

> "Differt a forma typica duabus tuberculis magnibus ad basine processorum..."

Although Georgewitsch's description noted the biradiate state as different from St. paradoxum, he did not make mention of the much smaller size and of the presence of the two protuberances at the base of the processes seen in his fig. 6. These protuberances are stressed by Grönblad (1945) and Florin (1957). It is doubtful that the variety cameloides can be clearly separated from St. tetracerum. Literature reports of St. tetracerum and observations of field and clonal material in this study show that the centre of the apex of St. tetracerum is in front view completely free of undulations or spines and is either straight or slightly concave. The undulations or small spines begin at the base of the processes and often appear like a protuberance on each side of the apex (Pl. 12 Fig. 1, 2).

g) St. tetracerum var. maximum Messikommer 1966 (p. 377-78;

pl. 1, fig. 16) Pl. K Fig. 13:

> "...Varietas nova praecipue differt dimensionibus multo maioribus. Long. sine process. 20,9 μ, cum process. 52,2 μ, lat. cum process. 64,3 μ, lat. isthm. 5,6 μ."

This variety was first found in East Germany and no other records were seen in the literature. Messikommer's figure 16 does not appear to belong to St. tetracerum. It is much larger, the isthmus is more widely open than in St. tetracerum and the apex of the cell in front view is undulate (Pl. K Fig. 13). The end view is triradiate and shows very clearly four verrucae located on the apex, a feature which is not seen in St. tetracerum.

3. Uncertain taxa of St. tetracerum

St. tetracerum var. subexcavatum Grönblad 1921

St. tetracerum f. tetragonum W. et G.S. West 1897c

St. tetracerum var. tortum (Teiling) Borge 1921

a) St. tetracerum var. subexcavatum Grönblad 1921

The original publication of this taxon was not available. Bourrelly (1961; pl. 22 fig. 3) illustrates St. tetracerum var. subexcavatum Grönblad f.? (Pl. K Fig. 10) from the Ivory Coast, which appears to represent only a large strongly ornamented form of St. tetracerum var. tetracerum. Only one other record was found in the literature and the illustration lacks details (Behre 1956).

b) St. tetracerum forma tetragonum W. et G.S. West 1897c (p. 495)

West and West may have found a tetraradiate form of St. tetracerum, although this does not seem to have been reported before. Prescott et al. (1982; p. 331) stress that without an illustration they cannot be certain that their "North American plants are identical with the type."

c) St. tetracerum var. tortum (Teiling) Borge 1921 (p. 22; pl. 2, fig. 22)

Basionym: St. iotanum var. tortum Teiling 1916 (p. 65)

The original publication of this taxon was not available but it is described in Prescott et al. (1982; p. 332) and they question its validity.

4. Conclusion

St. tetracerum is a distinct species. The semicells are often clearly twisted at the isthmus and the strongly denticulated processes are very characteristic. Nevertheless, the species is variable and the numerous varieties which have been added to it do not necessarily express stable taxonomic features.

TABLE 22

CELL DIMENSIONS AND RADIATION OF ST. TETRACERUM
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation; C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (µm) Average	Range	S.D.	C.V.	l(cp) (µm) Average	Range	S.D.	C.V.	Is (µm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 2	3	2-3
292	Munday 7-VI-80	24	18-27	2.64	10.36	26	17-34	3.69	13.77	6	5-7	0.67	10.72	0.94	97.3	0.7	2.0
368	Como 27-VI-80	21	18-26	2.35	10.87	23	19-28	2.68	11.19	8	7-9	0.62	8.27	0.92	98.6	0.7	0.7

Field material

Source	L(cp) (µm)	L(sp) (µm)	l(cp) (µm)	l(sp) (µm)	Is (µm)	L/l	Radiation 2	3
Como 28-V-79	26	11	24	13	5	1.07	X	
Como 14-VI-79	27	9	24	--	5	1.11	X	
Como 25-I-80	27	10	27	--	--	1.00		X
Como 18-VI-80	27	9	29	--	6	0.93	X	
Como 30-VIII-80	26	--	24	--	6	1.07	X	
Jacobs 26-VII-79	22	--	18	--	--	1.20	X	
" "	19	--	18	--	5	1.05	X	
" "	18	10	21	--	5	0.87	X	
Jacobs 22-VIII-79	23	16	19	--	--	1.22		X
Mike 10-VIII-79	23	8	19	--	5	1.19	X	
J.K. Henry 30-V-80	23	--	20, 17*	--	--	1.16, 1.38	X	

*Dichotypical cell

Plate 12

<u>St.</u> <u>tetracerum</u> var. <u>tetracerum</u>

SEM photographs

1-8. Clone HC 292

1. Cell in front view

2. Detail of front view; the arrow indicates the granules on the processes

3. Cell in front view showing the processes of different length; the arrow indicates the granules on the processes

4. Detail of the supraisthmial spines

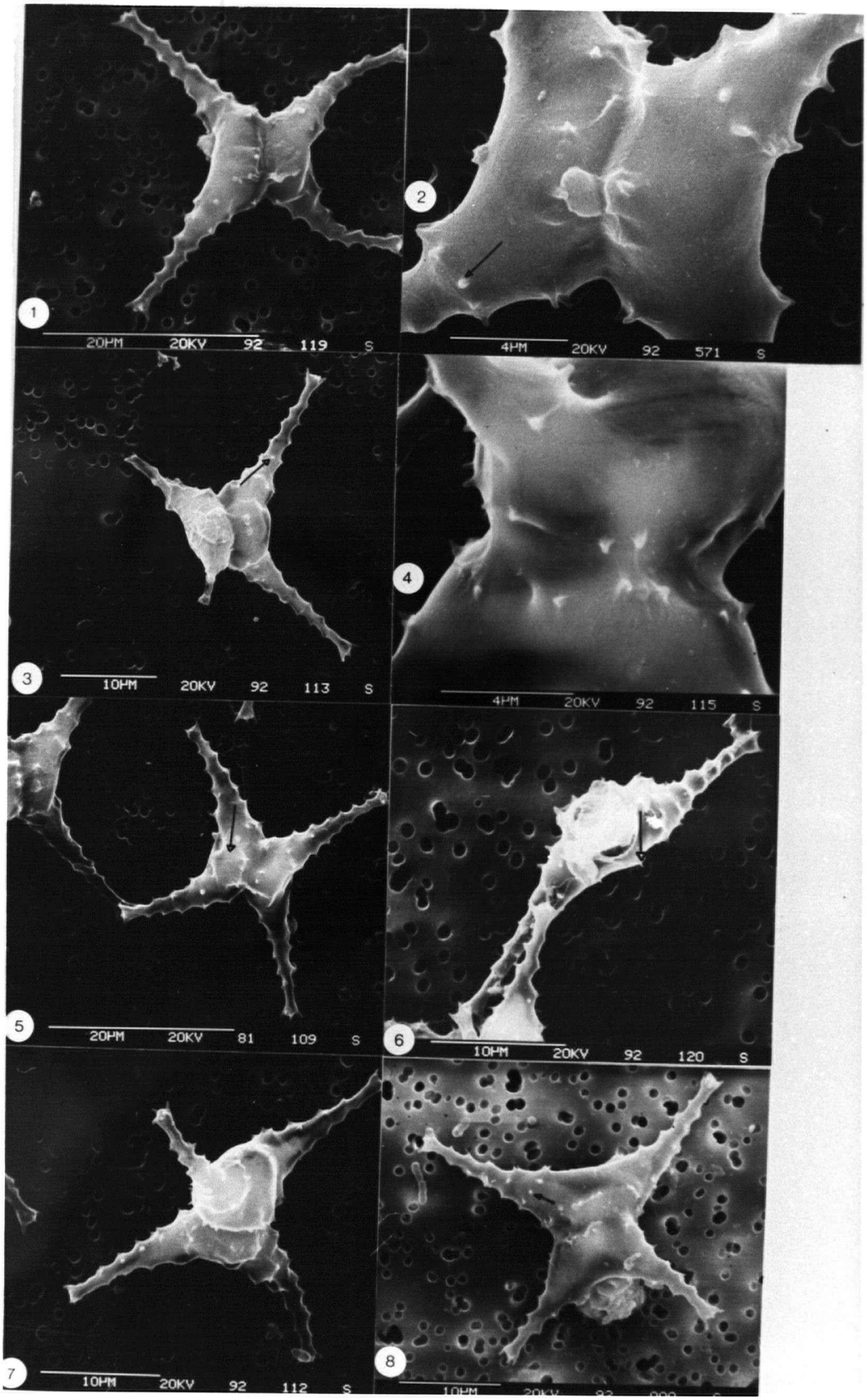
5. Cell in front view; the arrow indicates the front protuberances

6. Cell in basal view; the arrow indicates the subapical granules

7. Cell in front view twisted at the isthmus

8. Cell in front view showing the processes of different length in each semicell

285A



1
20µM 20KV 92 119 S
2
4µM 20KV 92 571 S
3
10µM 20KV 92 113 S
4
4µM 20KV 92 115 S
5
20µM 20KV 81 109 S
6
10µM 20KV 92 120 S
7
10µM 20KV 92 112 S
8
10µM

N. STAURASTRUM FURCIGERUM VAR. FURCIGERUM AND STAURASTRUM FURCIGERUM FORMA EUSTEPHANUM

Stein and Borden (unpublished) report 24 previous collections of *St. furcigerum* var. *furcigerum* in British Columbia, including Jacobs Lake. They also note seven records of *St. furcigerum* f. *armigerum* (Brébisson) Nordstedt, but none for f. *eustephanum*.

Clones examined: HC 211, *St. furcigerum* var. *furcigerum* from Jacobs Lake, 26-IV-80; HC 213 *St. furcigerum* f. *eustephanum* from Jacobs Lake, 26-IV-80 (Table 23).

Cells of *St. furcigerum* (clone HC 211) are slightly longer than broad (L/l = 1.08; Table 23) and are constricted by an open and acute sinus. The angles are extended into short, stout and strongly denticulated processes of variable length. Concentric rings of granules ornament the processes (Pl. 13 Fig. 1) which are tipped with two or three spines. The rest of the cell does not have ornamentation.

Three accessory processes are attached apically just above the angular processes (Pl. 13 Fig. 1, bottom semicell), so that in apical view, they are in the same vertical plane as the angular processes. The apical view is triradiate with straight sides. According to West *et al.* (1923, p. 190), the only difference between *St. furcigerum* var. *furcigerum* and the forma *eustephanum* is the number of accessory processes: three for the former, six for the latter.

The cells of *St. furcigerum* f. *eustephanum* have the same general features as the type species, but have a total of six accessory processes instead of three, that is two at each angle, located each side of the angular processes (Pl. 14 Fig. 2, 3). Clone HC 213 is also slightly bigger on average than clone HC 211 (Table 23), a feature which is not reported in the literature as a general distinction between f. eustephanum and the type species. The "granules" and filaments seen in SEM photographs are the result of incomplete cleaning of the mucilage during preparation for SEM observation.

A cell of f. eustephanum was observed from field material (Table 23). It was bigger than the cells in clonal culture and had strongly denticulated processes which varied in length in the two semicells.

The literature reports many dichotypical specimens with one semicell resembling var. furcigerum and the other f. eustephanum. Růžička (1973; pl. 16, fig. 7) observes such dichotypical specimens and claims that the number of accessory processes is a useless taxonomic characteristic. West et al. (1923; pl. 156, fig. 8) show conjugation between the two taxa. Both Förster (1970; pl. 16, fig. 5) and Lowe (1923; pl. 4, fig. 9) illustrate specimens of var. furcigerum in which one angle bears two accessory processes whereas the other angle bears only one process in the upper whorl. The two HC clones (HC 211, St. furcigerum and HC 213, St. furcigerum f. eustephanum) show no such variation in the number of accessory processes. In clone HC 211, no cells had more than three processes in the upper whorl, whereas in clone HC 213 all cells observed possessed the six accessory processes characteristic of

f. eustephanum. Both taxa are very common and are found in different areas of the world.

1. St. furcigerum (Brébisson ex Ralfs) Brébisson 1856 (p. 136):

Basionym: Staurastrum furcigerum Brébisson in Meneghini 1840 (p. 226)

Syn.: Didymocladon furcigerus Brébisson ex Ralfs 1848 (p. 144; pl. 23, fig. 12) Pl. L Fig. 2:

Ralfs' (1848) description is:

> "α . End view triangular.
> "β . End view quadrangular...
>
> "Frond comparatively large, rough with pearly granules, which being arranged on the processes in transverse lines, produce a crenate appearance on their margins. In the front view the processes are elongated, stout, tapering, bifid at the apex. The lateral processes of the one segment are usually parallel to those of the other; in Rochdale specimens however they are slightly curved outwards. The end view is triangular or quadrangular, and the elongated angles appear either acute and simple, or bifid, according as one or two forks of the processes may be visible.
>
> "Length of frond, including processes, 1/333 of an inch; length, excluding processes, 1/547; breadth, including processes, 1/357; breadth, excluding processes, 1/555; breadth at constriction 1/1666."

St. furcigerum was first described by de Brébisson in Meneghini (1840). Ralfs (1848) created the genus Didymocladon comprising one species, Didymocladon furcigerum (Brébisson) Ralfs characterised by the double processes which overlap each other at the angles. His classification did not attract much support.

De Brébisson (1856) refuted the new classification proposed by Ralfs and kept the species as St. furcigerum .

2. Proposed synonym of St. furcigerum var. furcigerum

St. furcigerum var. reductum W. et G.S. West 1906

St. furcigerum var. reductum W. et G.S. West 1906 (p. 104; pl. 11, fig. 12, pl. 9 fig. 5,2) Pl. L Fig. 3:

> "Var. processibus multe brevioribus, processibus superioribus brevissimis; semicellulae a vertice visae triangulares, lateribus paene rectis vel levissime convexis.
>
> "Long. 43 μ; lat. cum proc. 54 μ; lat. isthm. 21 μ...
>
> "This variety is principally distinguished by the great reduction of the superior processes. We have noticed one semicell in which they were altogether suppressed."

This variety was first described from Ireland and appears rare. It is difficult to accept, as it is based on the size of the processes which is a very variable feature as seen in clones HC 211 and 213. St. furcigerum var. reductum should be considered merely as a morpha of St. furcigerum .

3. St. furcigerum forma eustephanum (Ehrenberg ex Ralfs) Nordstedt 1888 (p. 207)

Basionym: Desmidium eustephanum Ehrenberg 1843 (p. 412; pl. 4, fig. 23)

Syn.: Staurastrum eustephanum Ehrenberg ex Ralfs 1848 (p. 215):

Ralfs' description is:

> "...end view triangular with six emarginate spines on the upper surface; each angle terminated by a short ray tipped with spines."

This taxon was first described by Ehrenberg (1843) as _Desmidium eustephanum_. Ralfs transferred it to the genus _Staurastrum_ and it was later established as forma _eustephanum_ of the species _St. furcigerum_ by Nordstedt (1888).

4. Proposed synonym of _St. furcigerum_ f. _eustephanum_

   St. furcigerum var. _montanum_ (Raciborski) W. et G.S. West _sensu_ Croasdale 1957

St. furcigerum var. _montanum_ _sensu_ Croasdale 1957 (pl. 9, fig. 132).

Croasdale (1957) illustrates a specimen that has one extra process at one angle and two at the other two angles. Its dimensions, 60 x 60 µm cp and 50 x 45 µm sp, are between Raciborski's (1885) for _St. montanum_ and Schröder's (1897) for _St. furcigerum_ var. _crassum_. Because of the double processes seen in Croasdale's vertical view of her taxon, I would rather classify this alga as f. _eustephanum_ than as var. _montanum_.

5. Other infraspecific taxa of _St. furcigerum_

The taxonomic features of the following varieties have not been found in the material studied here.

St. furcigerum f. _armigerum_ (Brébisson) Nordstedt 1888

St. furcigerum var. pseudofurcigerum (Reinsch) Nordstedt 1880

St. furcigerum var. montanum (Raciborski) W. et G.S. West 1898a

a) St furcigerum forma armigerum (Brébisson 1856) Nordstedt 1888 (p. 207)

Basionym: St. armigerum Brébisson 1856 (p. 136; pl. 1, fig. 22)

Pl. L Fig. 4:

Brébisson's description is:

"S. subgranulosum; hemisomatiis ventricosis extrorsum planis, a latere secundario triangularibus, angulis saepius bispinosis, marginibus spinulosis, spinis simplicibus aut bifidis.

"J'avais d'abord donné le nom de spinosum à cette espèce; mais par suite d'une erreur dont je suis sans doute le premier coupable, M. Ralfs a attribué ce nom à l'espèce précédente qu'il regarde comme le Xanthidium furcatum d'Ehrenberg, opinion partagée par M. Kützing. Pour éviter une nouvelle cause d'incertitudes dans la synonymie, je préfère adopter un autre nom.

"Cette espèce que j'ai trouvée près de Falaise où elle est assez rare, n'a point ses angles terminés par un prolongement muni de deux pointes; ils sont pourvus le plus souvent de deux épines divergentes. Au lieu des cornes que porte le disque des hémisomates des espèces précédentes, on ne remarque dans celle-ci que quelques épines simples ou bifides vers le sommet des angles.

"J'ai rencontré des individus ayant trois épines à chaque angle; d'autres, au contraire, n'avaient à ce point qu'une épine solitaire."

This taxon was first found in Normandy (France). It has since been reported from different regions of the world. It is similar to St. furcigerum f. eustephanum (Ehrenberg)

Nordstedt, in that it has two accessory processes at each angle compared to one for the type species, but the processes are longer and more prominently denticulated.

West et al. (1923, p. 191) adopted Nordstedt's classification but West and West (1890, 1892a, 1892b) had previously used the name St. furcatum var. armigerum. In subsequent publications, at least five authors (Borge, 1906; Smith, 1924; Taylor, 1935a; Irénée-Marie, 1957; Prescott et al.) cite the taxon incorrectly as a variety rather than a forma.

Proposed synonym of St. furcigerum f. armigerum (Brébisson) Nordstedt 1888

St. furcigerum var. armigerum forma gracillimum Smith 1924b (p. 123; pl. 83, fig. 8-11) Pl. L Fig. 5:

> "...Superior whorls containing six (not three) processes arising in pairs at the base of the processes of the inferior whorl and lying (in the vertical view) at right angles to the sides of the cell. Processes long and delicate and with their apices bifurcate. (Facultative planktont.)
>
> "Cells 63-68 μ long with processes, 30-32 μ long without processes; breadth with processes 67-73 μ, without processes 27-30 μ; breadth at isthmus 12-15 μ...
>
> "Three very similar species have been described in which there are three processes in the lower whorl and six in the upper. Nordstedt (l.c.) has shown that two of these become the varieties eustephanum (Ehrenberg) Nordstedt and armigerum (De Brébisson) Nordstedt of S. furcigerum ; while the third S. pseudofurcigerum Reinsch cannot be recognized but belongs in part to the variety armigerum and in part to the variety eustephanum. The variety armigerum is characterized by long delicate processes with undulate margins and bifid ends while the processes of the variety eustephanum are short and have the ornamentation of the type."

This taxon has been first found in Wisconsin and has not been recorded since. In his discussion of the taxon, Smith emphazises mostly the differences between the varieties armigerum, eustephanum and the species St. pseudofurcigerum. The need to establish the forma gracillimum is questioned as "Processes long and delicate and with their apices bifurcate" (Smith 1924b), only represents a variation of characteristics already distinguishing f. armigerum from the type species. Furthermore, comparison of Smith's and West et al.'s (1923; p. 191) dimensions suggest a major difference in the length of the processes.

Croasdale (1957; pl. 9, fig. 131) uses the name St. furcigerum f. armigerum for a specimen having processes of length intermediate between f. eustephanum and f. armigerum. This establishes a link between both formae.

One specimen found in Placid Lake (8-VIII-80) corresponds to f. armigerum as far as size and number of processes is concerned, but had slender processes and a wider isthmus. It had bifid spines at the tip of each proces. The dimensions were: L(sp): 35 μm; l(cp): 56 μm; Is: 17 μm. It is considered as f. armigerum.

Taylor (1935a) reports much variation in the length of the processes of a specimen of St. furcigerum (see his pl. 36 fig. 7) that "resembles var. armigerum ". The slender processes illustrated on the specimens of fig. 7 from Newfoundland recall illustrations by Smith (1924b; Pl. L Fig. 5) for his var. armigerum f. gracillimum. Taylor's specimen possesses only three accessory processes as in the type and not six as in f. armigerum. Růžička (1973) reports strong variation in the length of the processes with St. furcigerum var. furcigerum. Clones HC 211 and 213 also vary in the length of the processes.

It appears that length and stoutness of the processes is a variable feature and there is no reason to separate f. armigerum and var. armigerum f. gracillimum. Thus, var. armigerum f. gracillimum is a synonym of f. armigerum. Prescott et al. (1982; p. 207) keep it as a valid taxon and note that Smith (1924b) cites it as synonymous with var. armigerum. It is not certain what was Smith's intention in citing var. armigerum under the heading var. armigerum forma gracillimum n. forma. For forma gracillimum to be valid, var. armigerum must also have a valid description distinct from forma gracillimum.

b) St. furcigerum var. pseudofurcigerum (Reinsch) Nordstedt 1880 (p. 27)

Basionym: St. pseudofurcigerum Reinsch 1867b (p. 128; pl. 23C I, fig. 1-4) Pl. L Fig. 6:

Reinsch description is:

"Plantae corpus a fronte visum in medio utrimque acutangule excisum, corporis dimidia a fronte visa in ambitu regulariter elliptica, anguli laterales paulo producti et spina singula firma bidentata denticulata armati, margo superior ad spectatoris oculum adversus spinis binis (ut descript.) armatus; corporis dimidia e vertice visa trigona, margines laterales recti, anguli paulo producti, spina singula (ut descript.) armati, margines laterales spinis binis (ut descript.)

> ab angulis aeque distantibus paulo introrsum positis armati, angulorum respondentium binorum alius supra alium positus; spinarum longitudo corporis diametri longitudinalis aut transversalis (spin. exclus.) triens et paulo minor, spinarum latitudo longitudinis sexta usque quarta pars; articuli conjunctivi latitudo diametri transversalis (spin. exclus.) triens; corporis diameter transversalis (et spin. incl. et spin. exclus.) diametro longitudinali aequalis; membrana glabra.
>
> "Longit. (spin. exclus.) 0,046 -0,042 mm; 0,0211-0,0186"' rhen.
> "Latit. (spin. exclus.) 0,043-0,038 mm; 0,0191-0,0174"' rhen.
> "Spinarum longit. 0,015-0,013 mm; 0,0069-0,0061"' rhen.
> "Spinarum latit. 0,004 mm; 0,0017"' rhen."

West et al. (1923; p. 191) place St. pseudofurcigerum as a synonym of forma armigerum (Brébisson) Nordstedt. Smith (1924b; p. 123) states that it belongs partly to f. armigerum and partly to f. eustephanum and cannot be recognized. Neither de Brébisson nor Reinsch indicate the length of the processes, thus it is difficult to settle the question, but St. pseudofurcigerum does not appear to be a valid taxon.

c) St. furcigerum var. montanum (Raciborski 1885) W. et G.S. West 1898a (p. 334)

Basionyn.: St. montanum Raciborski 1885 (p. 90; pl. 12, fig. 11) Pl. M Fig. 1:

Syn.: St. furcigerum var. crassum Schröder 1897 (p. 64; pl. 4 fig. 6) Pl. L Fig. 7

Raciborski's description is:

> "S. mediocre, paullo latius quam longium, profundissime constrictum, incisura mediana intus sublineari, extrorsum valde ampliata. Semicellulae e

basi subreniformi (plus minusve) oblongo-ellipticae, dorso subrectae, angulis obtusis, non productis, aculeis 3-4, rectis subulatis achrois ornatis, dorso instructo processibus binis, validis, granulato-dentatis, apice aculeis (3-4) armatis. A vertice visae trigonae, lateribus rectis medio leviter concavis, angulis aculeatis. Membrana prope angulos denticulis parvis aspera, caeterum glabra, achroa.

"Corpus (aculeis exclusis) diametro transversali circiter quarta parte brevius. Latitudo isthmi fere triens diametri transversalis corporis.

"Habitu fere S. furcigeri Bréb. differt angulis (non productis) brachiis dorsalibus non bifurcatis, sed aculeis 3-4 parvis, subulatis ornatis...

"Long. cellul. acul. exclus. = 33 μ.
"Long. cellul. cum acul. = 35 μ.
"Latit. cellul. sine acul. = 43 μ.
"Latitudo cum acul. = 45-46 μ.
"Latit. apic. sine acul. = 26 μ.
"Latit. isthm. = 13 μ."

St. furcigerum var. montanum is a species seldom reported in the literature. It appears to be only a stout form of St. furcigerum as noted by West and West (1898). The Wests retain it as a variety of St. furcigerum. Their opinion is reluctantly accepted because the stoutness of the cell does not seem a sufficient feature upon which to base a variety. One record by Borge (1906; pl. 3, fig. 41c) shows a specimen with one of the accessory process reduced to a spine. Borge identifies this specimen as forma minor : L:32-33 μm; 1:58-59 μm. This is unnecessary since Borge's specimen is not smaller than the dimensions given by Raciborski (1885) for St. montanum.

St. furcigerum var. crassum Schröder 1897 (p. 64; pl. 4, fig. 6) Pl. L Fig. 7:

> "Fortsätze kurz, und namentlich diejenigen zu beiden Seiten des Isthmus dick, meist mit drei, seltener mit zwei Stacheln an den Enden versehen. 75-81 μ lang und ebenso breit."

West and West (1898; p. 334) consider this new taxon as "...a large form of S. montanum Racib. which itself is a stout small form of S. fuscigerum (sic) Bréb." It is placed as a synonym of St. furcigerum var. montanum.

6. Uncertain taxon of St. furcigerum

St. furcigerum forma longicornis Schmidle 1898 (p. 64; pl. 3, fig. 13)

The original publication of this forma was not available and it does not seem to have been further recorded. The name may imply longer processes as in f. armigerum.

7. Discussion

Teiling (1957) proposes a different classification of the St. furcigerum-armigerum complex, based on the fact that cells with one entire accessory process accompanied with only the rudiment of the second one were found by Hori (1945). He assumes that the varieties and forms with two accessory processes at each angle represent the primitive form and that the species should be based on one of those taxa. He recognizes two main lines based on the number of processes, in which existing forms or varieties are placed:

1. St. armigerum Brébisson

St. armigerum f. eustephanum (Ehrenberg) Teiling

St. armigerum f. gracillinum (G.M. Smith) Teiling

St. armigerum f. horii Teiling

St. armigerum fac. tetragona (Dick) Teiling

2. St. armigerum var. furcigerum (Brébisson) Teiling

St. armigerum f. crassum (Schröder) Teiling

St. armigerum f. reductum (W. et G.S. West)) Teiling

St. armigerum var. simplicissimum Brook.

Variation in the size of the processes is commonly seen. Therefore, it is questionable if so much importance should be given to the record of cells which show the reduction of one of the paired processes. Cells with reduced or missing accessory processes were seen in clonal cultures and seem to represent a malformation rather than a more evolved form. Borge (1906) and Croasdale (1957) found the same feature with St. furcigerum var. montanum.

The reports of dichotypical cells of St. furcigerum var. furcigerum and f. eustephanum show a strong link between these two taxa. According to Růžička (1973) the number of processes is an unreliable taxonomic criterion. The results of the present study did not support Růžička's conclusion. It is still difficult to accept a taxonomic scheme based on these criteria.

Teiling's new classification does not simplify the taxonomy of the species as he adds one more variety, var. simplicissimum and one forma, f. horii to the complex. This does not make the scheme more workable, as intermediate forms between his two groups are commonly reported.

TABLE 23

CELL DIMENSIONS AND RADIATION OF ST. FURCIGERUM AND ST. FURCIGERUM F. EUSTEPHANUM

(Clonal cultures: N=see Materials and Methods; SD=Standard deviation; C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone	Source	L(cp) (µm) Average	Range	S.D.	C.V.	l(cp) (µm) Average	Range	S.D.	C.V.	Is (µm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3
<u>St. furcigerum</u>															
211	Jacobs 26-IV-80	38	34-45	3.68	8.40	37	32-41	2.12	6.78	14	11-17	1.33	8.32	1.08	100.0
<u>St. furcigerum</u> f. <u>eustephanum</u>															
213	Jacobs 26-IV-80	44	41-49	1.93	4.38	42	37-46	2.47	5.84	17	13-20	2.22	13.6	1.04	100.0

Field material

Source	L(cp) (µm)	l(cp) (µm)	l(sp) (µm)	Is (µm)	L/l	Radiation 3
<u>St. furcigerum</u> f. <u>eustephanum</u>						
Jacobs 14-VI-79	52	48	28	--	1.09	X

Plate 13

_St._ _furcigerum_

SEM photographs

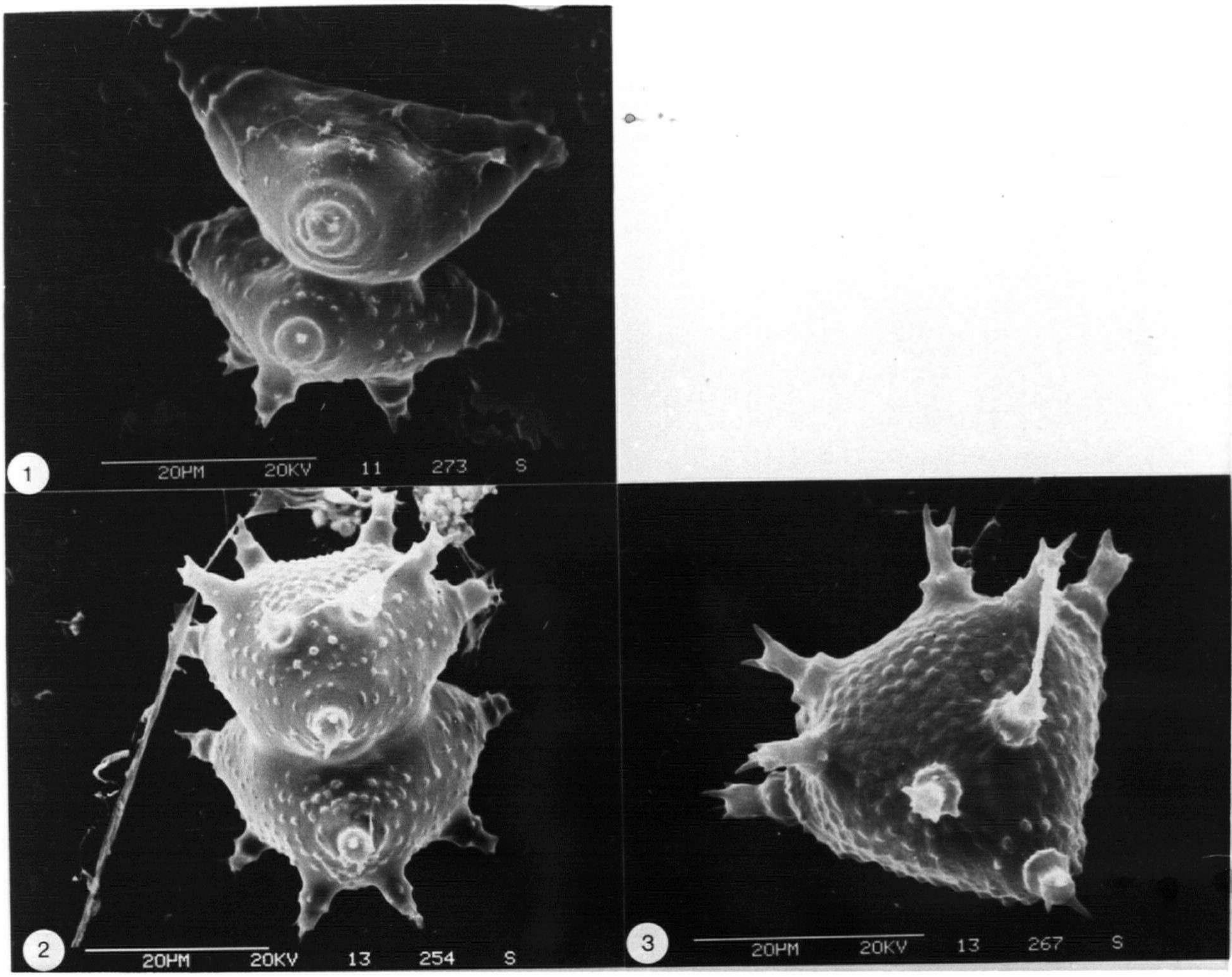
1. _St._ _furcigerum_ var. _furcigerum_, clone HC 211; the upper semicell is abnormal as it lacks the accessory processes

2, 3. _St._ _furcigerum_ f. _eustephanum_, clone HC 213

2. Cell in front view

3. Semicell in vertical view

300A



O. STAURASTRUM SENARIUM VAR. SENARIUM

St. senarium (Ehrenberg 1843) Ralfs 1848 (p. 216):

Basionym: Desmidium senarium Ehrenberg 1843 (p. 412; pl. 4 fig. 22)

Ralfs writes:

> "Ehrenberg's figure represents the end view as triangular, the angles terminating in short rays, which are tipped by minute spines: on each side are two short forked spines, and six others on the upper surface. His figure agrees in some respects with Staurastrum spinosum, consequently S. senarium may prove a variety of that very variable species."

Unfortunately, it was impossible to obtain Ehrenberg's original figure and Ralfs did not give an illustration of the species. The illustration of West et al. (1923; pl. 156, fig. 3) is shown on Pl. O Fig. 2.

St. senarium was not previously reported for British Columbia (Stein and Borden, unpublished). Only one clone was isolated and no field material was observed. St. furcatum was recorded 95 times, including collections from Munday, Lost and Mike Lakes.

Clone examined: HC 74 from Munday Lake, 26-VII-79 (Table 24).

The semicells in front view present an acute and open sinus (Pl. 14 Fig. 1). The angles are extended into processes divided into two, three or four spine-like parts at their extremities (Pl. 14 Fig. 4). The length of the processes and of the apices varies with the latter often curving inward (Pl. 14 Fig. 3-5).

The cells are triradiate in apical view as noted by Ralfs

a) St. hantzschii Reinsch 1867b (p. 129; pl. 22D II, fig. 1-6) Pl. L Fig. 8:

> "Plantae corpus a fronte visum in medio utrimque octangule excisum; corporis dimidia a fronte visa in ambitu regulariter elliptica, anguli laterales obtusi, non producti, spina singula firma bidentata denticulata aut glabra armati, anguli ad spectatoris oculum versi utrimque acie singula spinarum (ut descript.) ternarum superimpositarum armati, acierum spina summa in dimidii margine terminali, spina infima in dimidii basi, dimidii margo superior ad spectatoris oculum versus spinis binis (ut descript.) armatus; corporis dimidia e vertice visa trigona, anguli spina singula (ut descript. armati, margines laterales spinarum (ut descript.) paribus binis abangulis aeque distantibus paulo introrsum positis armati, angulorum respondentium binorum alius supra alium positus; spinarum longitudo corporis diametri longitudinalis aut transversalis (spin. exclus.) quarta pars et paulo minor, latitudinis duplum; articuli conjunctivi latitudo triens (et paulo magis) diametri transversalis; corporis diameter transversalis diametro longitudinali aequalis et paulo brevior; membrana glabra.
>
> "Longit. (spin. exclus.) 0,046-0,038 mm; 0,021-0,0174"' rhen.
> "Latit. (spin. exclus.) 0,042-0,038 mm; 0,0191-0,0174"'rhen.
> "Spinarum longit. 0,008 mm; 0,0036"' rhen.
> "Spinarum latit. 0,004 mm; 0,0019"' rhen..."

Grönblad (1960) discusses the relationship between St. hantzschii and St. senarium, concluding that:

> "The situation being very confused and the interpretation of S. senarium (Ehrenb.) Ralfs in Ralfs (1848, p. 216 without a figure), syn. Desmidium senarium Ehrenb. (1843, IV:22) being obscure I think it better to reject the name S. senarium and to use Reinsch's name S. Hantzschii which, indeed, being somewhat schematically drawn nevertheless can be identified without difficulties..."

I agree that both species should probably be combined because they are distinguished by the length of the processes which is a

(1848), but have a total of 12 accessory processes, four at each angle. Two of the processes are in the same horizontal plane as the angular processes and are located on each side of them, whereas the other two are inserted apically, just above the first two accessory processes (see Pl. O Fig. 2). Since each angle bears a total of five processes and the cell is triradiate, there is a total of 15 processes per semicell. The semicells of clone HC 74 characteristically have 15 processes, but one specimen with a lower number of processes was seen during SEM observation (Pl. 14 Fig.4).

The angular processes are never denticulate. West et al. (1923) mention the occurrence of cells in which one semicell has denticulate angular processes but, in the second semicell, the margins of the angular processes are smooth.

On Plate 14 Fig. 3, the top semicell has stunted processes. It also has some big "granules", which are probably pores with collars of dried mucilage. This heavy "granulation" was also occasionally seen with the light microscope.

1. Proposed synonyms of St. senarium var. senarium :

St. hantzschii Reinsch 1867b

St. hantzschii var. cornutum Turner 1892

St. tohopekaligense var. nonanum (Turner) Schmidle 1898 sensu Hughes 1950

St. tohopekaligense var. nonanum sensu Irénée-Marie 1939

St. tohopekaligense f. minus (Turner) Scott et Prescott 1961 sensu Hinode 1971 variable feature (Pl. L Fig. 8). However I disagree with the use of the name St. hantzschii. St. senarium was described at an earlier date (St. senarium Ehrenberg ex Ralfs 1848) and has priority. Furthermore, St. senarium is commonly reported whereas St. hantzschii is not. Prescott et al. (1982; p. 218) recognize St. hantzschii as a distinct taxon.

b) St. hantzschii var. cornutum Turner 1892 (p. 120; pl. 15, fig. 23) Pl. M Fig. 4:

> "Long. 24, lat. 20 (s. proc.); long. et lat. 30 (c. proc.); lat. isthm. 9, long. proc. 6-7 μ.
>
> "This variety though smaller in size, differs but little from Reinsch's form except in the length of the processes. It is nearly equal in dimensions to the Italian plant of Delponte. T. XV f. 23."

This variety differs mainly from St. hantzschii by its size and the length of the processes, a feature which has been shown to vary in clonal culture. This minor variation does not seem to justify the rank of variety.

c) St. tohopekaligense Wolle var. nonanum (Turner) Schmidle 1898 sensu Hughes 1950 (p. 49; pl. 3, fig. 8) Pl. M Fig. 5:

Hughes gives the following dimensions, width: 23-26 μm; isthmus:14-16 μm; length: 29-32 μm. Hughes' specimens have a total of 15 processes contrary to the nine of St. tohopekaligense (Wolle 1885; p. 128, pl. 51 fig. 4, 5) or its var. nonanum (Basionym: St. nonanum Turner 1892; p. 119, pl. 15 fig. 14) for the triradiate form. West et al. (1923, p. 179) however state that St. tohopekaligense has a total of nine or 15 processes in the triradiate form. This does not correspond to the original descriptions of St. tohopekaligense and St. nonanum. It is suggested that Hughes' illustration is of St. senarium.

d) St. tohopekaligense var. nonanum sensu Irénée-Marie 1939 (p. 327; pl. 55, fig. 13) Pl. M Fig. 6:

Irénée-Marie illustrates a specimen which bears a total number of 15 processes. Turner's original illustration of St. nonanum shows nine processes, which appear longer than those illustrated by Irénée-Marie. A comparison of measurements supports this. Turner's cells are longer and wider with processes (L(cp)= 80; l(cp)= 74 μm) than Irénée-Marie's (L(cp)= 44-48; l(cp)= 35-44 μm). It is suggested that Irénée-Marie's specimen belongs to St. senarium.

e) St. tohopekaligense forma minus (Turner) Scott et Prescott 1961 (p. 114, pl. 48, fig. 4-6) sensu Hinode 1971 (p. 127; fig. X:12) Pl. M Fig. 7:

Scott and Prescott (1961) transferred St. nonanum f. minor Turner 1892 (p. 119; pl. 15 fig. 15) as f. minus of St. tohopekaligense. Their three figures show one cell with the nine processes characteristic of St. tohopekaligense (fig. 4), one dichotypical cell with one semicell bearing nine processes and the other, 15 processes (fig. 5), and one cell with 15 processes in both semicells (fig. 6). The finding of these dichotypical specimens adds more weight to the close relationship existing between species with 15 processes (such as St. senarium) and species with nine processes (such as St. furcatum or St. tohopekaligense). Since Scott and Prescott's (1961) specimens stand between the two types, it is difficult to decide on either name.

Hinode (1971) shows a specimen of St. tohopekaligense f. minus with 15 processes in both semicells. The short processes illustrated do not seem to warrant its classification as St. tohopekaligense. Rather, this plant belongs to St. senarium.

2. Synonyms of St. senarium var. senarium

St. renardii var. congruum Raciborski 1890

St. hantzschii var. congruum (Raciborski) W. et G.S. West 1896b

St. hantzschii var. depauperatum Gutwinski 1892

St. intricatum Delponte 1877

Grönblad (1960) states that there does not seem to be any difference between St. hantzschii var. congruum (Raciborski) W. et G.S. West 1896b and St. hantzschii Reinsch 1867b. West and West (1896b) transferred St. renardii var. congruum to St. hantzschii. They also placed St. hantzschii var. depauperatum Gutwinski 1892 and the species St. intricatum Delponte 1877 as synonyms of St. hantzschii var. congruum. Thus according to Grönblad (1960) and West and West (1896b), St. hantzschii var. depauperatum, var. congruum and St. intricatum are all synonyms of St. hantzschii. Messikommer

(1935; p. 125) also agrees with the synonymy between *St. intricatum* Delp. and *St. hantzschii* Reinsch. Prescott *et al.* (1982; p. 219) accept *St. hantzschii* var. *congruum* as a valid taxon.

3. Infraspecific taxa of *St. senarium*

The taxonomic characteristics of the following taxa were not found in the material studied and no conclusions can be drawn. Some have been previously transferred to other taxa.

St. senarium var. *alpinum* f. *tatrica* Raciborski 1885

St. senarium var. *nigrae-silvae* Schmidle 1893

St. senarium var. *pseudowallichii* Grönblad 1920

a) *St. senarium* var. *alpinum* f. *tatrica* Raciborski 1885 (p. 88; pl. 3, fig. 7) Pl. L Fig. 9:

> "Processus hujus formae angulis sexies plures sunt, i.e. in semicellula formae triangularis 18 (6 dorsales, 12 mediani (=bini angulares et bini interangulares), formae quadrangularis 24 (8 dorsales, 16 mediani (=bini angulares et bini interangulares). Processus dorsales crassi, apice furcati vel trifidi. Processus mediani tenues, angulares subulati, interangulares subulati vel furcati. Membrana prope angulos granulis parvis ornata, caeterum glabra.
>
> "Long. cellul.(sine acul.)=26-29 μ
> "Latit. (sine acul.)=24-28 μ.
> "Latit. isthm. = 9-10 μ.
> "Long. process. dorsal. = 5-6 μ.
> "Crassit. process. dorsal. = 2 μ.
> "Longit. process. med. = 2.5-3 μ..."

Raciborski named his taxon *St. senarium* forma *tatrica* in the text, although in the table legend he indicates var. *alpinum* f. *tatrica*. West *et al.* (1923; p. 184) place var. *alpinum* f.

tatrica as a synonym of St. monticulosum Brébisson ex Ralfs var. bifarium Nordstedt 1873. Their interpretation is accepted.

b) St. senarium var. nigrae-silvae Schmidle 1893 (p. 553; pl. 28, fig. 19) Pl. M Fig. 2:

Syn.: St. subavicula W. et G.S. West var. nigrae-silvae (Schmidle) Grönblad 1942 (p. 43).

> "Membrana omnibus partibus granulato-punctata ad angulos binis vel ternis seriebus circularibus verrucarum ornata, ceterum ut in formis forma typica. Long. 42-56 µ, lat. 40-52 µ..."

This variety was transferred to the genus St. subavicula by Grönblad (1942). Prescott et al. (1982; p. 319) also accept the synonymy.

c) St. senarium var. pseudowallichii Grönblad 1920 (p. 76; pl. 2, fig. 20-23, pl. 5, fig. 51-53) Pl. M Fig. 3:

> "A vertice visae 3-angulatae processubus 6 superioribus longis et magnis; inferioribus 9 partim longis magnis: singulis in unoquoque angulo, - partim brevissimis: binis in unoquoque latere in ipso margine defixis. Ceterum membrana glabra. Long. 74, lat. 68, isthm. 16 µ..."

This variety is distinguished by its long apical and angular processes and short remaining accessory processes, located on each side and in the same plane as the angular ones. No such variation was observed in clone HC 74.

4. Uncertain taxa of St. senarium

The original publications of the following taxa were not available.

St. senarium var. bifarium Schmidle 1898

St. senarium var. pumillum Messikommer 1954

a) St. senarium var. bifarium Schmidle 1898 (P. 51; pl. 2, fig. 39)

West et al. (1923; p. 184) put this taxon as synonym to St. monticulosum var. bifarium.

b) St. senarium var. pumillum Messikommer 1954 (pl. 1, fig. 21)

This taxon was only cited in Grönblad (1960).

5. Taxa related to St. senarium

St. furcatum is closely related to St. senarium, and differs only by the presence of nine instead of 15 processes (West et al. 1923, p. 176). St. furcatum is at the present time recognized as a valid species, but St. renardii Reinsch is seen as a synonym of St. furcatum as discussed here.

St. furcatum (Ehrenberg ex Ralfs) Brébisson 1856 (p. 136):
Basionym: St. spinosum Ralfs 1848 (p. 143,; pl. 22, fig. 8)
Pl. M Fig. 9:

"...segments elliptic, furnished with a few bifid spines; lateral spines solitary, larger and more forked; end view triangular with two or three spines on each side and one terminating each angle.

"Frond deeply constricted at the middle; segments subelliptic, their outer margin usually more turgid than the inner; on each side is a conspicuous sessile spine, forked like the tail of a swallow, and on the outer margin are a few smaller spines, which are usually forked at the end, though sometimes simple. End view triangular, each angle terminated by a spine, which appears simple or forked according to its position when viewed; sides with two or three spines, which are sometimes simple and sometimes forked, and on the upper surface are six other spines, one opposite to each lateral spine.

"The sporangia of Staurastrum spinosum were first gathered by Mr. Broome near Bristol, and I have since found a few of them at Dolgelley. They are orbicular, and have numerous elongated spines which are divided at the apex.

"M. de Brébisson considers this plant identical with the Xanthidium furcatum, Ehr."

"Length of frond 1/859 of an inch; breadth 1/907; breadth at constriction 1/3267; diameter of sporangium 1/641; length of spine of sporangium 1/1408."

There is a close relationship between St. senarium and St. furcatum. This is shown especially by the observation of dichotypical cells where one semicell bears a total of 15 processes (as in St. senarium), whereas the other semicell, with only nine processes, answers to the description of St. furcatum (see also discussion by Turner, 1892; Grönblad, 1960). St. furcatum is another species which requires extensive revision. Following the same reasoning as with St. senarium and St. hantzschii, Grönblad (1960) proposes that St. furcatum (Ehrenberg 1843) Brébisson 1856 be dropped and included with St. renardii Reinsch 1867b.

a) Proposed synonym of St. furcatum var. furcatum

St. renardii Reinsch 1867b (p. 127, pl. 23 fig. AI) Pl. M Fig. 10:

"Plantae corpus a fronte visum in medio acutangule aut rectangule emarginatum, corporis dimidia a fronte visa in ambitu elliptica usque fere trapezica, anguli non producti, anguli laterales et superiores spina singula firma breviter truncata bidentata glabra aut crenulata armati; corporis dimidia e vertice visa trigona, margines laterales recti aut subconvexi, spinis binis firmis (ut descript.) ab angulis aeque distantibus armati, anguli obtusi spina singula (ut descript.) armati; spinarum longitudo corporis diametri transversalis sexta usque octava pars, latitudini aequalis; articuli conjunctivi latitudo corporis diametri transversalis duae quintae; corporis diameter transversalis (spin. except.) diametro longitudinali aequalis; membrana glabra.

"Longit. 0,028-0,019 mm; 0,0129-0,0085 "' rhen."
"Latit. 0,028-0,019 mm; 0,0129-0,0085 "'rhen..."

Since St. furcatum was published before St. renardii, it is suggested that St. renardii be a synonym of St. furcatum and not the reverse as suggested by Grönblad (1960). Prescott et al. (1982; p. 300) accept St. renardii as a valid species.

b) Uncertain infraspecific taxon of St. furcatum

St. furcatum var. iyaense Hinode 1962 (pl. III, fig. 98-99) Pl. M Fig. 8:

"Semicellulae marginibus ventralibus spinis duabus praeditis; e vertice visae intra marginem spinis binis bifurcatis ornatis unoquoque.

"Long. c. spin. 29 μ, s. spin. 25 μ; lat. c. spin. 29 μ, s. spin. 22 μ; isthm. 8 μ."

With its 15 processes, this variety would seem better classified in *St. senarium* than in *St. furcatum*. The presence of two spines at the base of the semicell in front view (Pl. M Fig. 8) may still justify it being recognized as a distinct variety of *St. senarium*. However, the small illustration and short description make it a doubtful taxon.

TABLE 24

CELL DIMENSIONS AND RADIATION OF ST. SENARIUM
(Clonal cultures: N=see Materials and Methods; S.D.=Standard deviation;
C.V.= Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (µm) Average	Range	S.D.	C.V.	l(cp) (µm) Average	Range	S.D.	C.V.	Is (µm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3
74	Munday 26-VII-79	41	36-47	3.40	8.40	38	32-42	2.16	5.62	16	13-17	1.12	7.03	1.05	100.0

Plate 14

St. senarium var. senarium

SEM photographs

1-5. Clone HC 74

1. Cell in front view

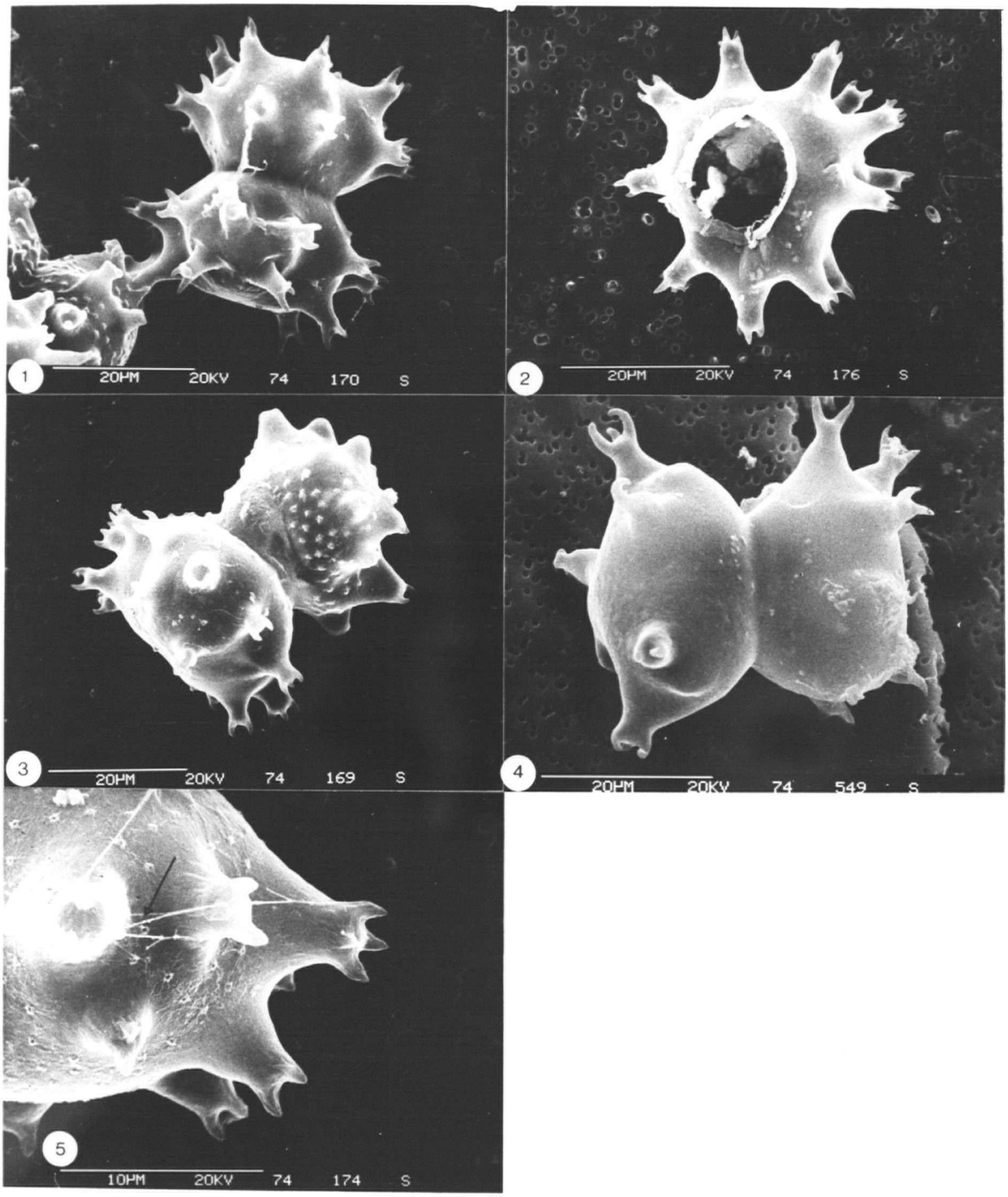
2. Cell in basal view

3. Cell in front view, the upper semicell has stunted processes and pores surrounded by dry mucilage.

4. Cell in front view with abnormal number of processes showing extremities

5. Detail of the processes and their extremities; the arrow indicates the pores and filaments of mucilage

314A


1
20µM 20KV 74 170 S
2
20µM 20KV 74 176 S
3
20µM 20KV 74 169 S
4
20µM 20KV 74 549 S
5
10µM 20KV 74 174 S

P. STAURASTRUM ARACHNE VAR. ARACHNE

St. arachne Ralfs ex Ralfs 1848 (p. 136; pl. 23, fig. 6) Pl. N Fig. 2:

> "...segments rough with minute granules, suborbicular, with elongated, slender, incurved processes; end view with five linear rays...
>
> "Frond minute, deeply constricted at the middle; segments about as long as broad, having on each side an elongated process, which is hyaline and incurved, and on account of its minute granules appears transversely striated. When the frond is viewed obliquely, so that three or more of the long curved processes are seen at once, its resemblance to an insect is considerable. The end view is circular with five slender rays.
>
> "This plant is remarkable for its slender processes, which will easily distinguish it from Staurastrum margaritaceum. It cannot be a five-rayed variety of S. gracile or S. polymorphum, for its rays are longer, more slender, remarkably incurved and also entire at the extremity.
>
> "Length of frond 1/1020 of an inch; breadth, excluding processes, 1/2040; including processes, 1/652; length of process 1/1858; breadth at constriction 1/2732."

St. arachne was found among aquatic plants and in plankton samples from Jacobs and Placid Lakes. Stein and Borden (unpublished) report 17 collections of St. arachne for British Columbia, including Jacobs Lake.

Clone examined: HC 115 from Jacobs Lake, 29-VIII-79 (Table 25).

The front view of clone HC 115 shows a slightly convex apex and parallel to slightly convergent processes (Pl. 15 Fig. 3). The length of the cells with processes is less than the width with processes (L/l= 0.82; Table 25). The semicells are subtriangular, the sinus forming a small notch in the middle of the semicell. Spines may be present on either side and just above the isthmus (Pl. 15 Fig. 3). The granulation pattern on the apex is variable, with some cells having only granules as seen on a semicell with stunted processes (Pl. 15 Fig. 2). Most well-developed cells show a distinct pattern of one double verruca between each process (Pl. 15 Fig. 4). This range of variation is known from the literature (Scott and Grönblad 1957, pl. 33, fig. 1-2; Croasdale 1957, pl. 6 fig. 104; Smith 1924b, textfig. 13 A, C; Irénée-Marie 1939, pl. 54 fig. 10; Grönblad 1948, fig. 28). Some authors do not represent any granules or verrucae in vertical view (Scott and Grönblad 1957, pl. 33 fig. 3; Prescott 1940, fig. 16 forma). Ralfs' description does not mention the apical verrucae illustrated by most authors. He also states that the end of the processes are entire, while the literature usually represent processes tipped with small spines. His plants are pentaradiate, whereas in the literature they vary from tri- to hexaradiate.

In clone HC 115, the processes always seem to present at least some pattern of granulation, varying from a few granules to a ring of granules or short spines surrounding the processes (Pl. 15 Fig. 4). According to Ralfs 1848, this characteristic makes them look "transversely striated".

The processes are usually tipped with two, three or four spines. Some cells have processes with rounded extremities, and without any spines. This appears to be due to an abnormal development of the cell, as it was seen only on cells which were otherwise deformed or stunted. Two dichotypical cells shown on

Pl. 15 Fig. 1 and 2 have one semicell bearing shorter processes with rounded extremities, whereas the other semicell has processes tipped with well developed spines. The processes are either undulate or denticulate; the undulations are tipped with short single spines (Pl. 15 Fig. 4).

As indicated in Table 25, cells in clonal culture are usually pentaradiate (95.2%), with 1.9% of the cells tetraradiate and 2.9% hexaradiate. One hexaradiate cell bore five normal processes and one process which was shorter and without terminal spines. A second hexaradiate cell bore two of these stunted processes. A pentaradiate cell had one process shorter but tipped with spines (Pl. 15 Fig. 1). Such abnormalities have been previously reported in the literature for pluriradiate species of Staurastrum. In field material, many cells were seen only in apical view and are not recorded in Table 25. The number of processes was always five.

1. Infraspecific taxa of St. arachne

The features of the following taxa have not been observed in the material of the present study. There is no reason not to accept them, although some have been placed by previous authors as synonyms of other taxa and are accepted as such.

St. arachne f. minor Boldt 1888

St. arachne var. arachnoides W. et G.S. West

St. arachne var. curvatum W. et G.S. West 1903

St. arachne var. gyrans (Johnson) Scott et Grönblad 1957

St. arachne var. sumatranum Scott et Prescott 1961

a) St. arachne forma minor Boldt 1888 (p. 39)

"Long. 19,2 μ; lat. 28,8 μ; lat. isthmi 3,4 μ."

The dimensions given by Boldt do not differ greatly from Ralfs' (1848) for St. arachne (L = 25; l(cp) = 39; Is = 9 μm) or from the range of variation observed in the present study, except for the width of the isthmus. No further mentions of the taxon were found in the literature. Irénée-Marie (1957; p. 150) also described a St. arachne f. minor (L: 20-26.5; l: 35-40; (sp): 13-14.5; Is: 7-8.5 μm). His dimensions do not differ from Ralfs' and this plant belongs to St. arachne. Prescott et al. (1982; p. 127) are doubtful about the validity of the taxon but accept it. However, since Boldt described his taxon first, the name St. arachne f. minor Irénée-Marie is not legitimate.

b) St. arachne var. arachnoides W. et G.S. West 1902b (p. 56)
Basionym: St. arachnoides W. West 1892a (p. 186; pl. 24, fig. 4) Pl. N Fig. 4:

The original description (West 1892a) is:

"S. mediocre, modice constrictuum, sinu lato et obtuso; semi-cellulae late campanulatae, apicibus truncatis granulis emarginatis praeditis, processibus longis gracillimis denticulatis leviter incurvatis ad angulos superiores, apicibus tridenticulatis; a vertice visae annulo granulorum novem intra marginem, pentaradiatae, processibus longis attenuatis subflexis.

"Long. 37 μ; lat. cum proc. 67-71 μ; lat. sine proc. 20 μ; long. proc. 25-27 μ; lat. isthm. 9 μ."

West and West (1902b) give slightly smaller dimensions for the width; that is,"...lat. s. proc. 15 μ, cum proc. 55 μ."

Scott and Grönblad (1957) propose to delete this variety since they "cannot see any difference between St. arachne, typical and var. arachnoides (W. West) W. et G.S. West." The Wests' taxon is both longer and larger than Ralfs' (see f. minor). Prescott (1966, pl. 8 fig. 1) illustrates a form of var. arachnoides with a diameter of only 44 μm and "...processes shorter than in the typical form", that is, more similar in dimensions to the type species than to var. arachnoides. Thomasson (1972) compares Prescott's specimen to his specimen of St. subradians Fritsch et Rich forma. However, this latter has strongly diverging processes and Prescott's alga has slightly convergent to parallel processes.

Although I agree with Scott and Grönblad (1957) that St. arachne var. arachnoides is similar to St. arachne, I disagree that it is the same as the type species.

c) St. arachne var. curvatum W. et G.S. West 1903 (p. 549; pl. 18, fig. 9) Pl. N Fig. 5:

> "Var. processibus leviter extrorsum curvatis; a vertice visae 4-vel 5-radiatae.
> "Long. 30 μ; lat. sine proc. 18 μ, cum proc. 57-70 μ; lat. isthm. 9 μ...

This variety was first found in Scotland. This is the only variety of St. arachne with diverging processes. West and West illustrate the taxon as lacking apical ornamentation. Smith (1924b; pl. 80 fig. 11-14) illustrates the variety with or without apical verrucae. As in var. arachnoides, this variety is wider than Ralfs' (1848) original description.

d) St. arachne var. gyrans (Johnson) Scott et Grönblad 1957 (p. 32; pl. 33, fig. 4-8)

Basionym: St. gyrans Johnson 1894 (p. 290; pl. 211, fig. 4)

Pl. N Fig. 6

Synonym: St. arachne f. gyrans (Johnson) Förster 1972 (p. 569; pl. 25, fig. 10, 11).

Johnson's original description is:

> "Length one-half the breadth. Semi-cells subcuneate, top slightly convex; angles prolonged into slender, slightly incurved rays. Margins of rays serrate-dentate, apices bearing each three short spines. In vertical view 5-radiate; at the base of each ray, on the left side, a strong horizontal spine. Length 20-25 μ; diameter with rays 40-48 μ, without rays 12 μ..."

This variety was first recorded in the United States. It has since been found in other areas of the world but does not appear to be common. In clone HC 115 or field material, no spines are ever observed at the base of the processes as in var. gyrans. Scott and Grönblad (1957) find dichotypical specimens of which one semicell belongs to St. arachne and the other to St. gyrans, and on this decide to rename St. gyrans as var. gyrans of St. arachne. Förster (1972) prefers to use the rank of forma instead of variety, since the Scott and Grönblad's transfer is based on the observation of dichotypical cells and thus represents a minor variation. The criteria for the establishment of varieties or forms are very subjective. It seems that at the present time, the transfer of var. gyrans to forma gyrans does not clarify the taxonomy of these taxa. Until further observations of actual variation is made, the interpretation of Scott and Grönblad should be accepted. Prescott et al. (1982; p. 128) also agree.

e) St. arachne var. sumatranum Scott et Prescott 1961 (p. 86; pl. 59, fig. 7) Pl. N Fig. 7:

> "Varietas magnitudine formaque speciei similis. Differt eo quod processus crassiores, atque dentes in marginibus dorsalibus processuum ac in superficie apicali prominentiores sunt...
>
> "L 23; W cpr 32-34; I 8."

This variety collected in Sumatra is based on characteristics which are variable, that is, stouter processes and more prominent "teeth on their dorsal margins and on the apical surface" (Scott and Prescott 1961). Such "teeth" or spines were not observed in this study.

2. Uncertain infraspecific taxa of St. arachne

The following taxa are doubtful and would need more thorough study before any conclusions are made.

St. arachne var. basiornatum Capdevielle et Couté 1980

St. arachne var. basiornatum f. pseudogyrans Capdevielle et Couté 1980

a) St. arachne var. basiornatum Capdevielle et Couté 1980 (p. 861; pl. 1, fig. 1-4, pl. 4, fig. 1-6) Pl. N Fig. 9

"A typo praeisthmialia corona quinque parvarum spinarum turbinatarum differt. Quaeque spina spatio inter duos processuum opposita est.

"Cellulae longitudo: 23-27 μm; latitudo: 47-50 μm; isthmus: 8-10 μm.

"Iconotypys tab. I, fig. 1-2-3-4; tab. IV, fig. 1-2-3-4-5-6.

"In paludibus: petit lac de Biscarosse, étang Hardy, 1978..."

Capdevielle and Couté (1980) provide excellent drawings as well as SEM photographs of their new variety. Since they do not record the presence of the type species, it is assumed they have found a large and pure population of the new taxon. The presence of isthmial spines on many cells of clone HC 115 but not on others, raises some doubts about the adequacy of this taxonomic feature. The spines observed by Capdevielle and Couté, as well as in the present study, may be seen as a more developed state of isthmial granules. Small isthmial granules can be very difficult to detect, especially on cells with protoplasm and thus could have been overlooked on cells of clone HC 115, but this seems doubtful. In view of the divergence between Capdevielle and Couté's observation and mine, I feel that observation of further clones and field material may be necessary before making any definite statement on the status of this new variety.

b) St. arachne var. basiornatum f. pseudogyrans Capdevielle et Couté 1980 (pl. 1; fig. 5-8, pl. 5, fig. 1-6) Pl. O Fig. 6:

"A varietate basiornatum spina unilaterali sub quoque processu differt.
"Cellulae longitudo: 26-27 µm; latitudo: 50-53 µm; isthmus 8-10 µm.
"Iconotypus tab. I, fig. 5-6-7-8; tab. V, fig. 1-2-3-4-5-6.
"In palude: petit lac de Biscarosse, 1978."

The only distinction between this taxon and St. arachne var. gyrans, is the presence of the isthmial spines characteristic of St. arachne var. basiornatum Capdevielle et Couté. Since this is a doubtful taxonomic criterion, it appears more appropriate to use var. gyrans forma basiornatum or simply var. gyrans morpha.

3. Conclusion

Although St. arachne seems to be a fairly well defined species, variation observed in the present study shows that the numerous infraspecific taxa described are closely related and some may not be valid. Some modern investigations (Scott and Grönblad 1957, Capdevielle and Couté 1980) have brought new data to the taxonomy of this species as well as interesting proposals for its taxonomic revision. Further observations of variation are necessary, in particular for the characteristics of var. gyrans and var. basiornatum.

TABLE 25

CELL DIMENSIONS AND RADIATION OF _ST._ _ARACHNE_
(Clonal cultures: N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(cp) (µm)				l(cp) (µm)				Is (µm)				L/l	Radiation (%)		
		Average	Range	S.D.	C.V.	Average	Range	S.D.	C.V.	Average	Range	S.D.	C.V.		4	5	6
115	Jacobs 29-VIII-79	25	23-29	1.35	5.35	31	26-35	2.31	7.47	12	10-13	0.69	6.03	0.82	1.9	95.2	2.9

Field material

Source	L(cp) (µm)	l(cp) (µm)	Is (µm)	L/l	Radiation 5
Jacobs 7-VI-80	27	42, 36*	10	0.64, 0.74	X

*Dichotypical cell

Plate 15

St. arachne var. arachne

SEM photographs

1-5. Clone HC 115

1. Cell in vertical view with the top semicell stunted and one shorter process on the bottom one

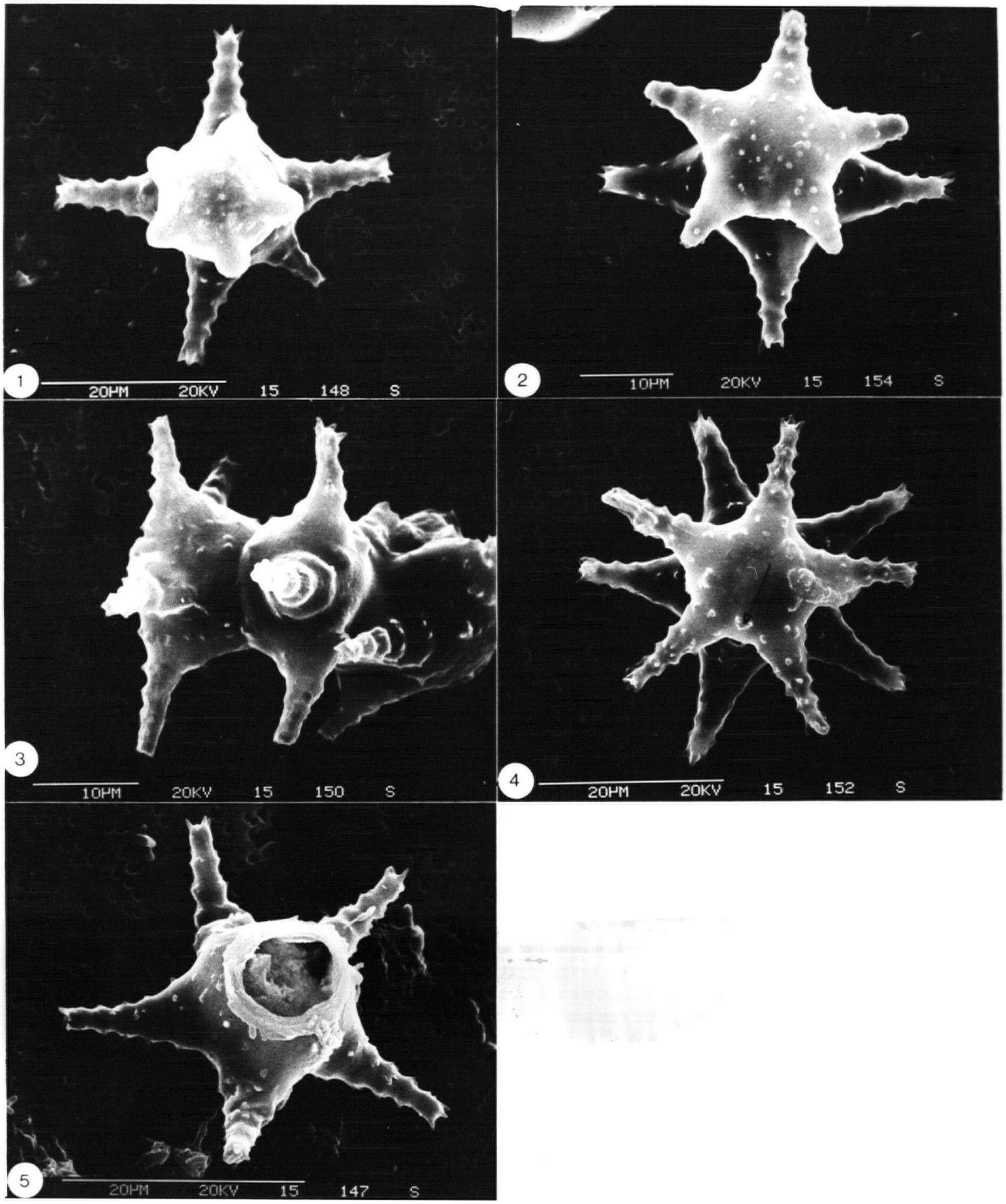
2. Cell in vertical view with the top semicell stunted

3. Cell in front view showing the supraisthmial spines

4. Cell in vertical view; the arrow indicates the apical double verrucae

5. Semicell in basal view

325A


1
20PM 20KV 15 148 S
2
10PM 20KV 15 154 S
3
10PM 20KV 15 150 S
4
20PM 20KV 15 152 S
5
20PM 20KV 15 147 S

Q. STAURASTRUM OPHIURA VAR. OPHIURA AND ST. PENTACERUM VAR. PENTACERUM

St. ophiura Lundell and St. pentacerum (Wolle)G.M. Smith will be treated together because they are closely related taxa as discussed in the conclusion to this section. They are also the only taxa studied which seem truly planktonic. St. pentacerum was originally a variety of St. ophiura but was placed in a separate species by G.M. Smith (1922). Clones of both species did not grow well. A number of clonal cultures were started but some of these were later discarded because of slow growth and malformation of the cells. Measurements were performed on one clone from Como Lake, five from Munday Lake, one from Lost Lake and two from Jacobs Lake (Table 26, 27). Radiation was counted on 13 supplementary clones of St. pentacerum var. pentacerum (Table 27). All clones usually had much shorter processes than in field material as seen on Table 26 and 27. Despite the poor growth, some observations were made and conclusions drawn.

Stein and Borden (unpublished) report two collections of St. pentacerum for British Columbia, including one for Munday Lake. St. ophiura on the other hand has 38 records including Jacobs, Placid, Munday and Lost Lakes; var. cambricum has two records, including Munday Lake.

1. St. ophiura Lundell 1871 (p. 69; pl. 4, fig. 7) Pl. P Fig. 8:

"S. permagnum, medio utrimque leviter emarginatum; semicellulae fere obovatae, sursum sensim dilatatae, in apice convexo papillis bifidis ornatae, angulis

> inferioribus papilla instructis, superioribus in radium valde elongatum, gracile, subachroum, strictum vel leviter incurvum, margine subtiliter denticulatum, apice uni-bidentatum productis; semicellulae a vertice visae 7-(raro 6- vel 8-) radiatae, radiis praelongis, apicem tridentatum versus sensim sensimque attenuatis, margine serrato-dentatis, in centro coronula papillarum 7 (raro 6 vel 8) quadrifidarum ornatae.
>
> "Long. 0,00256-323" = 65-82 μ; Lat. exclus. rad. 0,00134-157" = 34-40 μ; inclus. rad. 0,0055-61" = 140-155 μ; Maxima long. rad. 0,0025" = 63 μ; Lat. isthmi 0,00087" = 22 μ...
>
> "Formae hexagonae et octagonae tantum singula individua inventa sunt.
>
> " Habitu est Staurastri Arachnes Ralfs, sed multis partibus majus et papillis dorsalibus et basalibus distinctum."

One peculiar aspect of the description is pointed out by West and West (1894),

> "the apical papillae are described in front view as bifid, and in vertical view as quadrifid."

The presence of quadrifid verrucae do not seem to have been noted by any of the authors consulted (Smith 1922, pl. 12 fig. 4; 1924a, pl. 20 fig. 1, 2; 1924b, pl. 81 fig. 3, 4; Lowe 1927, pl. 1 fig. 13; Taylor 1935a, pl. 37 fig. 11, 13; Irénée-Marie 1939, pl. 57 fig. 4; Alcorn 1940, fig. 82; Prescott and Scott 1942, pl. 4 fig. 16; Schumacher 1969, fig. 102). Furthermore, Smith (1924b) notes that "Lundell states that these verrucae are quadrifid but I have only noted bifid apical verrucae". Although, in an earlier paper, Smith (1922) states in his description of St. pentacerum (see p. 12) that,

> "In a vertical view of S. ophiura there is a coronet

> of quadrifid papillae with one papilla between each two adjacent rays of the semicell."

These statements contradict each other.

Clones examined: HC 39 from Jacobs Lake, 14-VI-79; HC 150 from Jacobs Lake, 29-VIII-79 (Table 26).

The front view of St. ophiura shows a slightly constricted sinus with usually a small bulge just above it and straight to slightly convergent processes (Pl. 16 Fig. 1). Just above the isthmus, most cells show a row of granules (Pl. 16 Fig. 5). The number of processes varies between five and nine in clonal culture, and six and seven in field material (Table 26). The processes are tipped with three or four spines and lined on each side by two rows of verrucae which are bifid at the base of the process and simple at the extremity (Pl. 16 Fig. 3, 5). This feature is observed in field as well as in clonal material and is one of the features used by Smith to distinguish St. pentacerum and St. ophiura. St. pentacerum forma described by Bourrelly (1966, pl. 21 fig. 3, 4), is the only record consulted which shows the species pentacerum with strong double verrucae at the base of the processes. I think Bourrelly's species is closer to St. ophiura or to St. ankyroides Wolle, as he suggests.

The upper side of the processes have granules or single spines (Pl. 16 Fig. 1-3), whereas the ornamentation on the underside appears in front view to be reduced (Pl. 16 Fig. 1); a basal view shows that ornamentation (Pl. 16 Fig. 4). The length of the processes in clonal cultures varies and the cells in cultures have generally shorter processes than in the field (in clonal cultures, l(cp) = 56-108 μm; in field material, l(cp) =79-126 μm; Table 26).

The apical verrucae are well developed and emarginate to conical in shape (Pl. 16 Fig. 2, 3). They are located between the processes and usually there is a second smaller verruca just inside, that is closer to the centre of the apex (Pl. 16 Fig. 2, 3). The double verrucae may also be wanting, but this may be due to poor development, as it is seen on smaller or stunted cells. Two such cells are seen (Pl. 16 Fig. 6); the bottom one has particularly short processes.

A comparison of cell size and cell radiation shows that smaller cells have less radiation. For example, the two clones from Jacobs Lake vary in size (HC 39, l(cp) = 59-108 μm; HC 150, l(cp) = 56-89 μm) Both HC 39 and 150 are ca. 81% hexaradiate, but HC 39 is only 5% pentaradiate and has five to nine processes, whereas HC 150 is 14.9% pentaradiate and has five to seven processes. Field material from Jacobs Lake does show similar variation in size, from a width with processes of 97 μm for a specimen with six processes to 126 μm for one with seven. Ornamentation also tends to be less pronounced on the smaller and less radiate specimens.

2. Infraspecific taxa of <u>St. ophiura</u>

<u>St. ophiura</u> is a very common and widespread complex. Some of its infraspecific taxa are discussed here. Their taxonomic features have not been observed in the present study or require

more detailed study, thus many are accepted for now.

St. ophiura f. nonaradiata W. et G.S. West 1890

St. ophiura var. cambricum W. et G.S. West 1894

St. ophiura var. subcylindricum Borge 1913

St. ophiura var. perornatum Grönblad 1945

St. ophiura var. coronatum Scott 1950

St. ophiura var. horridum Scott 1950

St. ophiura var. longiradiatum Scott 1950

a) St. ophiura forma nonaradiata W. West 1890 (p. 29; pl. 5, fig. 15) Pl. N Fig. 10:

> "Forma a vertice nonaradiata.
>
> "End view with nine rays.
>
> "Of this beautiful species, two forms were noticed along with the type, one, a nine-rayed form, was seen several times, the other, a very long and slender armed one, measured 145 μ across the arms. Cooke and Wolle describe the end view as 7 (rarely 6 or 8) rayed; the forms from Capel Curig are almost all 8-rayed."

This alga does not seem to have been reported since it was first found in North Wales. It is not even noted in Nordstedt (1896, 1908). W. West's figure does not show the double apical verrucae typical of St. ophiura. Dichotypical specimens where one semicell has nine processes were seen in 1.2% of the cells of clone HC 39 (Table 26). Since W. West's description and illustration are poor and the alga appears rare, rejection of the name is suggested.

b) St. ophiura var. cambricum W. et G.S. West 1894a (p. 12):

"Var. cellulis 1 1/3-plo latioribus quam longioribus (cum processibus); semicellulae cuneatae, lateribus leviter concavis, apicibus cum annulo verrucarum conicarum (non emarginatarum) 8 ornatae, radiis brevioribus, denticulatioribus in margine superiore convexo; a vertice visae 8 (raro 6, 7 et 9) radiatae.

"Long. 75-80 μ; lat. cum proc. 98-110 (usque ad 145) μ; lat. isthm. 16-18.5 μ.

"This is the same as S. ophiura Lund. figured by Cooke and Wills, Grevillea, 1880), also in Cooke's Brit. Desm., pl. 59, f. 1, not the description on p. 172 (which is a translation of that of Lundell, where the apical papillae are described in front view as bifid, and in vertical view as quadrifid; Cooke's figure shows that the papillae of the British examples were entire, and not like the Swedish). The 8-rayed forms are the most common. At the base of each semicell there is a ring of 12 rather long papillae (not figured by Cooke)."

No figure of this alga was provided by the Wests (1894a). It has been reported in North America but does not appear to be common. This variety is mostly distinguished by its conical apical verrucae instead of bifid verrucae. The two kinds of ornamentation were observed in clonal cultures (Pl. 16 Fig. 2). However, no cells with only conical verrucae were observed and this variety is accepted pending more thorough investigation.

c) St. ophiura var. subcylindricum Borge 1913 (p. 22; fig. 14) Pl. Q Fig. 1:

"Lateribus semicellularum fere parallelis, supremis demum leviter divergentibus. Long. cell. 84 μ; lat. semicell. ad med. 22 μ; lat. cum brach. 165 μ, lat. isthm. 18 μ.- Zufolge der nach oben nicht oder nur wenig erweiterten Zellhälften erhält unsere Form ein schlankeres und von der Hauptform sehr abweichendes Aussehen, weshalb ich es für angemessen

> hielt, dieselbe als Varietät aufzustellen. - Das Pflänzchen ist von Herrn Dr. G.W.F. Carlson in einen See in Smaland gesammelt worden. Leider ist ihm die Probe verloren gegangen, aber Dr. C. hat mir die Figuren überlassen mit der Erlaubnis, dieselben zu publizieren..."

This is a fairly large variety of St. ophiura with strongly developed double verrucae as seen in Borge's illustration (Pl. Q Fig. 1)

d) St. ophiura var. perornatum Grönblad 1945 (fig. 241) Pl. P Fig. 7:

> "Differt a forma typica processibus apicalibus plus evolutis, brachiis seriebus binis verrucarum ornatis et plus incurvatis, granulis utrimque ad isthmum nullis. Long. 59-63, cum proc. lat. 101-108, ist. 13-14."

Variation in the degree of development and shape of the double verrucae was observed in clonal culture. Gerrath (1983) also notes variation in the shape of the "warts" for St. pentacerum, from "rounded to emarginate". Variation of the degree of curvature of the processes was not observed in the present study.

e) St. ophiura var. coronatum Scott 1950 (p. 248; pl. 1, fig. 1, 2) Pl. Q Fig. 2:

> "Size somewhat smaller than in the species. In front view processes almost straight, convergent, alternating, dorsal and ventral margins crenulate; supraisthmial granules absent; apical surface elevated, slightly convex, about seven or eight verrucae visible. In vertical view seven-radiate, processes very broad and stout, lateral margins

bearing six to eight emarginate verrucae on the proximal half and four to six crenations on distal half; ends of processes with four stout spines; centrally a group of 21 bifid or trifid verrucae arranged in a regular heptagon with retuse sides. Length 60-66 μ; width without processes 30-32 μ, with processes 92-106 μ; isthmus 15-18 μ.

"Varietas magnitudine paulo minor quam species. Processus a fronte visi fere recti, convergentes, alternates, marginibus dorsalibus ventralibusque crenulatis; granuli supraisthmiales desunt. Planta a vertice visa 7-radiata, processus latissimi crassissimique, marginibus lateralibus 6-8 verrucae emarginatas dimidio in proximali, atque 4-6 crenationes dimidio in distali ferentibus; extremitates processum 4 spinis crasses ornatae; in centro corona 21 verrucarum bifidarum aut trifidarum in heptagono regulari, lateribus retusis, ordinatorum. Long. 60-66 μ, lat. sine proc. 30-32 μ, cum proc. 92-106 μ; isthmus 15-18 μ."

This variety was found in Mississipi and Florida by Scott. It is very similar to St. coronulatum var. quebecense Irénée-Marie (discussed in section 3, following).

f) St. ophiura var. horridum Scott 1950 (p. 250; pl. 1, fig. 3, 4) Pl. Q Fig. 6:

"Size somewhat smaller than that of the species. In front view processes curved, convergent, opposite; dorsal margins of processes strongly undulate, each undulation bearing a short curved spine; ventral margins of processes slightly undulate, without spines; apical surface elevated, markedly convex, with three very large verrucae visible. In vertical view six-(seven-) radiate, lateral margins of processes strongly undulate, with an emarginate verruca or curved spine on each undulation, and a row of small spines centrally along each process; intramarginally between the processes, six large verrucae, each with three or four stout conical spines. Length 60-69 μ; width without processes 32-35 μ with processes 89-101 μ; isthmus 20 μ.

"Varietas magnitudine paulo minor quam species. Processus a fronte visi curvati, convergentes,

> oppositi; processum margines dorsales valde undulati, omnibus undulationibus spinam brevem curvatam ferentibus; margines ventrales subundulati, sine spinis; superficies apicalis elevata, valde convexa, 3 verrucis permagnis visibilibus. Planta a vertice visa 6-7 radiata, processum margines laterales valde undulati, verruca emarginata aut spina curvata in quaque undulatione, atque ordine spinarum parvarum secundum mediam partem cuiusque processus praediti; 6 verrucae magnae, omnes 3-4 spines breves, conicales, ferentes, inter processus intermarginaliter videntur. Long. 60-69 μ; lat. sine proc. 32-35 μ, cum proc. 89-101 μ; isthmus 20 μ."

This variety was collected by Scott in acid soils of Louisiana. It appears distinct from the type species.

g) St. ophiura var. longiradiatum Scott 1950 (p. 250; pl. 2, fig. 1-6) Pl. O Fig. 1:

> "Length somewhat less than in the species; width with processes much greater; processes much longer and relatively more slender. In front view processes recurved, divergent, alternating, dorsal and ventral margins slightly crenulate; apical surface elevated, convex, with three or four verrucae visible; supraisthmial granules absent, but sometimes replaced by low rounded swellings which may bear one or two very small granules. In vertical view six-radiate, processes very long and slender, proximal third of lateral margins bearing stout spines or bifid verrucae which are better developed than in the species, distal two-thirds of processes faintly crenulate, terminating in three spines; intramarginally between the processes six bifid to quadrifid verrucae. Length 45-54 μ; width without processes 25-27 μ, with processes 140-236 μ. Isthmus 15-16 μ. Zygospore, diam. without processes 54 μ, with processes 96 μ.
>
> "Varietas longitudine paulo minore quam species; latitudine, cum processibus, multo ampliore; processibus multo longioribus atque relative tenuioribus. Processus, a fronte visi, recurvati, divergentes, alternates, marginibus dorsalibus ventralibusque subcrenulatis; superficies apicalis elevata, convexa, 3 vel 4 verrucis visibilibus; granuli supraisthmiales desunt, interdum, autem, inflationibus depressis, rotundatis, 1 vel 2 granulas

minutas fortasse ferentibus substitutis. Planta a vertice visa 6-radiata, processibus longissimis tenuissimisque, proximali tertia parte marginum lateralium spinas crassas aut verrucae bifidas, quae magis effectae quam in specie sunt, ferente; distalibus duabus partibus tertis processum inconspicue crenulatis, in 3 spinis terminantibus; 6 verrucae bifidae ad quadrifidas intramarginaliter inter processus videntur. Long. 45-54 μ; lat. sine proc. 25-27 μ, cum proc. 140-236 μ; isthmus 15-16 μ. Zygospora diam. sine proc. 54 μ; cum proc. 96 μ."

This plant is mainly distinguished by its large size. No such variation in dimensions was observed in the present study and this taxon appears valid. It was found by Scott in Mississipi and Florida and by Förster in South America.

3. Taxon related to St. ophiura

St. coronulatum Wolle 1884b (p. 135; pl. 44, fig. 44) var. quebecense Irénée-Marie 1952a (p. 65; pl. 6, fig. 20) Pl. Q Fig. 3:

"...L: 32-45; l: 89-100; l(sp):32-33.5; Is: 14.5-16.5...

"Varietas satis similis S. Rotulae, sed sejuncta diametro apicali semper minore, ornamento poli coronati viginti arcuatis et emarginatis granulis, et dehiscit in 7 dentos radios, sicut in S. Ophiura et non sicut in S. Rotula, cum 4 vel 5 ultimis dentibus latis et emarginatis, 5 vel 6 sequentibus decrescentibus usque ad extremum radium, qui desinit in 3-4 parvas breves et divergentissimas spinas. Radii unius semicellulae variant vices cum alius. Ab apice visa, speciei Wolleani est. Est leviter cyathiformis, isthmo levi incisura notato; appendicibus semicellulae unius incurvis ad alius ita ut occurant et etiam trajiciant medium planum. Poli corona granulorum ornati. Heac est ex pulcherrimis desmidiis collectis in provincia Quebecensi."

Irénée-Marie states that this variety, found only in Québec (Canada), may belong to the type species and that the difference between the two taxa may be only due to the summary description of St. coronulatum given by Wolle (1884b). Figures of St. coronulatum var. quebecense appear similar to the alga described by Scott and named St. ophiura var. ornatum (Pl. Q Fig. 2), although Irénée-Marie's alga is shorter (L = 32-45 µm compared to 60-66 µm). The description and illustration provided by Wolle (1884b) for his St. coronulatum are inadequate as noted by Irénée-Marie. The type species and var. quebecense are thus of doubtful validity and both need to be reevaluated. Prescott et al. (1982; p. 168) accept it as valid.

4. St. pentacerum (Wolle) Smith 1922 (p. 356; pl. 12, fig. 19-22) Pl. O Fig. 7:
Basionym: St. ophiura var. pentacerum Wolle 1882 (p. 28; pl. 13, fig. 5) Pl. N Fig. 8:

Variety pentacerum of St. ophiura was described by Wolle for pentaradiate specimens of St. ophiura. Wolle only noted the pentaradiation and did not give a more explicit diagnosis. Smith (1922) raised the taxon to the level of species, on the basis of the following features:

> "...Length 28-30 µ; breadth (without processes) 17.5-22.5 µ, (with processes) 81-100 µ; breadth isthmus 7.5 µ.
>
> "In 1882 Wolle described the varieties tetracerum and

> pentacerum of S. Ophiura These have, as their name implies, four- and five-radiate semicells which are shaped somewhat like the semicells of S. Ophiura. In a vertical view of S. Ophiura there is a coronet of quadrifid papillae with one papilla between each two adjacent rays of the semicell. The arms have bifid projections at the base while the terminal portion is serrate and with a simple projection. The organism which I believe identical with Wolle's S. Ophiura var. pentacerum has an emarginate verruca between each two adjacent rays while the sides of the rays are denticulate and at times with a row of denticulations on the top. I have observed five-rayed specimens of S. Ophiura from New York, and in these individuals there is the typical marking of the seven- and eight-rayed individuals. I think, therefore, that Wolle's plant cannot be considered a variety of S. Ophiura but must be regarded as a distinct species. The number of rays is generally five, but may be six. The four-rayed specimens have the same marking and are discussed below in connection with the variety tetracerum. The specific name pentacerum has been chosen because the name tetracerum has already been used in another connection."

Clones measured: HC 69 from Como Lake, 26-VII-79; HC 91, 93, 97 from Munday Lake, 1-VIII-79; HC 100 from Munday Lake, 15-VIII-79; HC 497 from Munday Lake, 1-XI-80; HC 133 from Lost Lake, 5-IX-79. Other clones examined for radiation: HC 72, 73, 78 from Munday Lake, 26-VII-79; HC 82, 83, 85, 87, 98, 99 from Munday Lake, 1-VIII-79; HC 102 from Munday Lake, 15-VIII-79; HC 439, 448 from Munday Lake, 16-V-80; HC 134 from Lost Lake, 5-IX-79 (Table 27).

These clones are believed to belong to St. pentacerum var. pentacerum. In front view, the shape of the sinus is cylindrical (Pl. 16 Fig. 8) and the processes slightly incurved. The processes often have bifid verrucae at their base but they are less developed than in St. ophiura and sometimes reduced to single spines (Pl. 16 Fig. 10). The underside of the processes is smooth (Pl. 16 Fig. 8, 10). In clone HC 102, a clone with many deformed cells, presence of spines above the isthmus was observed (Pl. 16 Fig. 7)

In apical view, double verrucae are seen between the processes (Pl. 16 Fig. 9). The cells are smaller in culture than in field material (l(cp) = 42-86 µm in clonal cultures; l(cp) = 46-109 µm in field material). Cells of clonal cultures are mostly penta-, hexa or penta-hexaradiate, with a large variation among the clones. Field material is only pentaradiate (Table 27).

4. Synonyms of St. pentacerum var. pentacerum :

St. pentacerum var. tetracerum (Wolle) Smith 1922

St. pentacerum var. tetracerum f. major Smith 1922

St. pentacerum var. hexacerum Irénée-Marie 1957

These taxa are proposed by Gerrath (1983) as synonyms and the results of the present study agree.

a) St. pentacerum var. tetracerum (Wolle) Smith 1922 (pl. 13; fig. 3-5)

Basionym: St. ophiura var. tetracerum Wolle 1882 (p. 28; pl. 13, fig. 4) Pl. P Fig. 9

Smith's description is:

> "...In view of Wolle's rather diagrammatic figure of this variety, the determination rests upon the figure given by the Wests. The specimens that I have observed are not so long as the Wests state, and the breadth of the semicells with the processes may also be less. I have found the alga in quantity in several lakes without finding a single five-rayed individual

> and think, therefore, that it is a distinct variety. In some collections both four- and five-rayed individuals are present, but I consider this a mingling of the widespread type and variety and not a normal variation of the type.
>
> "The twisting of the semicells so that the rays of one semicell are equidistant between the rays of the other semicell is a constant character and furnishes another distinction between this species and S. Ophiura."

Gerrath's (1983) conclusion is followed, although tetraradiate specimens were rare in this study. This variety could be termed facies 4 in accordance with Grönblad and Růžička's (1959) recommendations. Prescott et al. (1982; p. 277) keep it as a valid variety.

b) St. pentacerum var. tetracerum forma major Smith 1922 (p. 358)

> "Processes much longer than in the foregoing, body of semicells of the same size as in the variety.
>
> "Breadth (with processes) 145-155 μ."

Gerrath (1983) considers this taxon "as part of the S. pentacerum morphological complex", because he observes variation in the length of the processes in material from the same lakes sampled by Smith (1922). Prescott et al. (1982; p. 277) accept this taxon but incorrectly report it as f. minor.

c) St. pentacerum var. hexacerum Irénée-Marie 1957 (p. 187; pl. 2, fig. 18) Pl. P Fig. 3:

> "L:36-44.5 mμ; l.:82.5-95 mμ; (sp):18-22 mμ; Is.: 10-12.8 mμ...
>
> "Variatas disjuncta a typo 6 processibus. Dimensiones typi sunt, interdum leviter minores."

Hexaradiate cells of St. pentacerum were common in clonal and field material from Como, Lost and Munday Lakes (Table 27). This could be termed facies 6 in accordance with Grönblad and Růžička (1959). Prescott et al. (1982; p. 276) accept this taxon.

5. An additional infraspecific taxon of St. pentacerum

St. pentacerum forma obesum Smith 1922 (pl. 13; fig. 1, 2) Pl. P Fig. 14:

> "Body of semicells stouter and apex more elevated.
>
> "Length 38-42 μ; breadth (without processes 25-27.5 μ, (with processes) 105-117 μ; breadth isthmus 14 μ."

It appears questionable whether such variation of the stoutness of the semicell deserves to be the basis of a different taxon. However, Gerrath (1981) observed material from the same lakes sampled by Smith (1922) and concluded that it is a good forma; Prescott et al. (1982; p. 276) also accept it. Their conclusion is followed.

6. Conclusion

From this summary observation of clones from Jacobs Munday, Lost and Como Lakes, it appears that the clones from Jacobs Lake are bigger, with more processes and stronger ornamentation. The latter agree with literature reports of St. ophiura. Clones of the second group from Munday, Lost and Como lakes are named St. pentacerum. Gerrath (1983) undertakes a detailed study of specimens of St. pentacerum from the same Ontario lakes sampled by Smith (1922). He finds that the morphological features, except radiation, are constant. He agrees with Smith who names a species distinct from St. ophiura. I accept this conclusion for the time being, but the variation observed in the present study does demonstrate a strong relation between St. pentacerum and St. ophiura. For example, bifid verrucae were observed with the SEM at the base of the processes of St. pentacerum (Pl. 16 Fig. 10) and supraisthmial spines were seen in clone HC 102 (Pl. 16 Fig. 7), which was however not further studied. Prescott and Scott (1942) state that they "find great variation in both the latter (Staurastrum ophiura) and in Staurastrum pentacerum (Wolle) Smith. Some of these variations intergrade sufficiently to warrant a reevaluation of the two species and to suggest the possibility of combining them." I think that a more detailed study, predominantly of field material is necessary, since clonal cultures grew poorly.

TABLE 26

CELL DIMENSIONS AND RADIATION OF ST. OPHIURA
(Clonal cultures: N=see Materials and Methods; S.D.=Standard deviation; C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone	Source	L(cp) (μm) Av.	Range	S.D.	C.V.	l(cp) (μm) Av.	Range	S.D.	C.V.	Is (μm) Av.	Range	S.D.	C.V.	L/l	Radiation (%) 5	6	7	5-6	5-7	6-7	6-9	8-9
39	Jacobs 14-VI-79	59	49-63	3.76	6.42	90	59-108	9.95	11.03	23	21-27	1.73	7.45	0.65	5.4	81.5	0.6	9.5	0.6	1.2	0.6	0.6
150	Jacobs 29-VIII-79	52	46-61	4.11	7.85	73	56-89	7.91	10.77	22	18-25	1.52	6.93	0.71	14.9	81.8	3.3	---	---	---	---	---

Field material

Source	L(cp) (μm)	l(cp) (μm)	l(sp) (μm)	Is (μm)	Pr (μm)	L/l	Radiation 6	7
Jacobs 28-VIII-79	---	97	---	---	14, 35, 28*	---	X	
Jacobs 16-V-80	---	126	37	20	---	---		X

*Dichotypical cell

TABLE 27

CELL DIMENSIONS AND RADIATION OF *ST. PENTACERUM*

(Clonal cultures: N=see Materials and Methods; S.D.=Standard deviation C.V.=Coefficient of variation. Field specimens: N=1; X=preserce)

Clonal cultures

Clone HC	Source	L(cp) (μm) Av.	Range	S.D.	C.V.	l(cp) (μm) Av.	Range	S.D.	C.V.	Is (μm) Av.	Range	S.D.	C.V.	L/l	Radiation (%) 4	5	6	7	8	9	4-6	4-5	5-6	5-7	6-7	6-9	8-9
69	Como 26-VII-79	43	35-51	2.67	6.15	63	51-73	5.52	8.81	16	15-18	1.26	7.71	0.69	---	27.4	63.2	0.9	---	---	---	---	8.5	---	---	---	---
72	Munday 26-VII-79	--	--	--	--	--	--	--	--	--	--	--	--	--	---	41.1	54.2	0.9	---	0.9	---	---	2.8	---	---	---	---
73	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	---	44.1	54.8	1.1	---	---	---	---	---	---	---	---	---
78	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	---	31.6	57.9	---	---	---	---	---	9.6	---	0.9	---	---
82	Munday 1-VIII-79	--	--	--	--	--	--	--	--	--	--	--	--	--	---	50.4	41.9	---	---	---	---	---	6.8	---	0.1	---	---
83	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	---	24.8	63.4	2.0	---	---	---	---	7.9	---	1.0	---	---
85	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	---	63.6	28.3	4.0	---	---	---	---	2.0	1.0	1.0	---	---
87	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	---	65.5	31.8	0.9	---	---	---	---	1.8	---	---	---	---
91	" "	45	38-50	2.65	5.97	70	53-86	9.49	13.63	16	13-17	1.11	7.12	0.64	---	90.5	3.2	3.2	---	---	---	---	2.1	---	---	---	---
93	" "	42	38-48	2.23	5.31	59	42-78	7.68	12.97	16	13-17	1.18	7.57	0.71	---	75.0	22.7	1.6	---	---	---	---	0.8	---	---	---	---
97	" "	44	38-48	2.35	5.38	63	51-74	5.31	8.48	17	15-19	1.25	7.25	0.70	---	66.2	31.6	2.2	---	---	---	---	---	---	---	---	---
98	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	---	31.3	53.4	---	---	---	---	---	12.7	1.7	0.8	---	---
99	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	---	26.4	38.2	---	---	---	---	---	33.3	1.4	0.7	---	---
100	Munday 15-VIII-79	43	38-51	3.20	7.49	63	42-82	9.23	14.70	17	15-19	1.17	6.73	0.68	---	67.7	30.6	0.8	0.8	---	---	---	---	---	---	---	---

continued

TABLE 27 (cont'd)

Clonal cultures

Clone HC	Source	L(cp) (μm) Av.	Range	S.D.	C.V.	l(cp) (μm) Av.	Range	S.D.	C.V.	Is (μm) Av.	Range	S.D.	C.V.	L/l	Radiation (%) 4	5	6	7	8	9	4-6	4-5	5-6	5-7	6-7	6-9	8-9
102	Munday 15-VIII-79	--	--	--	--	--	--	--	--	--	--	--	--	--	--	33.3	37.2	---	---	---	---	---	28.7	0.8	---	---	---
439	Munday 16-V-80	--	--	--	--	--	--	--	--	--	--	--	--	--	0.6	66.7	25.3	1.8	0.6	---	0.6	0.6	3.6	---	---	---	---
448	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	--	52.3	29.1	0.7	---	---	---	---	17.2	---	---	---	---
497	Munday 1-XI-80	44	38-48	2.41	6.50	63	53-78	6.86	10.86	18	17-23	6.58	16.56	0.70	--	59.5	39.5	---	---	---	---	---	1.0	---	---	---	---
133	Lost 5- IX-79	43	38-48	2.77	6.44	63	53-72	5.41	8.58	17	13-19	1.41	8.50	0.68	--	86.0	12.3	---	---	---	---	---	1.8	---	---	---	---
134	" "	--	--	--	--	--	--	--	--	--	--	--	--	--	--	68.8	20.5	---	---	---	---	---	10.7	---	---	---	---

Field material

Source	L(cp) (μm)	l(cp) (μm)	l(sp) (μm)	Is (μm)	L/l	Radiation 5
Munday 7-VI-79	---	---	108	---	---	X
Munday 14-VI-79	---	---	108	---	---	X
" "	---	---	82	---	---	X
Munday 1-VIII-79	---	---	45	---	---	X
Munday 15-VIII-79	46	99, 86*	20	11	0.47, 0.54	X
" "	---	94	20	---	---	X

*Dichotypical cell

continued

TABLE 27 . (cont'd)

Field material

Source	L(cp) (μm)	l(cp) (μm)	l(sp)	Is (μm)	L/l	Radiation 5
Munday 15-VIII-79	---	91	---	---	---	X
Munday 20-IX-79	---	99	22	---	---	X
" "	---	103	23	---	---	X
Lost 5-IX-79	---	80	---	---	---	X
" "	---	88	20	---	---	X
" "	---	83	---	---	---	X
Lost 12-IX-79	---	79	20	---	---	X
" "	---	79	23	---	---	X

Plate 16

St. *ophiura* var. *ophiura* and *St.* *pentacerum* var. *pentacerum*

SEM photographs

(marker = 10 μm unless indicated otherwise)

1-4. *St.* *ophiura* var. *ophiura*, clone HC 150

1. Cell in front view

2. Detail of vertical view showing variation in shape of the apical verrucae

3. Cell in a tilted position showing the apical verrucae and the bifid verrucae on the processes

4. Cell in basal view showing the ornamentation under the processes

5, 6. *St.* *ophiura* var. *ophiura*, clone HC 39

5. Cell viewed from the front and the apex; the arrow indicates the bifid verrucae at the base of the processes

6. Two cells of different size in vertical view showing the apical ornamentation

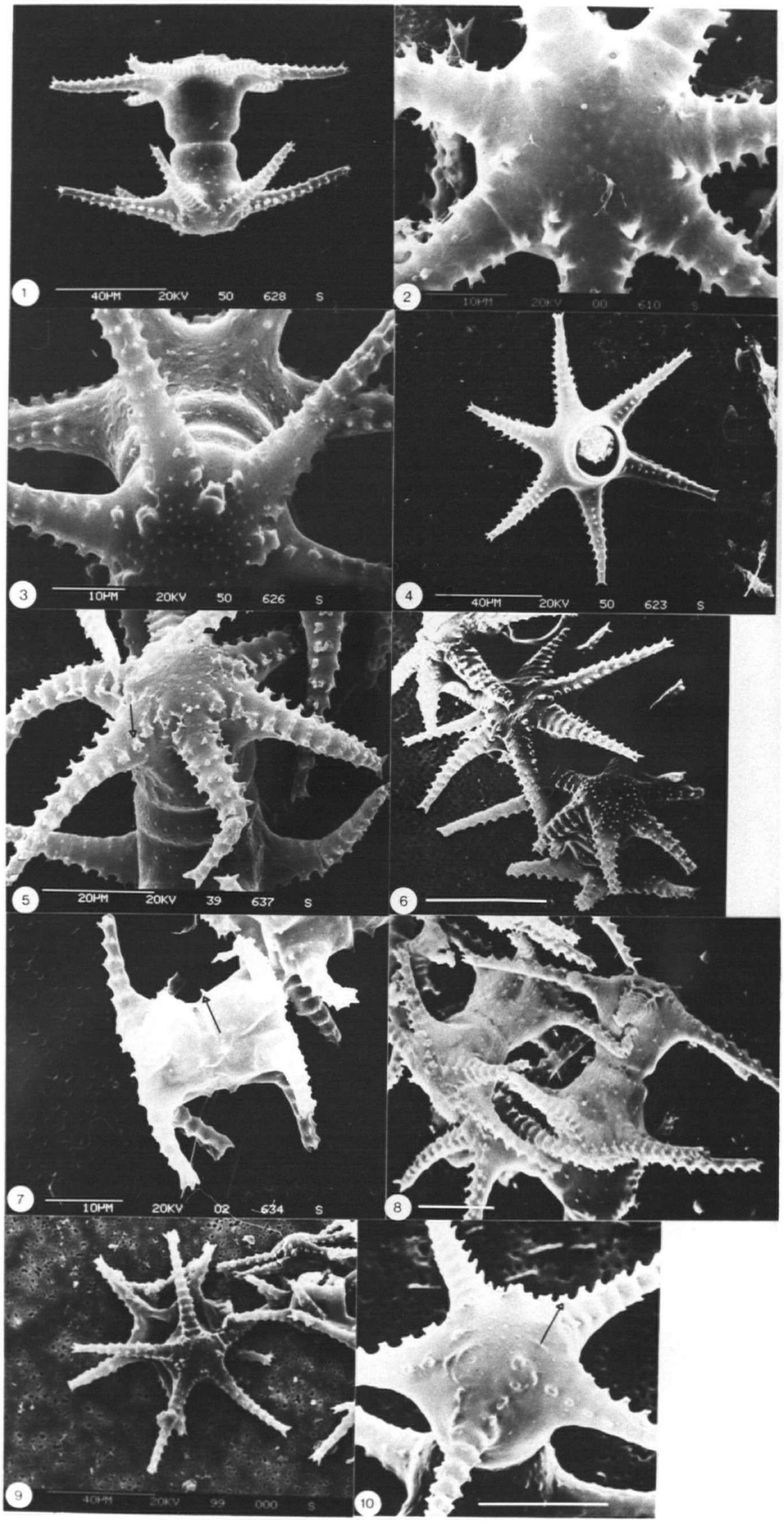
7. St. pentacerum var. pentacerum, clone HC 102; cell in front view, the arrow indicates the supraisthmial spines

8, 9. St. pentacerum var. pentacerum, clone HC 73

8. Cells in front view

9. Cell in vertical view

10. St. pentacerum var. pentacerum, clone HC 88; cell viewed from the front and the apex, the arrow indicates the bifid verrucae at the base of the processes


1
40µM 20KV 50 628 S
2
10µM 20KV 00 610 S
3
10µM 20KV 50 626 S
4
40µM 20KV 50 623 S
5
20µM 20KV 39 637 S
6
7
10µM 20KV 02 634 S
8
9
40µM 20KV 99 000 S
10

R. STAURASTRUM GRALLATORIUM VAR. FORCIPIGERUM INCLUDING ST. GRALLATORIUM VAR. GRALLATORIUM

St. grallatorium var. forcipigerum Lagerheim 1885 (p. 249; pl. 27, fig. 27) Pl. M Fig. 11:

> "Var. semicellulis supra basim saepe constrictis in dorso non crenato-dentato aculeis binis et verruculis binis praeditis; radii ad finem aculeis binis inaequalibus muniti.
>
> "Long. cell. 50-58 μ; lat. cell. c. rad. 115-120 μ; lat. bas. cell. 10 μ; lat. isthm. 7 μ."

St. grallatorium Nordstedt 1869 (p. 228; pl. 4, fig. 52) Pl. M Fig. 13:

> "S. submagnum; semicellulae quadrangulae dorso subproducto aculeis binis (vel quaternis?) parvis (a vertice visis quaternis (vel 8) instructae, angulis inferioribus rotundatis, superioribus in radium gracilem elongatum achroum margine crenato-dentatum apice bi-trifurcatum productis, a vertice visae ovales, utroque polo in radium elongatum margine integrum apice acuminatum vel trifurcatum productae.
>
> "Long. 0,0009"=23 μ. Lat. c. rad. 0,0031-41"=79-103 μ. Crass. 0,00052"=13 μ."

Variety forcipigerum appears to be a stouter form of St. grallatorium, having longer and stouter spines at the end of the processes, more developed apical verrucae, and two spines on each side of the apex. The literature reports commonly show much shorter processes than shown by Nordstedt for St. grallatorium.

In Stein and Borden (unpublished) there are only three records for St. grallatorium of which two are from Placid Lake; there are no records for var. forcipigerum.

The clone of St. grallatorium var. forcipigerum isolated from a sample collected in Jacobs Lake on 14-VI-79 (clone HC 63) contained many deformed cells. The culture was eventually discarded but a stub was prepared for SEM observation and three cells were measured (Table 28). Two cells of this taxon were observed in a field sample from Jacobs Lake (Table 28). Unfortunately, due to the many stunted and deformed cells in clone HC 63, it was not possible to observe variation in clonal culture. On Pl. 18 Fig. 5, 6 (see Std. dejectus) is a SEM photograph of a front and a vertical view. In front view (Pl. 18 Fig. 5), the upper semicell appears free of granules, whereas the lower one has an ornamentation similar to that described by Taylor (1935a; pl. 39, fig. 18), with some outline of a supraisthmial ring of granules and with granules covering the semicell body except for the centre of the ventral face. There are two spines on each side of the apex and, below them, two smaller spines or verrucae. The specimen observed in the sample from Jacobs Lake (26-VII-70) is shown on Pl. N Fig. 1. The two spines on each side of the apex are not well developed and approach the arrangement observed by Taylor.

Calculation of the ratio L/l for both original descriptions gives, 0.29-0.22 for St. grallatorium and 0.43 for St. grallatorium var. forcipigerum. Thus there is a large difference in the L/l ratio between the original description and both clone HC 63 and field material (Table 28).

Calculations of other records from the literature give the following results:

	L or L(sp)/l
St. grallatorium :	
Smith (1924b)	0.40-0.46
Taylor (1935a)	0.83
Irénée-Marie (1957)	0.64-0.66
St. grallatorium var. forcipigerum :	
Smith (1924b)	0.53-0.58
Irénée-Marie (1939)	0.56-0.96
Förster (1972)	0.47
St. grallatorium var. forcipigerum f. longispinum:	
Irénée-Marie (1952a)	0.66-0.67

It appears that Nordstedt's original illustration of St. grallatorium, is of a specimen with particularly long processes since subsequent literature reports indicate that the commonly encountered specimens of this species have shorter processes. As for the type description of var. forcipigerum, although the L/l ratio is small (0.43), it is closer than that of the type species to values observed in the present study and by the authors mentioned.

Some intermingling of the characteristics of the type species and its var. forcipigerum have been observed. For example, Taylor's (1935a) specimen possesses the two stout spines at the end of the processes characteristic of var. forcipigerum, but the cell apex does not have the typical two long spines. The cell is also longer than in both Nordstedt and Lagerheim's descriptions, and, in contrast to these, it has some granules on the semicell body. Förster (1972) suggests that Taylor's specimen probably belongs to var. forcipigerum, a conclusion which I endorse.

In summary, both type descriptions of St. grallatorium and var. forcipigerum diverge from other descriptions of the species found in the literature, and from the present study.

1. Proposed synonym of St. grallatorium var. forcipigerum

St. grallatorium var. forcipigerum f. longispinum Irénée-Marie 1952a

St. grallatorium var. forcipigerum f. longispinum Irénée-Marie 1952a (p. 74; pl. 7, fig. 9) Pl. M Fig. 12:

> "L: 53-56; l: 80-83.5; l(sp):53-54; Is: 10-10.5. "Forma disjuncta a typo profundissimis divisionibus appendicum in 2 brachia dissimilis longitudinis, longius attingens facile 16 mμ; minus, 13 mμ. Apex fert unum amplissimum granulum inter duas apicales spinas."

Irénée-Marie shows one big granule instead of two double verrucae between the two apical spines. The creation of forma longispinum seems unwarranted as it is based on a slight variation of size and development of the verrucae. Prescott et al. (1982; p. 214) accept it as a valid taxon.

2. Other varieties of St. grallatorium not discussed.

Other varieties of St. grallatorium found in the literature are var. americanum W. et G.S. West 1896b, var. ungulatum Wolle 1881, var. floridanum Scott et Grönblad 1957 and var. brasiliensis (Grönblad) Förster 1969. They appear distinct from var. forcipigerum but were not examined in detail as the culture material available was insufficient. Prescott et al. (1982; p. 214) place var. ungulatum as a synonym of var. forcipigerum.

TABLE 28

CELL DIMENSIONS AND RADIATION OF *ST. GRALLATORIUM* VAR. *FORCIPIGERUM*
(Clonal cultures: N=1 ; Field material: N=1; X=presence)

Clone HC	Source	L(cp) (um)	L(sp) (um)	l(cp) (um)	l(sp) (um)	Is (um)	Sp (um)	L/l	Radiation 2
Clonal cultures									
63	Jacobs 14-VI-79	68	53	76	25	11	10	0.66	X
"	" "	48	46	73	58	10	11	0.66	X
"	" "	57	48	76	--	10	11	0.66	X
Field material									
	Jacobs 26-VII-79	50	47	79	--	--	--	0.63	X
	Jacobs 26-IV-80	51	46	--	--	--	10, 8	0.80	X

S. STAURODESMUS MUCRONATUS VAR. DELICATULUS INCLUDING STD. MUCRONATUS VAR. MUCRONATUS

Std. mucronatus (Ralfs) Croasdale var. delicatulus (G.S. West) Teiling 1967 (p. 570; p. 18, fig. 6, 15)

Basionym: Staurastrum mucronatum var. delicatulum G.S. West 1905 (p. 72):

G.S. West (1905) described this taxon as:

"Var. semicellulis elliptico-fusiformibus, angulis lateralibus submamillatis et apiculatis. Long. 32.5-35 μ; lat. 34-37 μ; lat. isthm. 6-7 μ..."

It is only in 1909 that G.S. West published a figure of his taxon (G.S. West 1909b; Pl. P Fig. 10).

Std. mucronatus (Brébisson) Croasdale 1957 (p. 132; pl. 2, fig. 35, -36)

Basionym: Staurastrum mucronatum Ralfs 1845 (p. 152; pl. 10, fig. 5, 6) Pl. R Fig. 6:

Synonym: Staurastrum mucronatum (Ralfs) Brébisson 1856 (p. 142)

Ralfs' description is:

"Fronds smooth; end view three-lobed; lobes inflated, blunt, mucronate.
" α In the front view the segments are transversely elliptic, and the mucro straight.
" β Segments lunate, mucro curved outwatds.
" γ Mucro curved inwards...

"Fronds smooth, deeply constricted in the middle; segments broader than long, rounded at the sides, which are furnished with a mucro. In α . and γ . the segments are transversely elliptic, but in β . they are lunate. The end view shows three mammillate lobes or rays, each of which is terminated by a hair-like mucro.

> "The smooth frond, the peculiar inflated or mamillate form of the lobes in the end view, and the terminal hair-like points, well characterize this species..."

Many records of this taxon appear under the name Staurastrum, since Staurodesmus was proposed by Teiling (1948) and only in 1967 (Teiling 1967) did he publish a monograph on the genus. As Teiling (1967) points out, Ralfs' figures (1845; pl. 10 fig. 5, 6) of St. mucronatum represent Staurastrum nowadays known as several currently recognized species of Staurodesmus, that is Std. connatus (Lundell) Thomasson (Pl. R Fig. 6a, upper right corner), Std. mucronatus (Pl. R Fig. 6b, upper left corner and possibly front view just below it), and other unidentified cells.

Ralfs (1848) made St. mucronatum a synonym with St. dejectum described by de Brébisson in Meneghini (1840; p. 227). In his plate 20, fig. 5a (Pl. R Fig. 3b) is of St. dejectum sensu de Brébisson, whereas fig. 5e (Pl. R Fig. 3a) is considered by Teiling 1967 (p. 568) to represent the true St. mucronatum. De Brébisson 1856 (p. 142) reestablished the species St. dejectum and tried to emphazise the difference between his St. dejectum and Ralfs' St. mucronatum :

> "M. Ralfs n'a pas conservé cette espèce dans son dernier ouvrage the British Desmidieae et l'a réunie à la suivante. Je crois qu'elle en diffère. Dans le S. mucronatum les hémisomates sont ovoïdes, à dos convexe, et l'épine angulaire est droite ou un peu dirigée en dedans. Dans le S. dejectum les hémisomates sont turbinés, à dos plane et l'épine est déjetée en dehors."

Std. mucronatus var. delicatulus differs obviously from the type species. It has a "more slender shape, very short spines and more open sinus." (Teiling 1967, p. 570). In fact, the difference in the shape of the semicells is very striking, whereas _Std._ _mucronatus_ _sensu_ Teiling has oval semicells with convex apex, var. _delicatulus_ has subtriangular cells with apex slightly convex or straight.

Std. _mucronatus_ var. _delicatulus_ was first recorded in Australia. It appears to be rare and has not been found previously in North America. I collected it in J.K. Henry and Munday Lakes. Stein and Borden (unpublished) have two reports of _Std._ _mucronatus_ var. _mucronatus_, including one from Munday Lake, and two of its var. _subtriangularis_.

Clones examined: HC 173, 181, 185, 190 from J.K. Henry Lake, 18-IV-80; HC 288 from J.K. Henry Lake, 30-V-80; HC 79 from Munday Lake, 26-VII-79 (Table 29).

The cells of _Std._ _mucronatus_ var. _delicatulus_ are subtriangular in shape, with a straight or convex apex and a widely rounded sinus (Pl. R Fig. 1, 2). The angles are either rounded or bear converging spines or mucros of variable length. The longer spines are usually convergent.

The length of the spines varies and the angles are sometimes rounded and without spines (Pl. 17 Fig. 4, 8, 10). The spines are generally shorter in clone HC 79 (up to 2 µm) than in clones from J.K. Henry Lake (up to 4.5 µm). In field material from J.K. Henry Lake spines are also longer (up to 5 µm) than in clonal material. No field material from Munday Lake was observed.

Another peculiarity of clone HC 79 is the long isthmus observed on a few cells (Pl. 17 Fig. 1, 2). These SEM photographs of isolated semicells are very striking, but with the light microscope, no difference in the length of the isthmus was noted. Nevertheless, in Pl. 17, Fig. 2, the isthmus tube is three times longer than in Fig. 1. This does not seem to have been previously reported for Std. mucronatus var. mucronatus (however see Croasdale's report of Std. mucronatus var. subtriangularis).

The cell wall shows an hexagonal pattern (Pl. 17 Fig. 1, 5-7). Some pore openings are surrounded by a "collar" of mucilage (Pl. 17 Fig. 5-7). In apical view, the sides are slightly concave (Pl. 17 Fig. 4, 8, 9).

Table 29 shows that the clones collected in J.K. Henry Lake differ slightly in their average dimensions. For example, the average length is 42-46 µm, the average width of the semicell with spines or mucros is 40-46 µm and of the isthmus is 13-15 µm. Cells from field material vary considerably in the L/l ratio (0.69-0.86; Table 29). Clone HC 79 from Munday Lake is smaller than all clones from J.K. Henry Lake, with an average length of 37, and average width of the semicell with spines or mucros of 35 and an average width of the isthmus of 11 µm.

Clone HC 79 is triradiate (94.5%), whereas the five clones from J.K. Henry Lake are 47.9-70.4% triradiate, with most of the remaining cells tetraradiate, a few pentaradiate cells and dichotypical cells with one semicell triradiate and the other tetraradiate. All cells from field material are triradiate.

Two abnormal cells of clone HC 173 are seen on Pl. 18 Fig. 3 and 10). Fig. 10 shows an abnormal "process" half-way between the angles of the semicell. Cells of clone HC 79 from Munday Lake (Pl. R Fig. 1), and of clone HC 173 from J.K. Henry Lake (Pl. R Fig. 2) appears similar. Detailed observation of those clones reveals slight differences mostly in the length of the spines; clonal cultures isolated from J.K. Henry Lake have a higher proportion of tetraradiate cells, although none were seen in field material. Those differences are slight and relate to features which were shown to vary in this study. For this reason, the differences are not sufficient to separate clone HC 79 and clones from J.K. Henry Lake. The clones are believed to be better considered as morphae of the same taxon.

1. Infraspecific taxa of Std. mucronatus

The characteristics of the following taxa have not been found in this study and there is no reason not to accept them. Some have previously been made synonyms of other taxa of Std. mucronatus and are accepted as such.

Std. mucronatus var. parallelus (Nordstedt) Teiling 1967

St. mucronatum var. rectum Turner 1892

St. mucronatum var. rectum f. minor Turner 1892

Std. mucronatus var. subtriangularis (W. et G.S. West) Croasdale 1957

Std. mucronatus var. croasdalae Teiling 1967

Std. mucronatus var. groenbladii Teiling 1967

a) Std. mucronatus var. parallelus (Nordstedt 1888) Teiling 1967 (p. 570; pl. 18, fig. 11)

Basionym: St. dickiei var. parallelum Nordstedt 1888 (p. 39; pl. 4, fig. 15) Pl. P Fig. 12:

Nordstedt's description is:

"Minor; aculei breviores non convergentes, sed paralleli.

"Long. 23-24 μ; lat. sin. acul. 23-24 μ; lat. c. acul. 27 μ; lat. isthm. 7 μ...

"If the semicells had been more than twice as long, as they are broad, I should have considered it to be a form of St. mucronatum (between fig. 5b. and c. in Ralfs Brit. Desm. tab. 20)..."

This taxon, which was first recorded in New Zealand is more compressed and has smaller spines than the type species.

b) St. mucronatum var. rectum Turner 1892 (p. 106) and

c) St. mucronatum var. rectum f. minor Turner 1892 (p. 106; pl. 19, fig. 15):

"(Ralfs in Annals l.c. f. 5 a super. sinistr.; St. dejectum var. β Br. Desm. p.121, t.XX, f.5 c) F. minor (isthmo elongato).

"L. 16-18, lat. 18 (ac. incl.), lat. isth. 3-4; l. spin. 1.5-2.7 μ T. XIX, f. 15 (forma mostrosa, fide G.C.W. Mscr. No. 267, f. 3).

"The elongate isthmus of these Indian forms is peculiar: in this and in the next it is more noticeable than in the European plants, and might stand as F. Indica of both of them."

These taxa were first found in East India and do not seem to have been recorded since. Teiling (1967; p. 569) places them as synonym of Std. mucronatus.

d) Std. mucronatus var. subtriangularis (W. et G.S. West) Croasdale 1957 (p. 132; pl. 2, fig. 38).

Basionym: Staurastrum mucronatum var. subtriangulare W. et G.S. West 1903 (p. 545; pl. 17, fig. 11) Pl. P Fig. 11:

The Wests description is:

"Var. major, sinu apertiore, semicellulis cum dorso subrecto vel leviter convexo et ventre subsemicirculari.

"Long. 38,5 μ; lat. sine spin. 42-44 μ, cum spin. 51-53,5 μ; long. spin. 3.8-4.6 μ; lat. isthm. 9.5 μ."

This taxon was first recorded in Scotland and has since been found in Europe and North America. Literature reports of var. subtriangularis vary. Although the Wests' original figure has parallel spines and a short isthmus, Croasdale's (1962; pl. 6, fig. 117-118)) and Taylor's (1935a; pl. 33 fig. 4) figures of var. subtriangularis show cells with short and slightly divergent spines. Croasdale's specimens also have a long isthmus. Messikommer (1960, fig. 18) shows a semicell with mamillate angles and convex apex, which is almost identical to the original figure of var. delicatulum (Pl. P Fig. 10) and should be treated as such.

The shape of the cells of var. delicatulus resembles var. subtriangularis W. et G.S. West, but they differ by the usually shorter spines and, as represented by West and West's original figure of var. subtriangularis (Pl. P Fig. 12), by the parallel spines.

e) Std. mucronatus var. croasdaleae Teiling 1967 (p. 571; pl. 18, fig. 14) Pl. Q Fig. 4:

Syn.: Std. subulatus (Kützing) Thomasson 1963 sensu Croasdale 1957 (pl. 3 fig. 46).

> "Varietas differens ut semicellulae a fronte visae spinas super parte media laterum radialium, necnon formam triangularem, apice complanato, sinu latiore, praebent. Zygospora ut in var. mucronatus.
>
> "Differs in compressed shape with flattened apex and narrow sinus, spines rather long.
>
> "Dim. 40-42 x 39-42 x 12-18 μ, lo. sp. 6-8 μ."

This variety was first recorded as Std. subulatus by Croasdale in Alaska, and was later placed as a variety of Std. mucronatus by Teiling (1967). It has a closed sinus which differentiates it from all other varieties of Std. mucronatus. The spines are longer than in any specimens seen in the present study.

f) Std. mucronatus var. groenbladii Teiling 1967 (p. 571; pl. 18, fig. 12) Pl. Q Fig. 5:

> "Varietas apice convexiore, sinu angulari, late aperto, differens. Fac. 3, 4.
>
> "Dim. 26-32 x 22-24 x 8-10 μ.
> "Differs in more convex apex and widely open angular sinus, fac. 3, 4.
> "Dim. 26-32, 22-24 x 8-10 μ."

There are only two records of this variety, the original observation from Brazil and a record from Sweden. The cells are smaller than any cells observed in the present study. Variation in the degree of openness of the sinus was observed in connection with more or less depressed cells.

2. An uncertain taxon of Std. mucronatus

St. mucronatum var. debaryanum Turner 1892 (p. 105; pl. 16, fig. 20) Pl. P Fig. 13

> "...Cellulae plus minus incudiformes. Long. 25-28, lat. 30-33 (sp. incl.) lat. isth. 4-5, l. acul. 5-6 μ...
>
> "This form differs from those of Ralfs (β aculei parallel, and γ aculei convergent), in having the broadest part of the semicell apical and not lateral, and in having the spines so placed. In Nordstedt's form (De By l. c.) this is so; the Indian specimens having the aculei straight and mearly parallel..."

This taxon was first recorded in East India and does not appear to have been found since. It is not noted in Teiling's (1967) review of Staurodesmus. The deeply constricted isthmus and shape of the semicell do not justify its inclusion in Std. mucronatus. The validity of this taxon is doubtful.

TABLE 29

CELL DIMENSIONS AND RADIATION OF STD. MUCRONATUS VAR. DELICATULUS
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation; C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(csp) (µm) Average	L(csp) Range	L(csp) S.D.	L(csp) C.V.	l(csp) (µm) Average	l(csp) Range	l(csp) S.D.	l(csp) C.V.	Is (µm) Average	Is Range	Is S.D.	Is C.V.	L/l	Radiation (%) 3	4	5	3-4
173	J.K. Henry 18-IV-80	46	41-50	3.15	6.83	46	34-59	6.76	14.84	15	12-21	2.14	14.22	1.00	58.6	37.9	1.0	2.5
181	" "	45	40-54	2.47	5.49	45	40-54	5.42	12.02	14	13-16	1.82	14.04	0.99	50.0	50.0	---	---
185	" "	44	40-49	3.08	7.02	41	35-51	6.69	13.76	15	13-19	1.69	11.29	0.99	47.9	51.6	0.6	---
190	" "	42	36-47	2.49	5.81	45	32-54	5.30	11.80	13	11-14	0.93	7.25	0.95	70.4	25.9	3.7	---
288	J.K. Henry 30-V-80	43	37-50	3.04	7.01	40	36-59	4.58	11.37	14	12-16	0.82	6.69	1.08	64.1	32.0	3.9	---
79	Munday 26-VII-79	37	33-42	2.15	5.84	35	29-42	3.79	10.70	11	8-13	0.93	8.51	1.04	94.5	2.0	3.5	---

Field material

Source	L(csp) (µm)	l(csp) (µm)	l(ssp) (µm)	Is (µm)	Sp (µm)	L/l	Radiation 3
J.K. Henry 30-V-80	31	43	34	9	4, 5	0.73	X
" "	32	41	35	11	3	0.78	X
" "	32	46	36	10	4	0.69	X
" "	33	46	36	--	5	0.7	X
" "	31	36, 38*	32, 29*	9	2, 3	0.86, 0.81	X
" "	--	39, 42*	32, 33*	9	3, 4	---	X
" "	30	37, 39*	32	9	2, 3	0.81, 0.76	X

*Dichotypical cells

continued

TABLE 29 (cont'd)

Field material

Source:	L(csp) (μm)	l(csp) (μm)	l(ssp) (μm)	Is (μm)	Sp (μm)	L/l	Radiation 3
J.K. Henry 30-V-80	30	37, 39	32	9	2, 3	0.81, 0.76	X
" "	33	44	36	10	--	0.74	X
" "	30	37	33	9	3, 4	0.81	X
" "	31	37	33	10	2	0.83	X
" "	32	45	35	11	4	0.70	X
" "	--	48, 41*	37, 36*	--	2, 3, 5	0.70	X
" "	36	42, 48*	37	11	6, 2	0.85, 0.74	X
" "	32	39	32	10	2, 4	0.82	X
" "	--	42, 34*	32	10	5, 1	--	X

*Dichotypical cells

Plate 17

<u>Std.</u> <u>mucronatus</u> var. <u>delicatulus</u>

SEM photographs

1, 2. Clone HC 79, isolated semicells in front view showing a long isthmus

3-5. Clone HC 173

3. Abnormal semicell in vertical view

4. Tetraradiate semicell with rounded angles in basal view

5. Vertical view showing pores with dry mucilage

6, 7. Clone HC 181

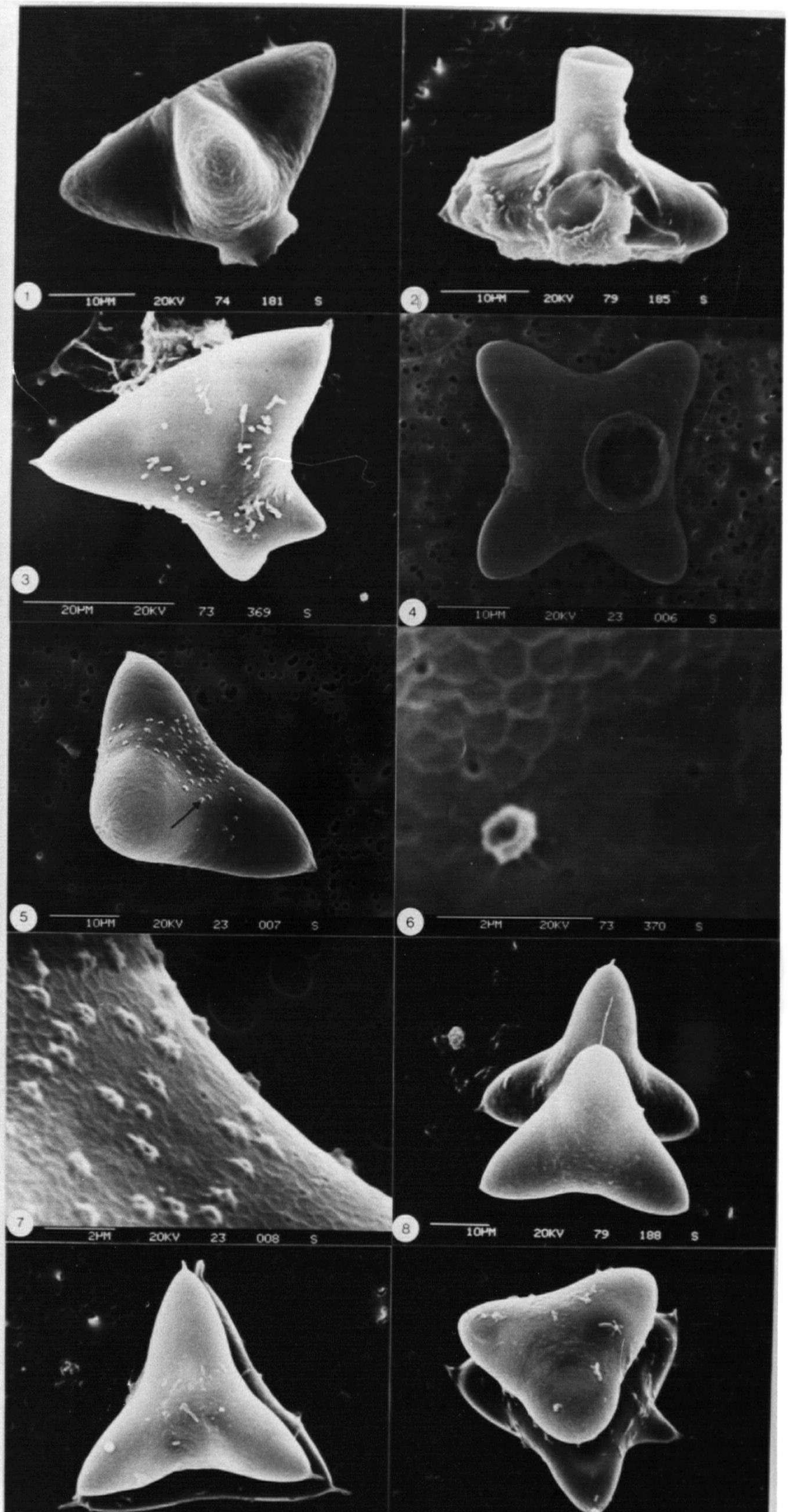
6. Detailed view of the cell wall showing the hexagonal pattern and the pores; the arrow indicates a pore lined by dry mucilage

7. Detailed view of the pores

8, 9. Clone HC 79; cells in vertical view showing the variation in the angular spines or mucros

10. Clone HC 173; abnormal cell in vertical view

365A



1 10µM 20KV 74 181 S
2 10µM 20KV 79 185 S
3 20µM 20KV 73 369 S
4 10µM 20KV 23 006 S
5 10µM 20KV 23 007 S
6 2µM 20KV 73 370 S
7 2µM 20KV 23 008 S
8 10µM 20KV 79 188 S
9 10µM 20KV 79 186 S
10 20µM 20KV 73 368 S

T. STAURODESMUS DEJECTUS VAR. DEJECTUS

Std. dejectus (Brébisson ex Ralfs 1848) Teiling 1954 (p. 128); 1967 (p. 529; pl. 9, fig. 1-5, 7) Pl. R Fig. 8:

Syn.: St. dejectum Brébisson in Meneghini 1840 (p. 227), 1856 (p. 142)

Ralfs' (1848; p. 121, pl. 20 fig. 5; Pl. R Fig. 8) description is:

> "...segments smooth, lunate or elliptic; constricted portion very short; end view with inflated awned lobes.
> " α Segments externally lunate, awns directed outwards.
> " β Segments elliptic, awns parallel.
> " γ Awns converging.
>
> "Frond smooth, deeply constricted at the middle; segments broader than long, lunate or elliptic, awned, the awns subulate, varying in length and direction. The end view shows three or four mammillate lobes or rays, each terminated by a hair-like mucro or awn...
>
> " Staurastrum dejectum and a few other species form a distinct group, distinguished by their smooth fronds, the peculiar inflated or mammillate form of their angles, or rather lobes, in the end view, and by their terminal awn-like spines. In some respects they have more resemblance to the two plants placed in Arthrodesmus than to the other species of this genus. Should any change be required, I would rather remove them to Arthrodesmus than unite that genus with Staurastrum.
>
> " Staurastrum dejectum is larger than S. cuspidatum, its spines are shorter, and its segments are connected either without a band or by a very short one.
>
> "Length of frond 1/833 of an inch; breadth 1/757; breadth at constriction 1/2732; length of awn 1/3937; diameter of sporangium 1/714; length of spine of sporangium from 1/2500 to 1/1250."

Ralfs' concept did not follow de Brébisson's original idea

(1835; in Meneghini 1840) and was later rectified by de Brébisson (1856; p. 142; see under Std. mucronatus var. delicatulus). Since Ralfs' description does not correspond to the true description, that of Teiling is given here:

> "Facies 3, 4. Semicell cup-shaped with divergent, rarely vertical short spines, isthmus elongate, apex mostly slightly convex with concave margins, sinus open and rounded at the isthmus, zygospore spherical, spinous.
>
> "Dim. 10-20 x 16-27 x 5-10 μ, formae majores 24-40 x 19-36 x 5-10 μ. Zygospore diam. c. 23 μ ssp.
> "Distr. ubiquitous.
> "Facies 3."

Std. dejectus is a common species which I found in Como, Lost, Munday and J.K. Henry Lakes. In Stein and Borden (unpublished), there are 31 records of the type species including Jacobs and Munday Lakes. Variety apiculatus counts 26 records including Jacobs, Munday and Como Lakes.

Clones examined: HC 306 from Munday Lake, 7-VI-80; HC 336, 340, 364, 365, 367, 399 from Como Lake, 27-VI-80; HC 419 from Como Lake 18-VII-80 (Table 30).

In both field and clonal material variation is observed in the length of the spines which are sometimes totally wanting (Pl. 18 Fig. 1-4). In one field record from J.K. Henry Lake (Table 30) the four angles are different: at three angles, the spines are 1, 3 and 5 μm respectively and one angle has rounded angles without spines. The direction of the spines also varies from upwardly directed (Pl. 18 Fig. 1; Pl. O Fig. 2) to slightly diverging (Pl. P Fig. 4). This variation is important since the apically inserted vertical spines represent the main distinction between Std. dejectus and Std. dejectus var. apiculatus (Brébisson) Teiling. The sinus is open, rounded and more or less elongated (Pl. P Fig. 2, 4, 6; Pl. O Fig. 4). The semicells are cup-shaped and the apex is flat or slightly convex.

In apical view, the sides are slightly concave (Pl. 18 Fig. 2). Some small variation in dimensions exists among the clones, clone HC 306 from Munday Lake and clone HC 419 from Como Lake being the smallest. Most cells of clonal culture are triradiate (Table 30), with up to 6.4% (clone HC 340) of tetraradiate cells. Only two dichotypical cells, with one semicell triradiate and the other tetraradiate, were observed (clone HC 419).

Most records of this species are as Staurastrum dejectum, since Teiling only described the genus Staurodesmus in 1948. Teiling 1967 (p. 524-531) traces a thorough historical survey of the species Std. dejectus. As discussed under Std. mucronatus var. delicatulus, Ralfs' interpretation of St. dejectum (Pl. R Fig. 3) is misleading. Teiling examines some unpublished drawings made by de Brébisson and on this basis, judges that only Ralfs' figure 5a (pl. 20; Pl. R Fig. 3b) was really St. dejectum, and other figures (5 b, c) belonged to St. mucronatum (see Teiling 1967, p. 525).

For many years, the concept of St. dejectum was very confused and this confusion may have been prompted by the interpretation given by West et al. (1923; p. 7, pl. 129 fig. 9-12). The Wests' illustration of St. dejectum (Pl. R

Fig. 7) shows long diverging spines and a widely open sinus, differing from Teiling's figures (Pl. R Fig. 8) of Std. dejectus which show shorter and upwardly directed spines. Teiling points out that a record of Std. dejectus without illustration has little meaning.

1. Proposed synonyms of Std. dejectus

Std. dejectus var. apiculatus (Brébisson) Teiling 1954

Std. dejectus forma β Croasdale 1957

a) Std. dejectus var. apiculatus (Brébisson) Teiling 1954 (p. 128); Teiling 1967 (p. 530; pl. 9 fig. 6)

Synonyms for this taxon include:

St. apiculatum Brébisson 1856 (p. 142; pl. 1, fig. 23) Pl. R Fig. 4

St. dejectum var. apiculatum (Brébisson) Lundell 1871 (p. 59)

Std. apiculatus (Brébisson) Lillieroth 1950 (p. 264)

Std. apiculatus (Brébisson) Florin 1957

Std. dejectus f.? apiculatus (Brébisson) Croasdale 1957 (p. 128; pl. 2 fig. 31).

De Brébisson's (1856) description is:

"S. parvulum, laeve, hemisomatiis turbinatis e dorso planis subconcavis, angulis rotundatis, spinula angulari brevi dejecta.

"Marais de Percy, près de Mézidon.

"Cette espèce est plus petite que le S. dejectum.

> Ses angles sont arrondis et portent un peu au dessous du sommet une très courte épine dirigée en dehors et par conséquent perpendiculaire au disque qui est plane, quelquefois même légèrement concave. Les sporanges sont couverts de pointes coniques à large base et souvent très obtuses."

According to de Brébisson, this species differs from St. dejectum by its smaller size and its spines which are inserted on the apical side of rounded angles and directed upwardly. As Teiling (1967) states, many true St. dejectum have been called St. apiculatum following the confusion on St. dejectum 's concept.

St. apiculatum was transferred to St. dejectum as variety apiculatum, by Lundell 1871 (p. 59). Since 1948, three authors have made the transfer of this taxon from Staurastrum to Staurodesmus. Florin (1957) transferred St. apiculatum to Std. apiculatum (sic). However, earlier, Lillieroth (1950; p. 264) had made the transfer. Croasdale (1957; p. 128) used the varietal rank in her text, but in the legend of her figure (pl. 2 fig. 31) she uses the name Std. dejectus f. apiculatus. Teiling (1967; p. 530) reports Croasdale's new combination as Std. dejectus f. apiculatus. His reference indicates that he established the taxon Std. dejectus var. apiculatus in 1955. In his bibliography there is no reference to Teiling 1955 and this was not found anywhere. Prescott et al. (1982; p. 179) credit the transfer to Teiling 1954.

Most illustrations compiled from the literature under the name apiculatum would be better called dejectum. The degree of divergence of the spines varies, and only Grönblad (1960;

fig. 152, 153) and Croasdale (1957; pl. 2 fig. 31) show short spines. Yamagishi and Kobayasi (1971, fig. 73) illustrate longer spines that are upwardly directed. Teiling (1967; p. 531) states that:

> "The single locality makes probable that Brébisson has found a local variation of dejectus, since I have among my figures found no desmid, that in all characters agree with Brébisson's."

Teiling (p. 525) reports de Brébisson's unpublished notes on St. apiculatum :

> "Voisin du dejectum dont il diffère par la taille plus petite, sa point (sic) courte et placée en dehors de l'angle arrondi. Perey, juillet 1847."
>
> "à Brimoy il se trouve avec des pointes très allongées et un peu flèchies (sic) en dehors. Il est aussi plus grand."

Based on these literature reports and the variation in the direction of the spines observed in clonal cultures, it is suggested that the characteristics of the spines are too variable to be used as a taxonomic criterion for this taxon. Lundell's decision to transfer St. apiculatum to var. apiculatum of St. dejectum was certainly wise, although it seems that the basic characteristics do not justify the varietal rank. Turner (1892) agrees that, "Brébisson's St. apiculatum is only a small form of his St. dejectum."

Variety apiculatus would be, in my opinion, better integrated as part of Std. dejectus.

b) Std. dejectus forma β Croasdale 1957 (p. 128; fig. 28) Pl. O

Fig. 3:

Croasdale's figure shows striking resemblance to a cell from clone HC 340 (Pl. P Fig. 6). Since the length or presence of spines is a variable characteristic, there is no need for a new forma based on those.

An important number of varieties and forms of Std. dejectus (as St. dejectum) have been described, and many have been later transferred to other taxa or rejected as true taxonomic units. West et al. (1923) note in their index, 13 varieties or forms of St. dejectum not including the type species. Of these, they accept only three. Since the taxonomy of Std. dejectus has been so confused and the object of constant changes, only taxa for which the original publication was available are reported here.

2. An additional infraspecific taxon of Std. dejectus

The following taxon is accepted as a valid variety of Std. dejectus

Std. dejectus var. borealis Croasdale 1965 (p. 328; pl. 7, fig. 4-7) Pl. P Fig. 5:

> "Cellulae 38-45 μ x 33-46 μ sine spinis, x 36-60 μ cum spinis, isth. 9-11 μ, spinae 4-9 μ long. Cellulae tetragonae, isthmus satis elongatus, sinu rotundo; apex valde convexus; spinae crasse divergentes, lineam marginis ventralis continuantes aut aliquantulum sursum curvatae; Varietas a var. dejecto differens quod maior, et apex convexior et spinae crassiores divergentioresque; et quod semicellulae semper tetragonae..."

This taxon was first found in the Northwest Territories. It is bigger than Std. dejectus and also differs in its more convex apex and stouter and more diverging spines. According to Croasdale, it is always tetraradiate and should be compared with her forma *a* (Croasdale 1957; p. 128, fig. 27; Pl. O Fig. 8). Teiling 1967 (p. 531) recognizes it as a good variety of Std. dejectus. Coesel (1979; p. 394, pl. 22 fig. 6, 7) illustrates two specimens of var. borealis with different degree of elongation of the sinus. He does not give any dimensions.

2. Uncertain taxa of Std. dejectus

The status of the following taxa is uncertain. Varieties subglabrum and paucidens have not been treated by Teiling (1967) and their validity is questioned. The two others have been published only as provisory names or without any name.

St. dejectum var. subglabrum Grönblad 1920

St. dejectum var. paucidens Beck-Mannagetta 1931

Std. dejectus f. angustus Teiling 1954

Std. dejectus f. *a* Croasdale 1957

a) St. dejectum var. subglabrum Grönblad 1920 (pl. 3; fig. 105, 106) Pl. O Fig. 5:

> "Cellulae a fronte visae ut in S. deject. var. Debaryano (Jacobs.) Nordst. (syn.= S. deject. apud De Bary, Unters. üb. Conj. t. 6 f. 25-32), sed a vertice visae ut in S. glabro (Ehr.) Ralfs (apud West, N.-Amer. t. 16 f. 8). Cfr. etiam S. deject. v. Debaryanum forma Borge, Vestergötl. t. 3 f. 36, quae forma a Westio postea(s. Borge in litt.) ad S. glabrum translata est. Semicellulae a fronte visae subtriangulares angulis spuperioribus primum

divergentibus, tum subito in spinas longas convergentes excurrentibus, lateribus (inferioribus) convexis, dorso quasi concavo sed medio conspicue etsi levissime tumido velut triundulato; a vertice visae triangulae lateribus rectis angulis spinis longis rectis instructis. Cum spin. long. 21,5, lat. 41,4, isthm. 7,5, sine spin. lat. 16,1, long. spinae max. 13,8 μ."

This variety was first found in Finland and does not appear to have been reported since. Teiling (1967) does not discuss it. It differs obviously from St. dejectus in the shape of its semicells and the direction of its spines. It is similar to Std. dickiei (Ralfs) Lillieroth var. rhomboideus (W. et G.S. West) Lilieroth 1950 (p. 264), but is more compressed and has longer spines than stated and figured by West and West 1903 (p. 545; pl. 16, fig. 9).

b) St. dejectum var. paucidens Beck-Mannagetta 1931

"Aculei in angulis aspectus verticalis 1-2."

This "variety" was noted as var. paucidens "n.f.". The laconic description without illustration, does not state any characteristic to justify the naming of a new variety or forma. No further records were found.

c) Std. dejectus forma angustus Teiling 1954 (p. 129):

This forma was created by Teiling as a provisory name to distinguish cells with an acute sinus. None of the cells observed in the present study had an acute sinus. Croasdale (1957, p. 128; fig. 29, 30) figures, as f. angustus, two specimens with a broad isthmus and acute sinus. Prescott *et al.* (1982; p. 181) place it as a synonym of *St. dejectum* var. *patens* Nordstedt (see later).

d) *Std. dejectus* forma *a* Croasdale 1957 (p. 128; fig. 27) Pl. O Fig. 8:

The features of this forma from Alaska, which is distinguished by its larger size (40 x 40 μm csp) and more convex apex, have not been observed in clonal or field material. Croasdale states that it is a "doubtful form".

3. Related taxa to *Std. dejectus*

The following *St. dejectum* taxa have been transferred to *Std. patens* and this conclusion is accepted for the time being.

Std. patens (Nordstedt) Croasdale 1957

Std. patens f. *inflatus* (W. West) Teiling 1967

a) *Std. patens* (Nordstedt) Croasdale 1957 (p. 134; pl. 2, fig. 32-34)

Basionym: *St. dejectum* var. *patens* Nordstedt 1888 (p. 39; pl. 4, fig. 16) Pl. R Fig. 5:

Nordstedt's description is:

> "Forma aculeis (parvis) patentibus (divergentibus, non parallelis), semicellulis isthmo non elongato connatis. Cum figura superiora sinistra tab. 5, fig. 51 in Denot. Desm. Ital. fere prorsus congruit.
>
> "Long. 23 μ; lat. sin. acul. 24 μ; lat. isthm. 6 μ; long. acul. ad 2,5 μ."

This taxon was first found in New Zealand and has since been reported from different regions of the world. Croasdale (1957) renamed it Std. patens (Nordstedt) Croasdale. The semicells have more convex sides than Std. dejectus and an acute sinus with short isthmus. The spines are short and divergent. Those characteristics appear to warrant the segregation of Std. patens as a different species, although observations of figures of Std. patens or St. dejectum var. patens in the literature show variations which often make it difficult to distinguish between Std. dejectus and Std. patens.

West et al. stress the presence of an acute-angled sinus (1923; p. 9, pl. 130 fig. 2). In another figure (pl. 130 fig. 2), the sinus may be interpreted as slightly rounded. This has probably led to misinterpretation of the taxon. For example, Grönblad (1960; p. 154) and Taylor (1935a; pl. 33, fig. 1), illustrate cells with obviously rounded sinus and slightly elongated isthmus. Förster (1965, pl. 9 fig. 18) and Coesel (1979, pl. 22 fig. 11) represent a more or less rounded sinus similar to that in West et al. (1923; pl. 130 fig. 2). Coesel notes that his specimens of Std. patens are not always easily distinguishable from Std. dejectus. Prescott et al. (1982; p. 181) retain it as var. patens of St. dejectum.

b) Std. patens f. inflatus (W. West) Teiling 1967 (p. 544; pl. 11, fig. 25).

Basionym: St. dejectum var. inflatum W. West 1892a (p. 170; pl. 22, fig. 11) Pl. P Fig. 1:

W. West's description is:

"Var. multo major, semicellulis ellipticioribus et inflatis, spinis brevioribus (extrorsum versis).

"Long. sine spin. 43 μ; lat. sine spin. 52 μ; lat. isthm. 12 μ."

This taxon first found in the West of Ireland was renamed forma _inflatus_ of _Std. patens_ by Teiling (1967; p. 544). Prescott _et al._ (1982; p. 180) retain it as _St. dejectum_ var. _patens_. It differs from _Std. patens_ by its more inflated cells and narrow sinus, variation which may not justify a distinct taxon.

TABLE 30

CELL DIMENSIONS AND RADIATION OF STD. DEJECTUS
(Clonal cultures; N=see Materials and Methods; S.D.=Standard deviation;
C.V.=Coefficient of variation. Field specimens: N=1; X=presence)

Clonal cultures

Clone HC	Source	L(csp) (μm) Average	Range	S.D.	C.V.	l(csp) (μm) Average	Range	S.D.	C.V.	Is (μm) Average	Range	S.D.	C.V.	L/l	Radiation (%) 3	4	3-4
306	Munday 7-VI-80	22	20-27	2.12	9.69	24	20-28	1.85	8.67	8	6-8	0.57	7.39	1.02	98.6	1.4	---
336	Como 27-VI-80	26	24-28	1.27	4.87	26	22-29	1.60	6.08	8	7-9	0.65	8.00	0.98	100.0	---	---
340	" "	26	22-35	3.14	11.93	26	22-41	4.17	16.86	8	7-11	1.09	13.28	1.01	93.5	6.4	---
364	" "	25	22-27	1.21	4.83	25	20-28	1.73	6.88	8	7-8	0.45	6.82	0.99	99.3	0.7	---
365	" "	26	25-28	1.02	3.82	27	24-32	1.62	6.02	8	7-9	0.65	6.72	0.97	100.0	---	---
367	" "	27	25-29	1.40	6.11	28	23-32	1.81	6.89	8	7-9	0.68	8.24	0.98	98.4	0.6	---
399	" "	25	23-26	1.39	5.54	25	23-26	1.30	5.19	8	7-9	0.50	6.61	1.00	100.0	---	---
419	Como 18-VII-80	24	20-27	2.44	9.98	24	19-27	1.79	7.57	7	5-8	2.44	9.98	1.03	98.6	---	1.4

Field material

Source	L(csp) (μm)	L(ssp) (μm)	l(csp) (μm)	l(ssp) (μm)	Is (μm)	Sp (μm)	L/l	Radiation 3
Lost 5-IX-79	31	27	28	28	7	4, 2*	1.10	X
J.K. Henry 18-IV-80	26	--	26	26	6	1, 3*	1.00	X
J.K. Henry 30-V-80	21	21	24	21	6	--	0.87	X
" "	25	21	21	21	6	5, 3, 1, 0*	1.05	X
" "	23	20	22	19	6	3, 4*	1.05	X

*Dichotypical cells

continued

TABLE 30 (cont'd)

Field material

Source	L(csp) (μm)	L(ssp) (μm)	l(csp) (μm)	l(ssp) (μm)	Is (μm)	Sp (μm)	L/l	Radiation 3
J.K. Henry 30-V-80	24	24	24, 23*	23	6	1, 4	1.00, 1.04	X
Como 16-V-79	28	21	24	24	5	--	1.15	X
Como 18-VII-80	26	17	21	18	5	5, 4	1.25	X
Como 11-X-80	--	--	21	19	6	4	--	X

*Dichotypical cell

Plate 18

SEM photographs

1-4. Std. dejectus var. dejectus, clone HC 340

1. Two semicells, the left one in vertical view without angular spines and the right one in front view with upwardly directed spines

2. Semicell in basal view without angular spines

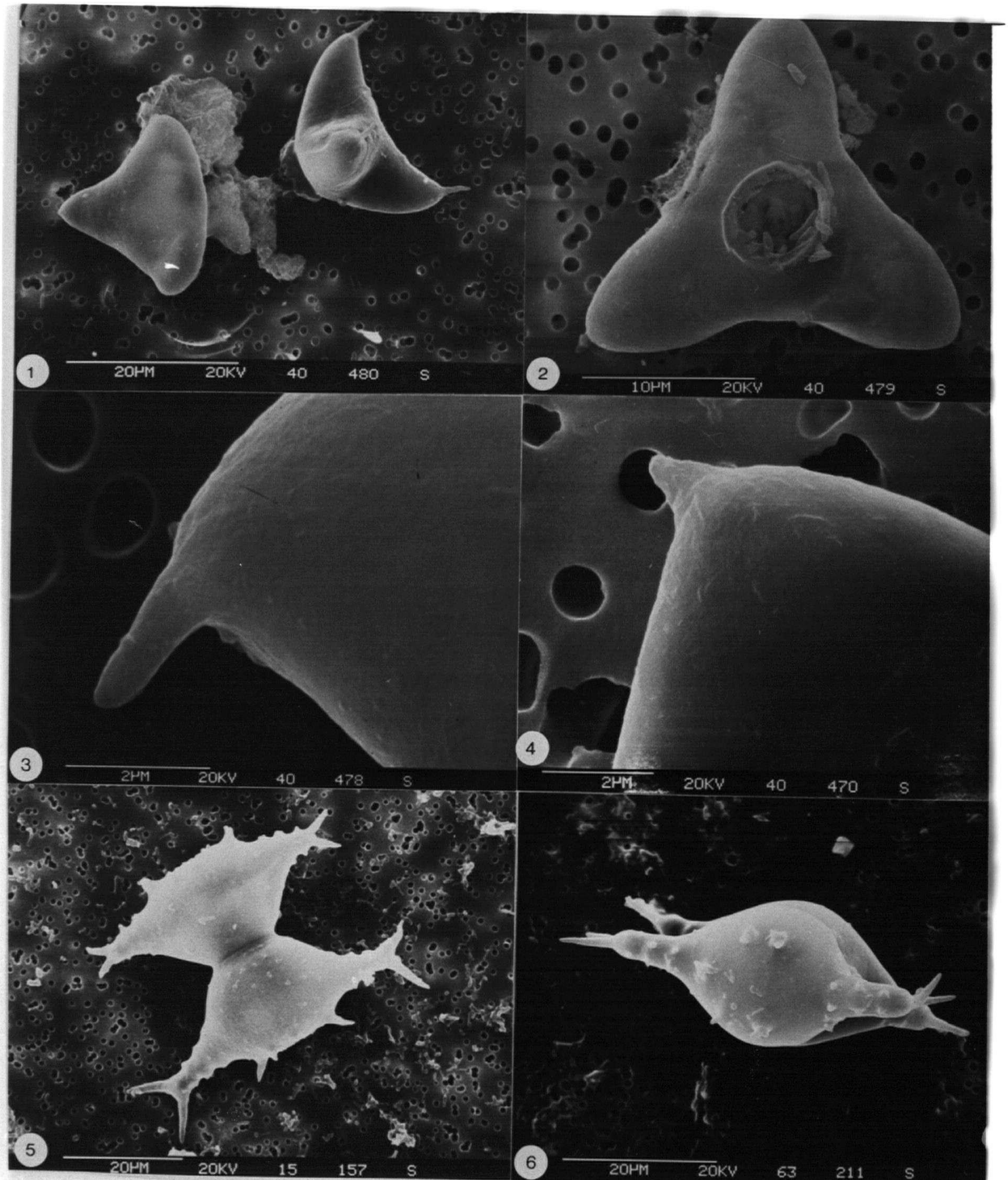
3, 4. Detail of angles showing the variation in the length of the angular spines

5, 6. St. grallatorium var. forcipigerum, clone HC 63

5. Cell in front view

6. Cell in vertical view

380A


1
20PM 20KV 40 480 S
2
10PM 20KV 40 479 S
3
2PM 20KV 40 478 S
4
2PM 20KV 40 470 S
5
20PM 20KV 15 157 S
6
20PM 20KV 63 211 S

VI. SUMMARY AND CONCLUSION

A. SUMMARY

The present study is a contribution toward a better knowledge of the genera Staurastrum (St.) and Staurodesmus (Std.). It examined critically a number of taxa found in a definite geographic area, the lower Fraser Valley (British Columbia, Canada). Field material, clonal culture material and literature reports were investigated. The four main study sites were characterized physico-chemically (pH, temperature, irradiation, alkalinity, calcium, dissolved oxygen, nitrate, phosphate). Morphological variation and growth rate in different environmental conditions (media, irradiation, temperature, pH) were followed in one clone (St. inflexum, clone HC 18). Observations of morphological variation were carried out with a SEM and a light microscope. Dimensions and radiation of field and clonal material were measured. The standard deviation and coefficient of variation of cell dimensions were calculated for clonal cultures. Original publications of the taxa in culture, infraspecific and related taxa were compared with the material studied and showed that many taxonomic characteristics are not stable. The taxa examined and the changes proposed are listed hereafter.

1. Staurastrum brebissonii (Brébisson) Archer in Pritchard 1861

   Proposed synonyms:

   St. brebissonii f. minor Boldt 1888; var.

brevispinum W. West 1892

St. erasum Brébisson 1856

Other infraspecific taxa:

St. brebissonii var. *heteracanthum* W. et G.S. West 1896; var. *paucispinum* Smith 1922; var. *truncatum* Grönblad 1926; var. *laticeps* Grönblad 1942; var. *brasiliense* Grönblad 1945; var. *curvispinum* Grönblad 1945; var. *maximum* Cedercreutz 1932

2. *St. gladiosum* Turner 1885

Proposed synonyms:

St. breviaculeatum Smith 1924 (*St. breviaculeatum* var. *karelicum* Grönblad 1936; var. *macracanthum* Scott et Grönblad 1957)

St. claviferum W. et G.S. West *sensu* Bourrelly 1966

Other infraspecific taxa:

St. gladiosum var. *longispinum* Turner 1892; var. *delicatulum* W. et G.S. West 1900.

Uncertain infraspecific taxon:

St. gladiosum f. *ornata* Laporte 1931

Related taxa:

St. teliferum Ralfs 1848; var. *ordinatum* Börgesen 1894; var. *subteliferum* (Roy et Bisset) Förster 1970

3. *St. alternans* Brébisson ex Ralfs 1848

Proposed synonyms:

St. alternans var. *subalternans* Maskell 1888

<u>St.</u> <u>punctulatum</u> f. <u>ellipticum</u> Lewin 1888

Other infraspecific taxa:

<u>St.</u> <u>alternans</u> var. <u>pulchrum</u> Wille 1879; var. <u>minus</u> Turner 1892; var. <u>basichondrum</u> Schmidle 1898; var. <u>basichondrum</u> f. <u>tetragonum</u> Croasdale et Grönblad 1964; var. <u>divergens</u> W. et G.S. West 1902; var. <u>spinulosum</u> Irénée-Marie et Hilliard 1963

Related taxa:

<u>St.</u> <u>punctulatum</u> Brébisson ex Ralfs 1848; var. <u>subproductum</u> W. et G.S. West 1912; var. <u>striatum</u> W. et G.S. West 1912

4. <u>St.</u> <u>muricatum</u> Brébisson ex Ralfs 1848

Proposed synonyms:

<u>St.</u> <u>muricatum</u> var. <u>denudatum</u> Brébisson 1856

Other infraspecific taxa:

<u>St.</u> <u>muricatum</u> var. <u>acutum</u> W. West 1890; var. <u>borholmiense</u> Gutwinski 1890; var. <u>australis</u> Raciborski 1892; var. <u>subturgescens</u> Schmidle 1893

Uncertain infraspecific taxa:

<u>St.</u> <u>muricatum</u> var. <u>trapezicum</u> Gutwinski 1890; var. <u>turgescens</u> Schmidle ?; var. <u>dimidiatum</u> Comère 1901

Related species:

<u>St.</u> <u>hirsutum</u> (Ehrenberg) Brébisson ex Ralfs 1848

<u>St.</u> <u>botrophilum</u> Wolle 1881

<u>St.</u> <u>trapezicum</u> Boldt 1888

<u>St.</u> <u>arnellii</u> Boldt 1885

5. St. *avicula* Brébisson ex Ralfs 1848

Proposed synonyms:

St. *avicula* var. *brevispinum* Harvey 1892; var. *subarcuatum* (Wolle) W. et G.S. West 1894; var. *subarcuatum* f. *quadrata* Irénée-Marie 1957; var. *verrucosum* W. West 1892

Closely Related taxa:

St. *denticulatum* (Nägeli) Archer in Pritchard 1861

St. *lunatum* Ralfs 1848; var. *subarmatum* W. et G.S. West 1894; var. *triangularis* Börgesen 1894; var. *planctonicum* W. et G.S. West 1903; var. *ovale* Grönblad 1942; var. *tvaerminneense* Grönblad 1942

Other infraspecific taxa:

St. *avicula* var. *aciculiferum* W. West 1889; var. *inerme* Irénée-Marie 1949

Uncertain varieties:

St. *avicula* var. *rotundatum* W. et G.S. West 1907; var. *exornatum* Messikommer 1929

Related species:

St. *caronense* Irénée-Marie 1949

St. *granulosum* (Ehrenberg) Ralfs 1848

6. St. *proboscideum* (Ralfs) Archer in Pritchard 1861

Synonyms:

St. *borgeanum* Schmidle 1898

St. *proboscideum* var. *productum* Messikommer 1942

St. *proboscideum* f. *minor* (Schmidle) Prescott, Bicudo et

Vinyard 1982

Proposed synonym for _St._ _proboscideum_ f. _minor_:

_St._ _borgeanum_ var. _parvum_ Messikommer 1949

Species related to _St._ _proboscideum_ f. _minor_:

_St._ _polymorphum_ Brébisson ex Ralfs 1848

Other infraspecific taxa:

_St._ _proboscideum_ var. _americanum_ Wolle 1882; var. _altum_ Boldt 1885; var. _brasiliense_ Börgesen 1890; var. _subglabrum_ W. et G.S. West 1890; var. _compactum_ (Grönblad) Prescott, Bicudo et Vinyard 1982

Uncertain infraspecific taxon

_St._ _proboscideum_ f. _javanica_ Nordstedt 1880

7. _St._ _sexcostatum_ Brébisson ex Ralfs 1848

Proposed synonym:

_St._ _sexcostatum_ var. _truncatum_ Raciborski 1885

_St._ _sexcostatum_ var. _productum_ W. West 1892

Synonym for _St._ _sexcostatum_ var. _productum_:

_St._ _aculeatum_ var. _ornatum_ forma _simplex_ Boldt 1888

An additional infraspecific taxon:

_St._ _sexcostatum_ var. _ornatum_ (Nordstedt) Förster 1963

Uncertain taxon:

_St._ _sexcostatum_ var. _depauperatum_ Gutwinski 1896

8. _St._ _crenulatum_ (Nägeli) Delponte 1877

Uncertain infraspecific taxa:

_St._ _crenulatum_ var. _continentale_ Messikommer 1927;

var. britannicum Messikommer 1927

An additional infraspecific taxon:

St. crenulatum var. continentale f. mammiferum Prescott et Scott 1952

9. St. manfeldtii Delponte 1877

Related taxa:

St. sebaldi Reinsch 1867

St. sebaldi var. ornatum Nordstedt 1873

Infraspecific taxon: St. sebaldi var. ornatum f. minor Bourrelly 1957

St. manfeldtii var. parvum Messikommer 1942

Other infraspecific taxa:

St. manfeldtii var. bispinatum Turner 1892; var. pinnatum Turner 1892; forma spinulosa Lutkemüller 1900; var. annulatum W. et G.S. West 1902

Uncertain infraspecific taxa:

St. manfeldtii var. planctonicum Lutkemüller ?; var. fluminense Schumacher et Whitford 1961

10. St. vestitum Ralfs 1848

Synonym:

St. anatinum f. vestitum (Ralfs) Brook 1959

Proposed synonyms:

St. vestitum var. splendidum Grönblad 1920; var. cedercreutzii Croasdale in Croasdale et Grönblad 1964

Other infraspecific taxa:

St. vestitum var. *diplacanthum* Rabenhorst 1868; var. *distortum* Wolle 1883; var. *denudatum* Nordstedt 1869; var. *ornatum* Istvanffi 1887; var. *semivestitum* W. West 1892; var. *subanatinum* W. et G.S. West 1902; var. *gymnocephalum* Scott et Prescott 1961

Uncertain intraspecific taxa:

St. vestitum var. *tortum* W. et G.S. West 1898; f. *minor* Schmidle 1898

11. *St. inflexum* Brébisson 1856

Proposed synonym:

St. brachycerum Brébisson 1856

St. cyrtocerum Brébisson ex Ralfs 1848 *sensu* Croasdale 1957, 1965, 1973

Related taxon:

St. cyrtocerum Brébisson ex Ralfs 1848

12. *St. tetracerum* (Kützing) Ralfs 1848

Proposed synonyms:

St. tetracerum f. *biradiata* Borge 1925; forma Borge 1936; f. *trigonum* Lundell 1871

Other infraspecific taxa:

St. tetracerum var. *undulatum* W. et G.S West 1895; var. *validum* W. et G.S. West 1897; var. *evolutum* W. et G.S. West 1905; var. *trigranulatum* W. et G.S. West 1907; var. *evolutum* f. *minor* Irénée-Marie 1957; var. *cameloides* Florin 1957; var. *maximum*

Messikommer 1966

Uncertain taxa:

St. tetracerum var. *subexcavatum* Grönblad 1921; f. *tetragonum* W. et G.S. West 1897; var. *tortum* (Teiling) Borge 1921

13. *St. furcigerum* (Ralfs) Brébisson 1856

Proposed synonym:

St. furcigerum var. *reductum* W. et G.S. West 1906

St. furcigerum f. *eustephanum* (Ralfs) Nordstedt 1888

Proposed synonym for *St. furcigerum* f. *eustephanum*:

St. furcigerum var. *montanum* (Raciborski) W. et G.S. West *sensu* Croasdale 1957

Other infraspecific taxa:

St. furcigerum f. *armigerum* (Brébisson) Nordstedt 1888

Proposed synonym for *St. furcigerum* f. *armigerum*:

St. furcigerum var. *armigerum* f. *gracillimum* G.M. Smith 1924

St. furcigerum var. *pseudofurcigerum* (Reinsch) Nordstedt 1880; var. *montanum* (Raciborski) W. et G.S. West 1898; var. *crassum* Schröder 1897

Uncertain taxon:

St. furcigerum f. *longicornis* Schmidle 1898

14. *St. senarium* (Ehrenberg) Ralfs 1848

Proposed synonyms:

St. hantzschii Reinsch 1867; var. *cornutum* Turner 1892; *St. tohopekaligense* Wolle var. *nonanum* (Turner) Schmidle 1898 *sensu* Hughes 1950 and *sensu* Irénée-Marie 1939; f. *minus* (Turner) Scott et Prescott 1961 *sensu* Hinode 1971

Synonyms:

St. renardii var. *congruum* Raciborski 1890

St. hantzschii var. congruum (Raciborski) W. et G.S. West 1896; var. *depauperatum* Gutwinski 1892

St. intricatum Delponte 1877

Infraspecific taxa:

St. senarium var. *alpinum* f. *tatrica* Raciborski 1885; var. *nigrae-silvae* Schmidle 1893; var. *pseudowallichii* Grönblad 1920

Uncertain taxa:

St. senarium var. *bifarium* Schmidle 1898; var. *pumillum* Messikommer 1954

Related taxa:

St. furcatum (Ralfs) Brébisson 1856

Proposed synonym:

St. renardii Reinsch 1867

Uncertain taxon:

St. furcatum var. *iyaense* Hinode 1962

15. *St. arachne* Ralfs 1848

Infraspecific taxa:

St. arachne f. *minor* Boldt 1888; var. *arachnoides*

(W. West) W. et G.S. West 1902; var. _curvatum_ W. et G.S. West 1903; var. _gyrans_ (Johnson) Scott et Grönblad 1957; var. _sumatranum_ Scott et Prescott 1961

Uncertain infraspecific taxa:

St. arachne var. _basiornatum_ Capdevielle et Couté 1980; var. _basiornatum_ f. _pseudogyrans_ Capdevielle et Couté 1980

16. _St. ophiura_ Lundell 1871

Infraspecific taxa:

St. ophiura f. _nonaradiata_ W. et G.S. West 1890; var. _cambricum_ W. et G.S. West 1894; var. _subcylindricum_ Borge 1913; var. _perornatum_ Grönblad 1945; var. _coronatum_ Scott 1950; var. _horridum_ Scott 1950; var. _longiradiatum_ Scott 1950

Related taxon:

St. coronulatum Wolle var. _quebecense_ Irénée-Marie 1952

17. _St. pentacerum_ (Wolle) Smith 1922

Synonyms:

St. pentacerum var. _tetracerum_ (Wolle) Smith 1922; var. _tetracerum_ f. _major_ Smith 1922; var. _hexacerum_ Irénée-Marie 1957

An additional infraspecific taxon:

St. pentacerum f. _obesum_ Smith 1922

18. _St. grallatorium_ Nordstedt 1869

St. grallatorium var. forcipigerum Lagerheim 1885

Proposed synonym for St. grallatorium var. forcipigerum:

St. grallatorium var. forcipigerum f. longispinum Irénée-Marie 1952

Other varieties not discussed:

St. grallatorium var. americanum W. et G. S. West 1896; var. ungulatum Wolle 1881; var. floridanum Scott et Grönblad 1957; var. brasiliense (Grönblad) Förster 1969

19. Staurodesmus mucronatus (Brébisson) Croasdale 1957

Staurodesmus mucronatus var. delicatulus (G.S. West) Teiling 1967

Infraspecific taxa:

Std. mucronatus var. parallelus (Nordstedt) Teiling 1967; St. mucronatum var. rectum Turner 1892; var. rectum f. minor Turner 1892; Std. mucronatus var. subtriangularis (W. et G.S. West) Croasdale 1957; var. croasdaleae Teiling 1967; var. groenbladii Teiling 1967

An uncertain taxon:

St. mucronatum var. debaryanum Turner 1892

20. Std. dejectus (Ralfs) Teiling 1954

Proposed synonyms:

Std. dejectus var. apiculatus (Brébisson) Teiling 1954; forma β Croasdale 1957

An additional infraspecific taxon:

Std. dejectus var. borealis Croasdale 1965

Uncertain taxa:

St. dejectum var. subglabrum Grönblad 1920; var. paucidens Beck-Mannagetta 1931; f. angustus Teiling 1954; forma *a* Croasdale 1957

Related taxa:

Std. patens (Nordstedt) Croasdale 1957; f. inflatus (W. West) Teiling 1967

B. CONCLUSION

This study confirms that the numerous taxa of the genus Staurastrum differ significantly in their morphology and need to be subdivided into different genera. Palamar-Mordvintseva (1976) proposed scheme comprising four genera, Cylindiastrum, Comoastrum, Raphidiastrum and Staurastrum has yet to gain wide acceptance among desmidiologists. Previous attempts to split the genus Staurastrum into more workable units have been largely unsuccessful, except for Teiling's (1948, 1967) genus Staurodesmus. The main reason is that the authors have merely proposed new subdivisions, without providing detailed studies of the taxa involved, in contrast to Teiling's complete work.

I believe that a reevaluation of the numerous described taxa of Staurastrum is the first task to accomplish, but it is a major undertaking. Taxa have been described for slight morphological variation and are found in the most obscure publications. Many taxa have been described in the nineteenth or the beginning of the twentieth centuries. Sometimes no illustration is given, or if there is one, it may be so sketchy that the main features cannot be distinguished. Descriptions are often brief and lack observations on morphological variation. The fact that these are unicellular puts some limit on the number of characteristics that can be studied.

This reevaluation ideally encompasses culture, field and literature work. Clonal culture work provides genetically homogenous material but "unnatural" conditions. Comparison of variation in field material is useful to detect any abnormalities of the cells in culture. As described in the thesis for example, cells in culture tend to be stouter with shorter processes. Reference to original descriptions and illustrations is of prime importance as many taxa have been broadly interpreted. This approach was pursued with a limited number of species in my study.

More modern methods of investigation have not been extensively used with the desmids. A few observations were done with the SEM as noted in the introduction. This tool proved to be very useful in my study of morphological variation. Details of the cell structure are often difficult to distinguish with the light microscope, especially when the protoplasm is still present. However, use of the SEM is a time consuming and costly method of study which may explain why it has been so scarcely used by other workers. TEM work has provided useful data to the classification of desmids above the species level but is even more time consuming and costly. This means was not used in my study. Observation of the structure of the pore apparatus or other cell structures could reveal interesting differences between taxa. For example, I observed a previously unreported pore apparatus with an external protuberance in Staurastrum gladiosum var. gladiosum.

Study of chromosome numbers and level of ploidy may also be useful. Brandham (1965b) states that polyploidy occurs spontaneously in culture and is usually characterized by a bigger cell with a higher level of radiation. He notes that infraspecific and specific taxa are likely to have been described for polyploid cells of known taxa. Many varieties or forms called minor or major may enter this category.

Chemical taxonomy has not, to my knowledge, been used with desmids. However, it would be interesting to compare the chemical composition of such products as the mucilage secreted by different taxa of desmids. This could provide the basis for new taxonomic characteristics. Fritsch (1953) states that "one may even suspect that some of the finer granulations of the wall recorded in various species, may be nothing else than the consolidated mucilage excreted from the pores." In one clone of Cosmarium sp., I observed with the SEM that the cell wall had an hexagonal pattern which appeared to be formed by threads of mucilage. A literature search suggested that such a pattern was observed by other workers in field material and was the basis for the description of new taxa of Cosmarium and Xanthidium. Conjugation, when present, may also be studied in a chemical point of view. It has been shown in Chlamydomonas (Wiese 1965), that a chemical present on the flagellar tip acts as an attractant between cells. Although no conjugation was observed in my work, pairing of cells was observed (see Results and Discussion). It would be interesting to investigate the cause for this pairing. This work could be most valuable in understanding the process of sexual reproduction or lack of it in desmids.

Based on their own and other workers' cytological and biochemical studies, Stewart and Mattox (1975) devised a new classification of the Chlorophyceae. The Zygnematales were shown to have a particular mode of cytokinesis where the persistent interzonal spindle is eventually cut off by a furrow. In addition, they produce glycolate oxidase which is also found in all terrestrial plants, in contrast to the glycolate dehydrogenase present in most green algae. These features are shared with other groups of green algae which Stewart and Mattox grouped in the class Charophyceae. The conclusion reached for the Zygnematales is based on studies done with Spirogyra sp., Cosmarium botrytis, Closterium littorale and Micrasterias fimbriata Ralfs (Fowke and Pickett-Heaps 1969a, 1969b; Pickett-Heaps 1972; Pickett-Heaps and Fowke 1970; Tourte 1972). Other species and genera of Zygnematales, namely Staurastrum and Staurodesmus, have not been investigated. Such cytological and biochemical studies would be most valuable to establish the relationship among the Zygnematales or between them and other genera of green algae. Studies using other enzyme systems might help differentiate between taxa but nothing has been explored in this area.

My study is limited in that field material is too scarce and literature includes only 350 publications which could be gathered in the time and with the means available. It is interesting to note that in the bibliography of Prescott et al. (1982), there are only 340 publications cited; the most recent one was published in 1976. Observations of the conjugation process in Staurastrum and Staurodesmus would have been useful in order to evaluate the amount of genetic variation in a population. But the few reports found in the literature and the lack of success achieved in this study, make this difficult. However, some desmid taxa seem not to reproduce sexually. A classification based on the morphological features of the zygospore, used extensively for the filamentous Zygnematales, would thus be impractical.

In my opinion, the most valuable work that could be undertaken to complete my study, would be an investigation of material from other geographic areas and a more thorough literature search. Genetic, chemical and cytological studies could be very fruitful. However, the taxonomy of desmids at the specific and infraspecific levels is still based on morphology and relies mainly on work done a hundred years ago. I believe that it is first necessary to reevaluate the many taxa, on the basis of their morphological description, before attempting to use other means of classification; this has been the approach adopted by most modern desmid taxonomists.

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APPENDIX A

SAMPLING DATES FOR THE MAIN SITES

(X= Collection made)

Date		Jacobs Lake	Munday Lake	Lost Lake	Como Lake
1979,	16 May	---	X	---	X
	7 June	---	X	---	X
	14 June	X	X	---	X
	28 June	---	X	---	X
	6 July	---	---	---	X
	26 July	X	X	---	X
	1 August		X	---	X
	10 August	X	---	---	
	15 August		X	---	X
	22 August	X	X	---	X
	29 August	X	X	---	X
	5 September	---	X	X	X
	12 September	X	X	X	X
	30 September	---	X	X	X
	28 December	X	---	---	
1980,	25 January	X	X	---	X
	23 February	---	X	X	X
	23 March	X	X	X	X
	5 April	X	X	X	X
	26 April	X	X	X	X
	16 May	X	X	X	X
	7 June	X	X	X	X
	27 June	X	X	X	X
	18 July	X	X	X	X
	8 August	X	X	X	X
	30 August	X	X	X	X
	20 September	X	X	X	X
	11 October	X	X	X	X
	1 November	X	X	X	X
	22 November	X	X	X	X

APPENDIX A (cont'd)

Date	Jacobs Lake	Munday Lake	Lost Lake	Como Lake
1981, 11 January	X	X	X	X
1 February	X	X	X	X
22 February	X	X	X	X
13 March	X	X	X	X
7 April	X	X	X	X
27 April	X	X	X	X
17 May	X	X	X	X
9 June	X	X	X	X
30 June	X	X	X	X
22 July	X	X	X	X
11 August	X	X	X	X
28 August	X	X	X	X

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APPENDIX C - NUMERICAL LIST OF CLONES STUDIED

Clone HC	Taxon	Origin
2	Staurastrum proboscideum f. minor	Como Lake
4	" " "	"
6	" " "	"
12	St. avicula var. avicula	"
18	St. inflexum var. inflexum	"
20	St. avicula var. avicula	"
22	" " "	"
24	" " "	"
39	St. ophiura var. ophiura	Jacobs Lake
45	St. manfeldtii var. parvum	"
49	St. vestitum var. vestitum	"
58	St. avicula var. avicula	"
60	" " "	"
62	St. proboscideum f. minor	Como Lake
63	St. grallatorium var. forcipigerum	Jacobs Lake
66	St. vestitum var. vestitum	"
67	St. manfeldtii var. parvum	"
68	St. inflexum var. inflexum	Como Lake
69	St. pentacerum var. pentacerum	"
70	St. brebissonii var. brebissonii	Jacobs Lake
71	St. gladiosum var. gladiosum	Lost Lake
72	St. pentacerum var. pentacerum	Munday Lake
73	" " "	"
74	St. senarium var. senarium	"
78	St. pentacerum var. pentacerum	"
79	Staurodesmus mucronatus var. delicatulus	"
82	St. pentacerum var. pentacerum	"
83	" " "	"
85	" " "	"
87	" " "	"
91	" " "	"
93	" " "	"
97	" " "	"
98	" " "	"
99	" " "	"
100	" " "	"
102	" " "	"
110	St. gladiosum var. gladiosum	Lost Lake
115	St. arachne var. arachne	Jacobs Lake
132	St. gladiosum var. gladiosum	Lost Lake
133	St. pentacerum var. pentacerum	"
134	" " "	"
135	St. gladiosum var. gladiosum	"
148	" " "	"
150	St. ophiura var. ophiura	Jacobs Lake
151	St. vestitum var. vestitum	"
153	" " "	"
154	" " "	"

173	Std. mucronatus var. delicatulus	J.K. Henry Lake
181	" " "	"
185	" " "	"
190	" " "	"
205	St. alternans var. alternans	"
210	St. vestitum var. vestitum	Jacobs Lake
211	St. furcigerum var. furcigerum	"
213	St. furcigerum f. eustephanum	"
226	St. vestitum var. vestitum	"
242	St. proboscideum f. minor	Como Lake
271	St. vestitum var. vestitum	Jacobs Lake
272	" " "	"
275	St. muricatum var. muricatum	Munday Lake
276	" " "	"
278	St. proboscideum f. minor	Como Lake
283	St. muricatum var. muricatum	Munday Lake
284	" " "	"
288	Std. mucronatus var. delicatulus	J.K. Henry Lake
292	St. tetracerum var. tetracerum	Munday Lake
293	St. proboscideum f. minor	Munday Lake
294	St. inflexum var. inflexum	"
295	St. proboscideum f. minor	"
296	St. inflexum var. inflexum	"
297	" " "	"
301	St. proboscideum f. minor	"
302	St. inflexum var. inflexum	"
306	Std. dejectus var. dejectus	"
311	St. vestitum var. vestitum	Jacobs Lake
323	St. gladiosum var. gladiosum	Como Lake
325	St. avicula var. avicula	"
331	" " "	"
333	St. proboscideum f. minor	"
334	" " "	"
336	Std. dejectus var. dejectus	"
340	" " "	"
347	St. inflexum var. inflexum	"
354	St. avicula var. avicula	"
355	St. inflexum var. inflexum	"
362	St. proboscideum f. minor	"
363	" " "	"
364	Std. dejectus var. dejectus	"
367	" " "	"
368	St. tetracerum var. tetracerum	"
369	St. avicula var. avicula	"
370	St. proboscideum f. minor	"
378	" " "	"
381	" " "	"
383	St. avicula var. avicula	"
386	" " "	"
388	St. proboscideum f. minor	"
389	" " "	"

399	Std. dejectus var. dejectus	"
403	St. inflexum var. inflexum	Como Lake
408	St. muricatum var. muricatum	Lost Lake
409	" " "	"
410	" " "	"
411	" " "	"
414	" " "	"
415	" " "	"
417	" " "	"
418	" " "	"
419	Std. dejectus var. dejectus	Como Lake
420	St. avicula var. avicula	"
422	St. proboscideum f. minor	"
424	St. avicula var. avicula	"
427	St. sexcostatum var. productum	Jacobs Lake
430	" " "	"
433	St. proboscideum f. minor	VanDusen Botanical Garden
435	St. crenulatum var. crenulatum	"
437	St. inflexum var. inflexum	Como Lake
438	St. alternans var. alternans	Munday Lake
439	St. pentacerum var. pentacerum	"
448	" " "	"
468	St. vestitum var. vestitum	Jacobs Lake
469	St. sexcostatum var. productum	"
479	St. vestitum var. vestitum	Placid Lake
490	St. inflexum var. inflexum	Como Lake
492	St. muricatum var. muricatum	Lost Lake
496	St. gladiosum var. gladiosum	Munday Lake
497	St. pentacerum var. pentacerum	"

APPENDIX D - DRAWINGS, INCLUDING PUBLISHED ILLUSTRATIONS OF TAXA STUDIED

This appendix presents figures redrawn from original illustrations under the original name used, and some camera lucida drawings of material studied. No permission has been requested for official publication of the illustrations redrawn from other authors. Synonyms accepted in this study are given in parenthesis. Each measurement marker corresponds to 10μm; omission of the marker means that the author did not give any indication of dimensions or that these dimensions were not available. Most specimens are illustrated in front and vertical views; these are defined in Fig. 1 (section A of Introduction).

Plate A

(marker = 10 μm)

1. St. pilosum Brébisson 1856 (pl. 2, fig. 49) (= St. brebissonii var. brebissonii)

2. St. brebissonii Ralfs f. minor Boldt 1888 (pl. 2, fig. 45) (= St. brebissonii var. brebissonii)

3. St. brebissonii var. brevispinum W. West 1892b (pl. 9, fig. 26) (= St. brebissonii var. brebissonii)

4. St. erasum Brébisson 1856 (pl. 1, fig. 28) (= St. brebissonii var. brebissonii)

5. St. brebissonii var. heteracanthum W. et G.S. West 1896b (pl. 16, fig. 26)

6. St. brebissonii var. paucispinum Smith 1922 (pl. 10, fig. 25; pl. 11, fig.. 1-5)

7. St. brebissonii var. truncatum Grönblad 1926 (pl. 2 fig. 85, 86)

8. St. brebissonii var. laticeps Grönblad 1941 (pl. 4, fig. 16, 17)

9. St. brebissonii var. brasiliense Grönblad 1945 (pl. 9, fig. 198)

10. St. brebissonii var. curvispinum Grönblad 1945 (fig. 199)

11. St. gladiosum Turner 1885 (pl. 16, fig. 21)

12. St. breviaculeatum Smith 1924b (pl. 70, fig. 10-18) (= St. gladiosum var. gladiosum)

13. St. teliferum var. ordinatum Börgesen 1894 (pl. 2, fig. 23)

14. St. gladiosum var. longispinum Turner 1892 (pl. 17, fig. 2)

15. St. gladiosum var. delicatulum W. et G.S. West 1900 (pl. 412, fig. 14)

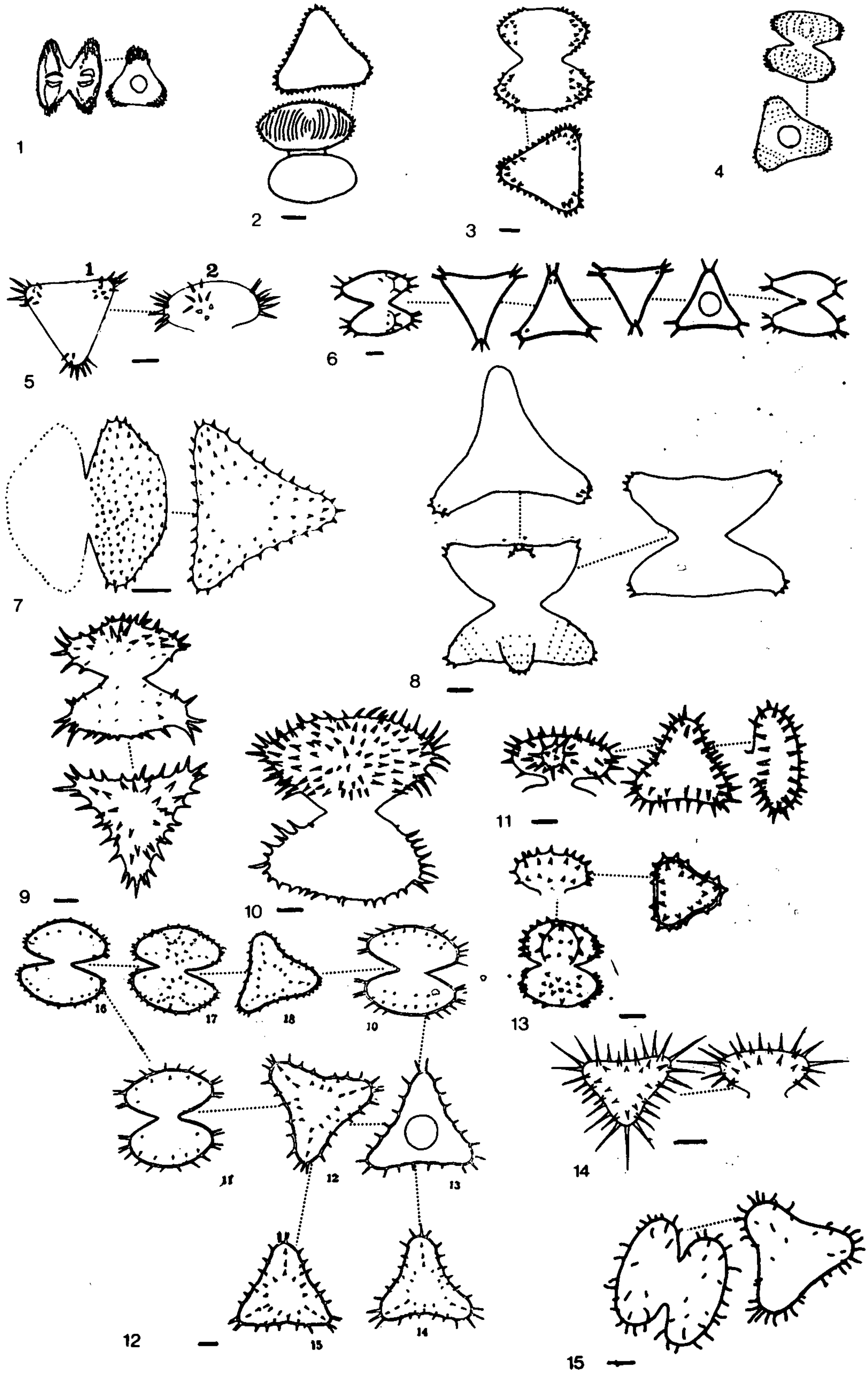
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Plate B

(marker = 10 μm)

1. St. breviaculeatum var. karelicum Grönblad 1936 (fig. 23, 24)

2. St. breviaculeatum var. macracanthum Scott et Grönblad 1957 (pl. 18, fig. 1, 2)

3. St. teliferum Ralfs 1848 (pl. 22, fig. 4; pl. 34, fig. 14) (a= zygote)

4. St. teliferum var. subteliferum (Roy et Bisset) Förster 1970 (pl. 27, fig. 16, 17)

5. St. subteliferum Roy et Bisset 1886 (pl. 268, fig. 1)

6. St. muricatum var. australis Raciborski 1892 (pl. 7, fig. 19)

7. St. claviferum W. et G.S. West 1896b in Bourrelly 1966 (pl. 20, fig. 5, 6) (= St. gladiosum var. gladiosum)

8, 9. St. gladiosum var. gladiosum, clone HC 71; cell in vertical view showing spine pattern

10. St. alternans Brébisson ex Ralfs 1848 (pl. 21, fig. 7)

11. St. alternans var. subalternans Maskell 1888 (pl. 4, fig. 38) (= St. alternans var. alternans)

12. St. punctulatum f. ellipticum Lewin 1888 in Krieger 1932 (pl. 15, fig. 10) (= St. alternans var. alternans)

13. St. alternans var. pulchrum Wille 1879 (pl. 13, fig. 66)

440A

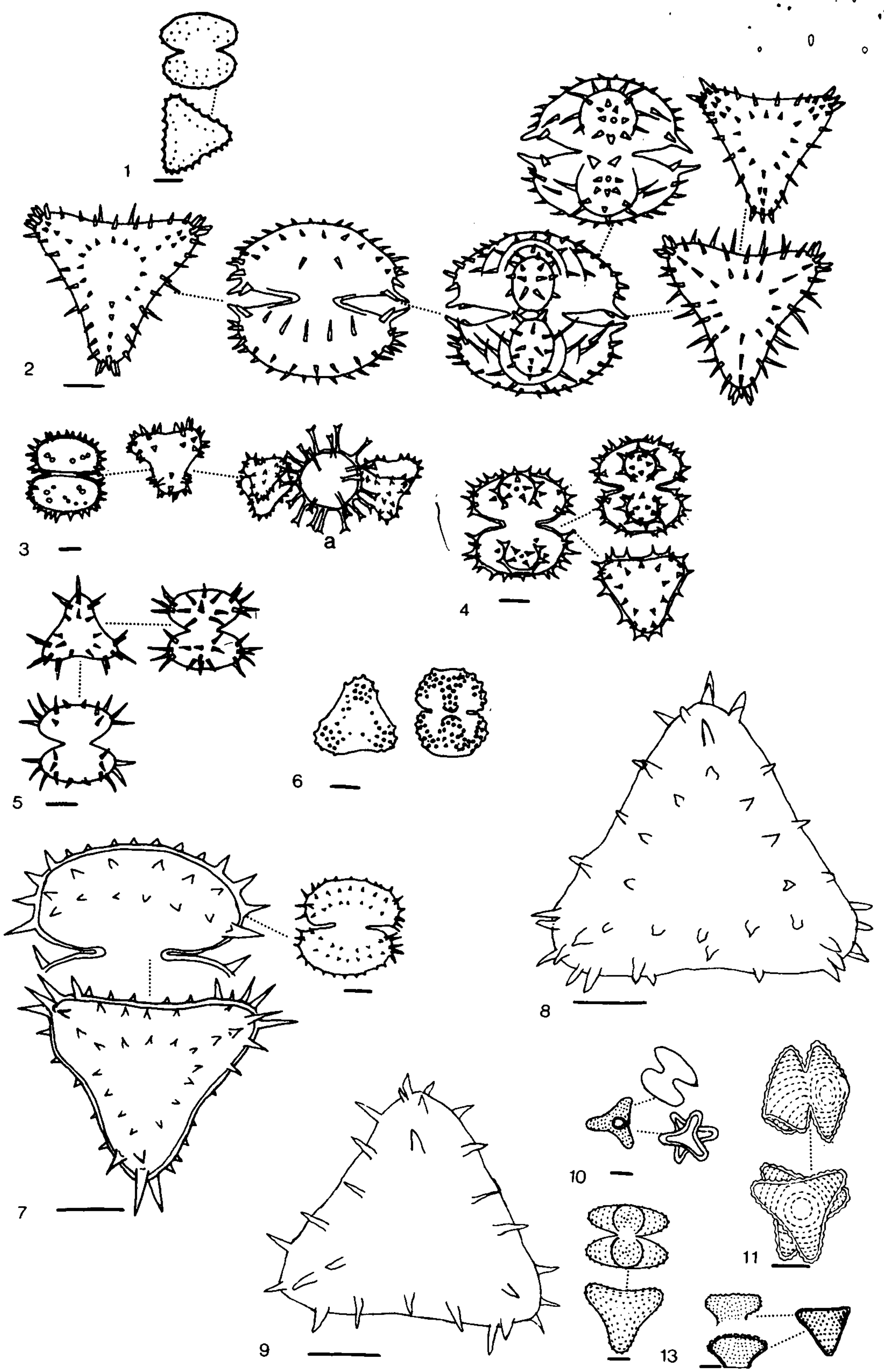

Plate C
(marker = 10 μm)

1. St. alternans var. minus Turner 1892 (pl. 16, fig. 6)

2. St. alternans var. basichondrum Schmidle 1898 (pl. 3, fig. 6)

3. St. alternans var. divergens W. et G.S. West 1902a (pl. 21, fig. 18)

4. St. alternans var. spinulosum Irénée-Marie et Hiliard 1963 (pl. 1, fig. 3)

5. St. alternans var. basichondrum f. tetragonum Croasdale et Grönblad 1964 (pl. 18, fig. 4, 5)

6. St. punctulatum Brébisson ex Ralfs 1848 (pl. 22, fig. 1) (4= smaller cell, 5= larger cell; see text)

7. St. punctulatum var. subproductum W. et G.S. West 1912 (pl. 127, fig. 15)

8. St. punctulatum var. striatum W. et G.S. West 1912 (pl. 128, fig. 5, 6)

9. St. muricatum Brébisson ex Ralfs 1848 (pl. 22, fig. 2)

10. St. muricatum in Ralfs 1845 (pl. 11, fig. 1)

11. St. muricatum var. acutum W. West 1890 (pl. 5, fig. 14)

12. St. muricatum var. subturgescens Schmidle 1893 (pl. 28, fig. 20)

13. St. hisurtum (Ehrenberg) Brébisson ex Ralfs 1848 (pl. 22, fig. 3) (a= zygote)

14. St. arnellii Boldt 1885 (pl. 5, fig. 21)

15. St. botrophilum Wolle 1881 (pl. 6, fig. 13)

16. St. trapezicum Boldt 1888 (pl. 2, fig. 46)

17. St. avicula var. inerme Irénée-Marie 1949a (pl. 1, fig. 1)

18. St. avicula Brébisson ex Ralfs 1848 (pl. 23, fig. 11)

19. St. avicula var. brevispinum Harvey 1892 (pl. 126, fig. 13) (= St. avicula var. avicula)

20. St. avicula var. verrucosum W. West 1892a (pl. 23, fig. 2) (= St. avicula var. avicula)

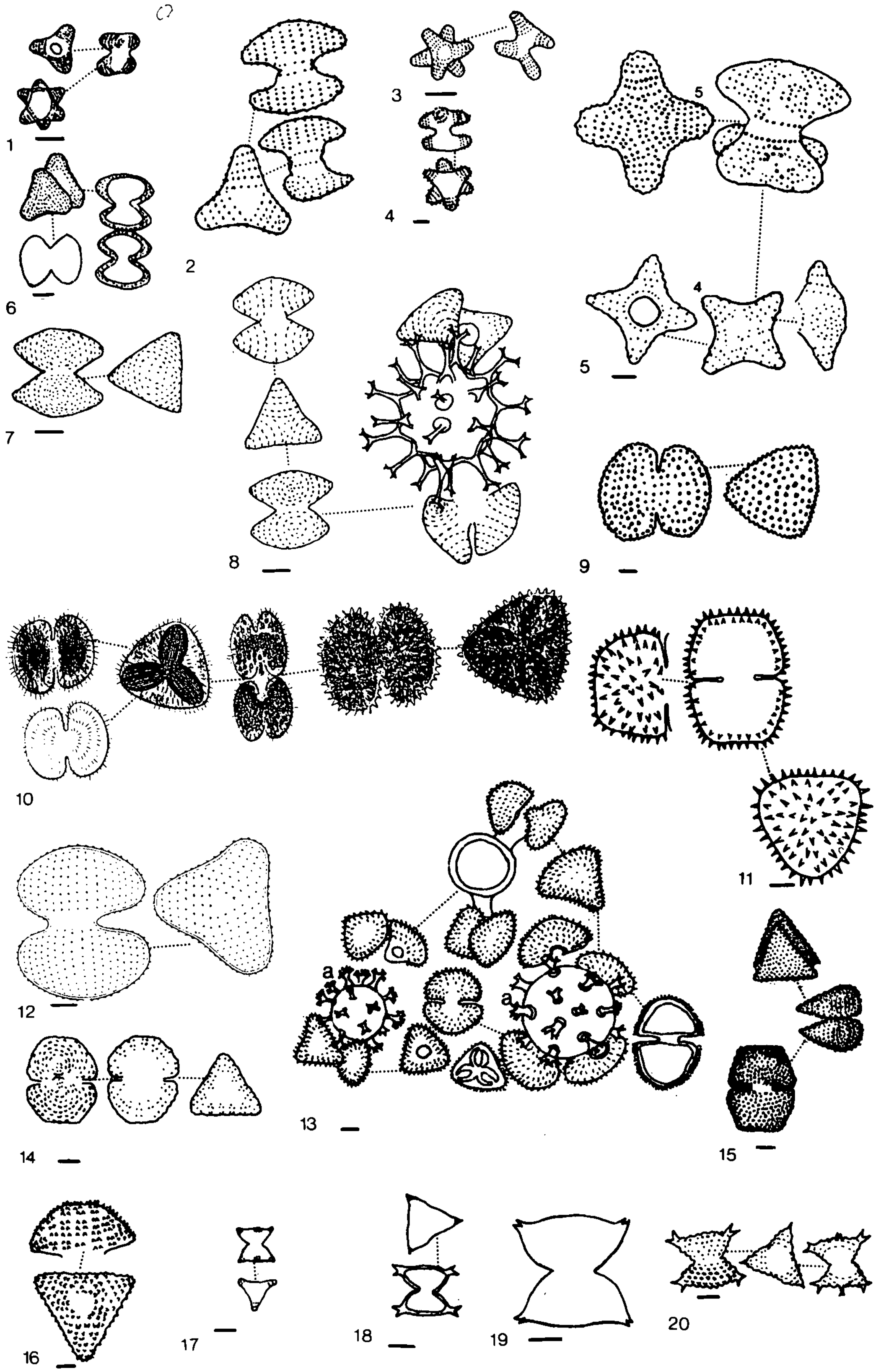
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Plate D

(marker = 10 μm)

1, 2. St. muricatum var. muricatum, clone HC 275; showing shape of the cell in front view.

3. St. subarcuatum Wolle 1880 (pl. 5, fig. D) (= St. avicula var. avicula)

4. St. avicula var. aciculiferum W. West 1889 (pl. 291, fig. 12)

5. St. avicula var. rotundatum W. et G.S. West 1907 (pl. 15, fig. 25)

6. St. avicula var. exornatum Messikommer 1929 in Coesel 1979 (pl. 25, fig. 5, 6)

7. St. avicula var. subarcuatum f. quadrata Irénée-Marie 1957 (pl. 1, fig. 3) (= St. avicula var. avicula)

8. St. caronense Irénée-Marie 1949 (pl. 1, fig. 3)

9. Phycastrum denticulatum Nägeli 1849 (pl. 8c, fig. 3) (= St. denticulatum var. denticulatum)

10. St. lunatum Ralfs 1848 (pl. 34, fig. 12)

11. St. lunatum var. subarmatum W. et G.S. West 1894 (pl. 2, fig. 47)

12. St. lunatum var. triangularis Börgesen 1894 (pl. 2, fig. 24)

13. St. lunatum var. planctonicum W. et G.S. West 1903 (pl. 16, fig. 11, 12)

14. St. lunatum f. Grönblad 1960 (fig. 208-212)

15. St. lunatum var. ovale Grönblad 1942 (pl. 5, fig. 1, 2)

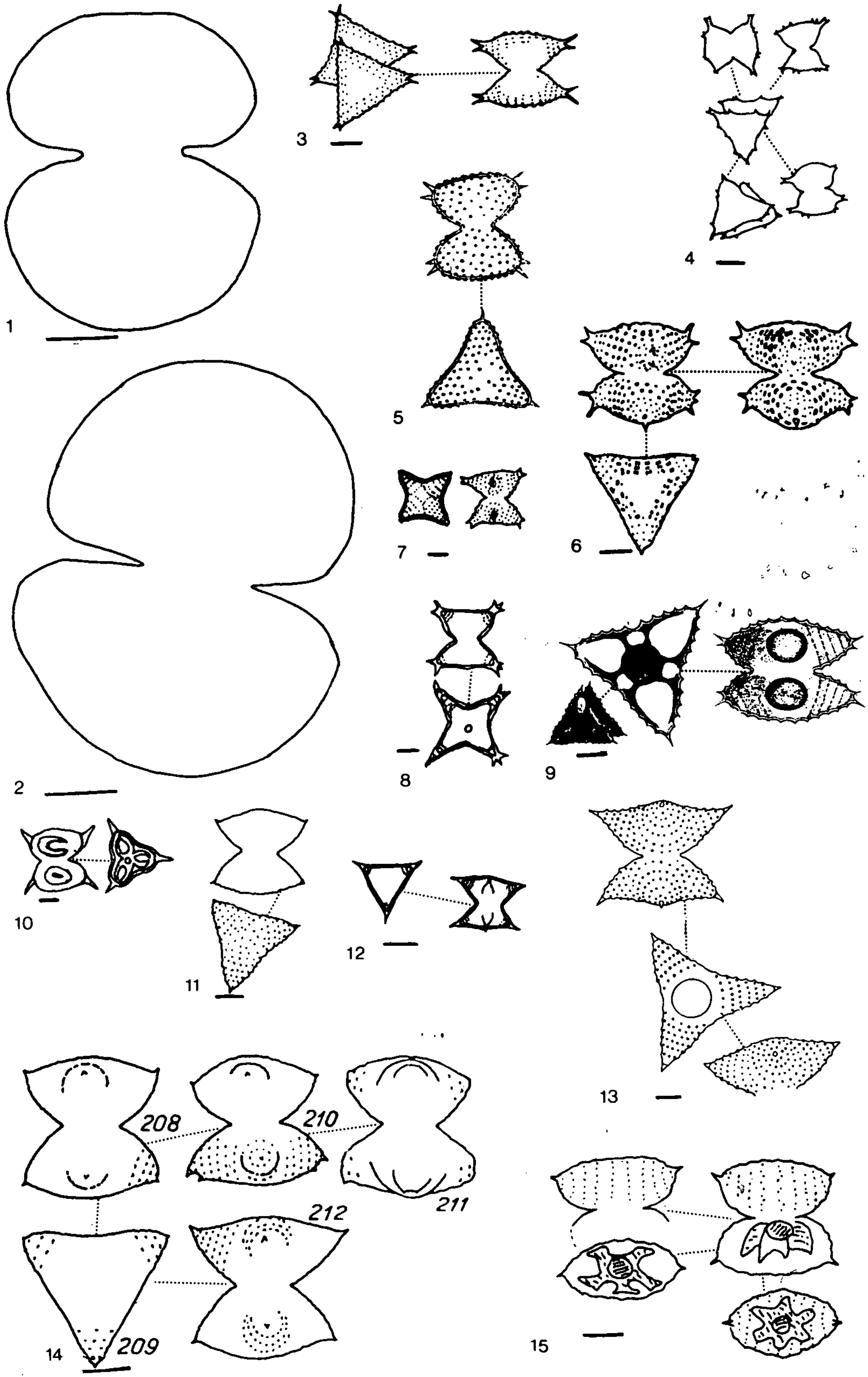
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Plate E

(marker = 10 μm)

1-9. St. avicula var. avicula, showing variation in angular spines and shape of the cells

1, 2. Clone HC 22

3. Clone HC 331

4. Clone HC 12

5. Como Lake 1-VIII-79

6. Clone HC 12

7. Clone HC 331

8. Clone HC 20

9. Clone HC 24

10. St. borgeanum Schmidle f. minor Schmidle 1898 (pl. 3, fig. 16) (= St. proboscideum f. minor)

11. St. borgeanum Schmidle 1898 (pl. 3, fig. 7) (= St. proboscideum var. proboscideum)

12. St. asperum var. proboscideum Ralfs 1848 (pl. 22, fig. 6; pl. 23, fig. 12)(= St. proboscideum var. proboscideum)

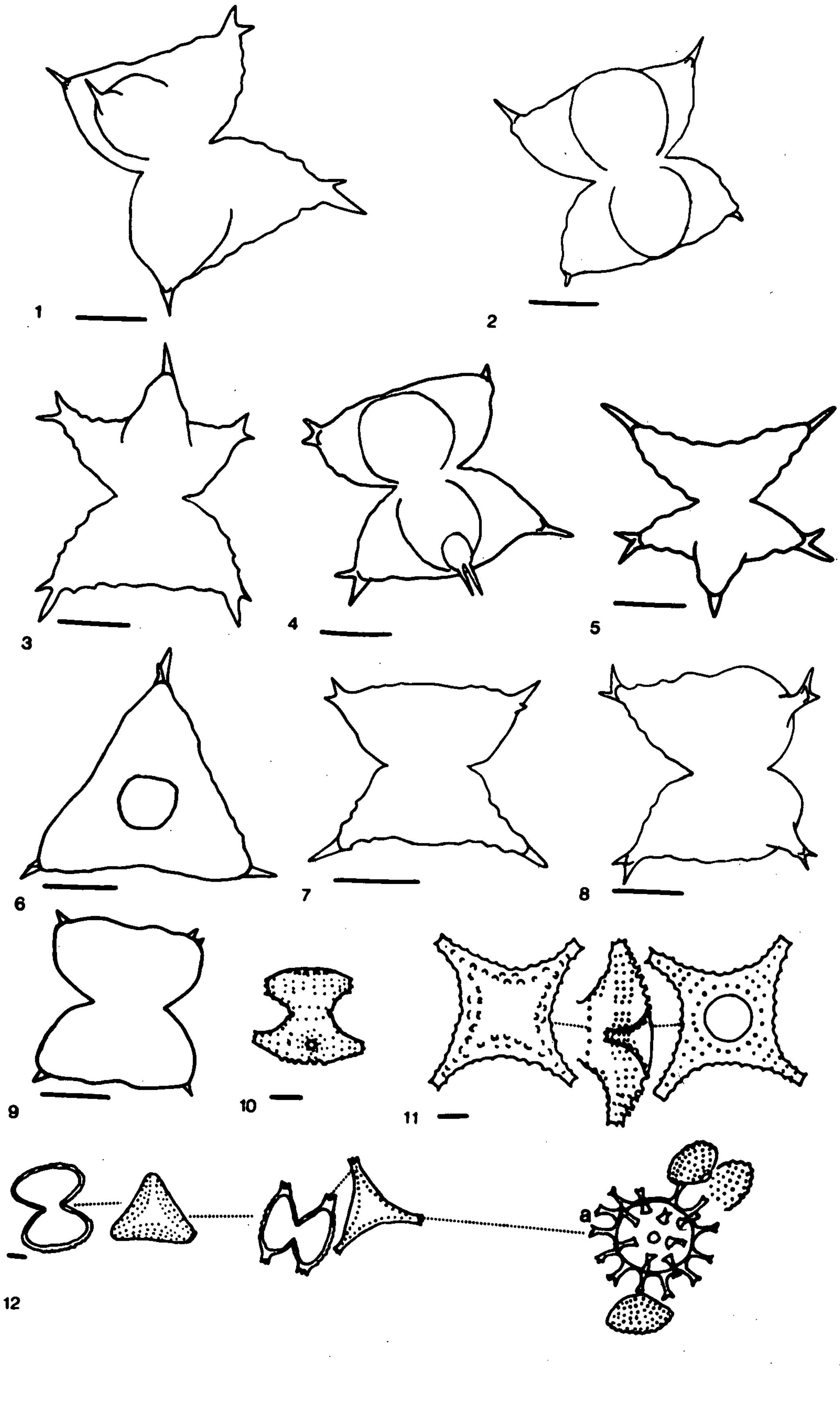
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Plate F

(marker = 10 μm)

1. St. proboscideum var. productum Messikommer 1942 (pl. 17, fig. 3) (= St. proboscideum var. proboscideum)

2. St. proboscideum var. americanum Wolle 1882 (pl. 13, fig. 10)

3. St. proboscideum var. altum Boldt 1885 (pl. 6, fig. 34)

4. St. proboscideum var. brasiliense Börgesen 1890 (pl. 5, fig. 49)

5. St. proboscideum var. subglabrum W. West 1890 (pl. 6, fig. 35)

6. St. borgeanum var. compactum Grönblad 1926 (fig. 89, 90) (= St. proboscideum var. compactum)

7. St. borgeanum var. parvum Messikommer 1949 (pl. 1, fig. 17) (= St. proboscideum f. minor)

8. St. polymorphum Brébisson ex Ralfs 1848 (pl. 22, fig. 9; pl. 34, fig. 6) (a= zygote)

9. St. sexcostatum Ralfs 1848 (pl. 23, fig. 5)

10. St. sexcostatum var. truncatum Raciborski 1885 (pl. 121, fig. 14) (= St. sexcostatum var. sexcostatum)

11. St. sexcostatum var. ornatum (Nordstedt) Förster 1963 in Förster 1965 (pl. 9, fig. 10)

12. St. aculeatum var. ornatum Nordstedt 1872 (pl. 7, fig. 27)

13. St. aculeatum var. ornatum f. simplex Boldt 1888 (pl. 2, fig. 49) (= St. sexcostatum var. productum

14. St. sexcostatum var. productum W. West 1892b (pl. 9, fig. 34)

15. St. crenulatum var. continentale f. mammiferum Prescott et Scott 1952 (pl. 5, fig. 3)

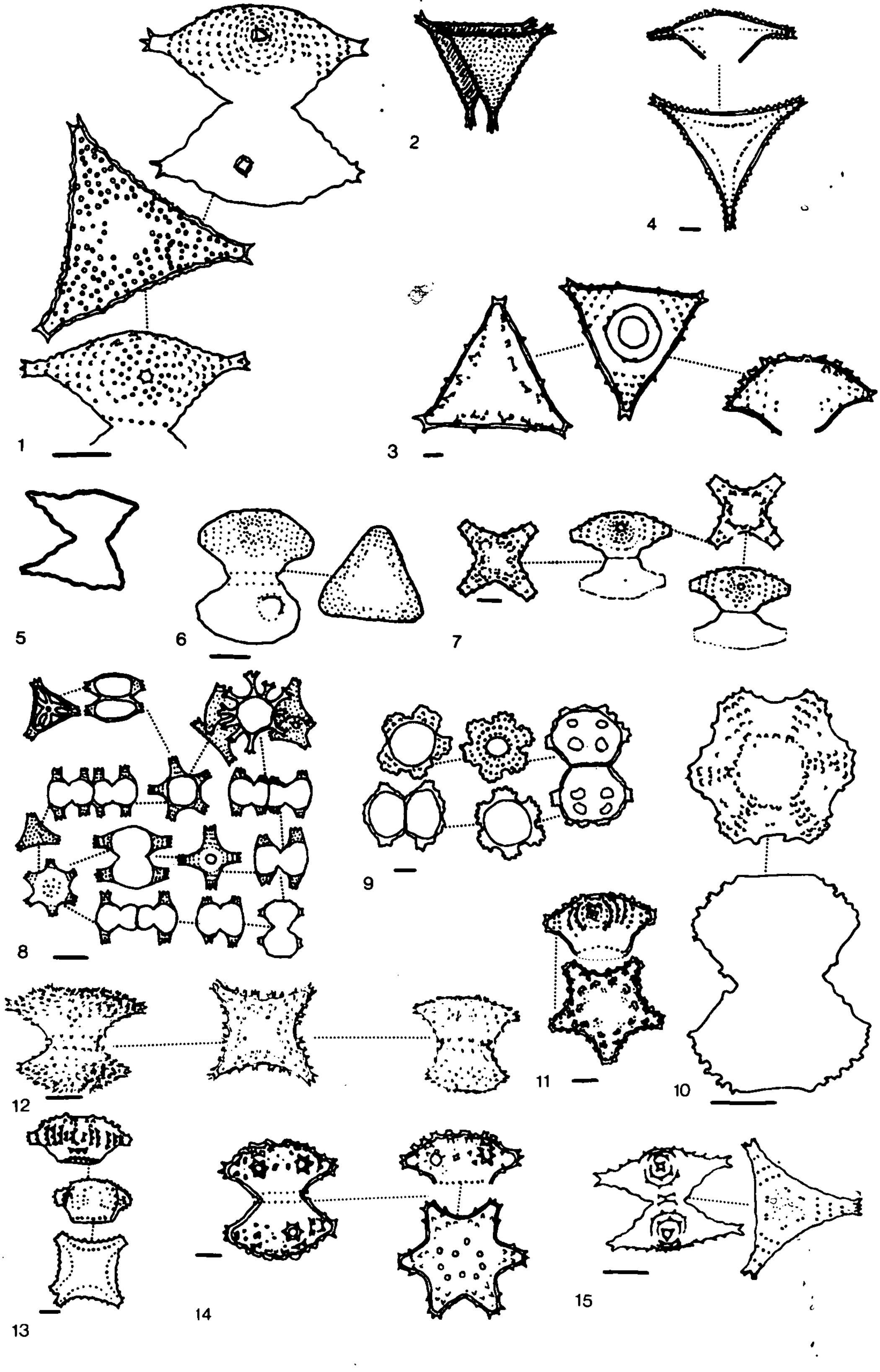
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Plate G

(marker = 10 μm)

1, 2. St. sexcostatum var. productum

1. Clone HC 427

2. Clone HC 469

3. Phycastrum crenulatum Nägeli 1849 (fig. 8B) (= St. crenulatum var. crenulatum)

4. St. pingue Teiling 1942 (fig. 3-5)

5. St. planctonicum Teiling 1946 (fig. 30, 32)

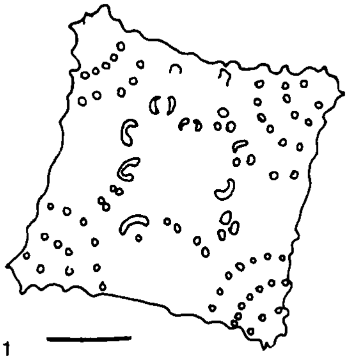
6. St. sebaldi var. ornatum f. minor Bourrelly 1957 (pl. 16, fig. 141)

7. St. manfeldtii var. bispinatum Turner 1892 (pl. 16, fig. 11, 12)

8. St. manfeldtii var. pinnatum Turner 1892 (pl. 16, fig. 10)

9. St. manfeldtii f. spinulosa Lutkemüller 1900b (pl. 6, fig. 32, 33)

10. St. manfeldtii var. annulatum W. et G.S. West 1902b (pl. 1, fig. 30, 31)



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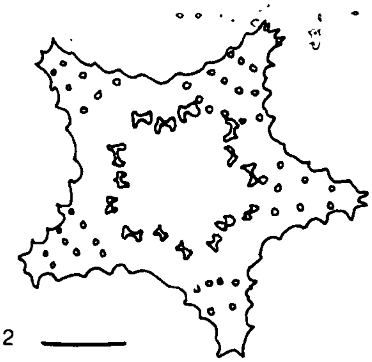

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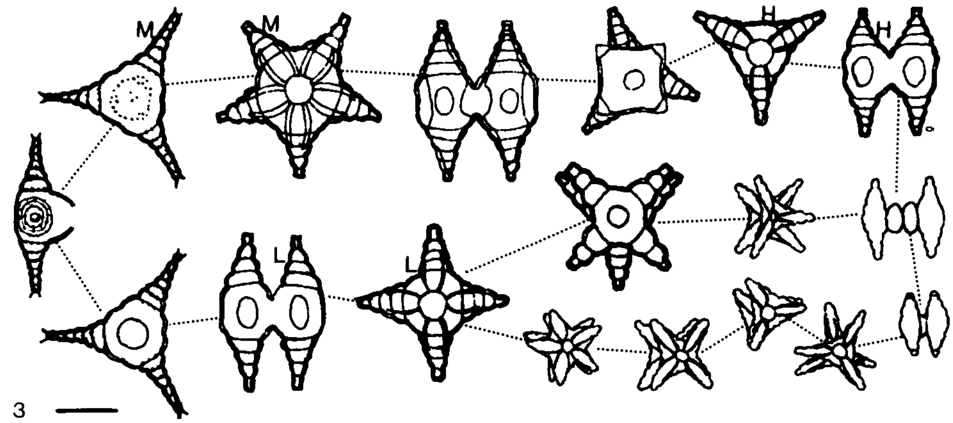

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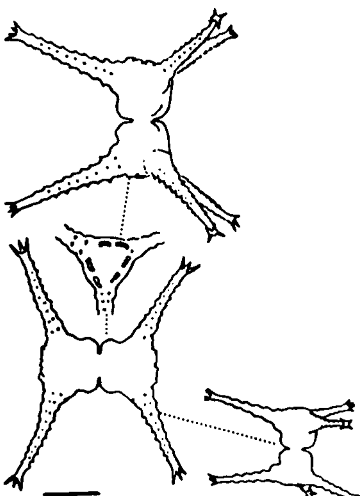

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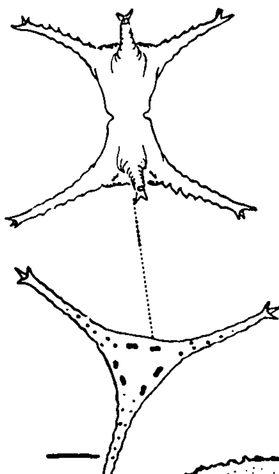

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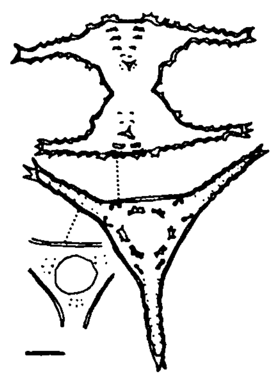

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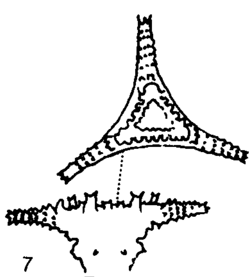

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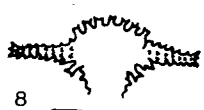

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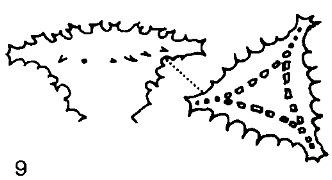

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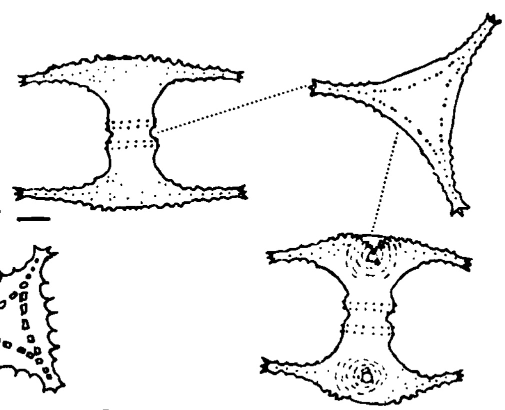

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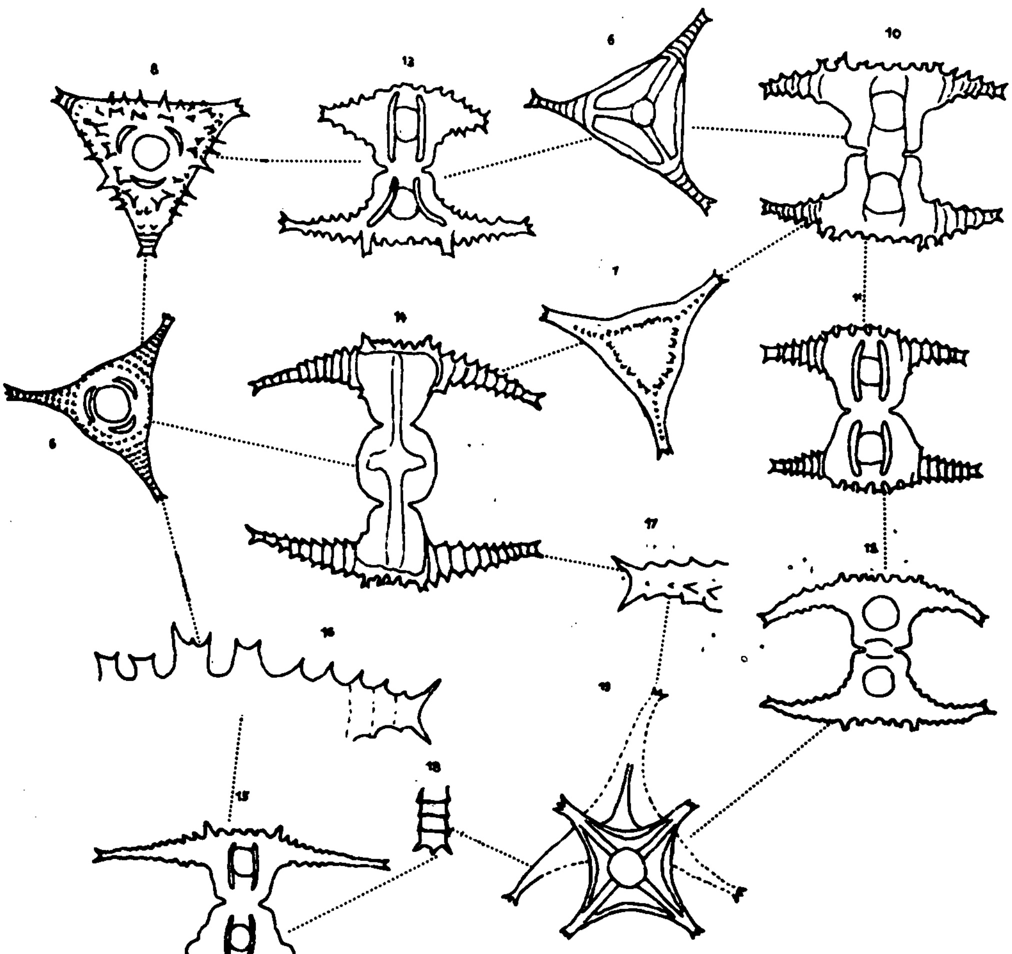
Plate H

(marker = 10 μm)

1. St. manfeldtii Delponte 1877 (pl. 13, fig. 6-19)
2. St. sebaldi Reinsch 1867b (pl. 24D-I, fig. 1-3)
3. St. sebaldi var. ornatum Nordstedt 1873 (pl. 1, fig. 15)
4. St. vestitum Ralfs 1848 (pl. 23, fig. 1)



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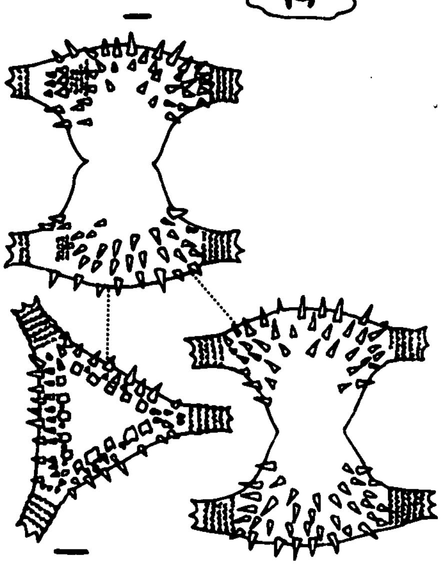

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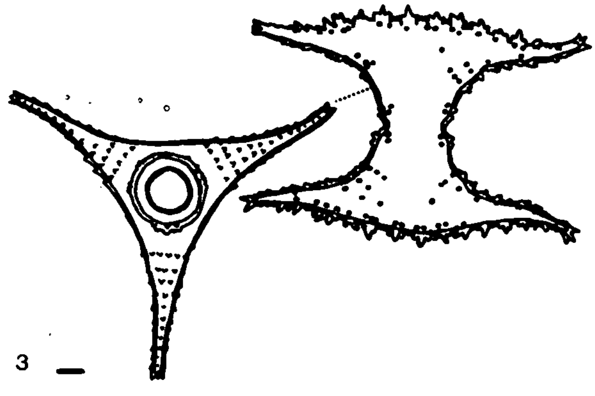

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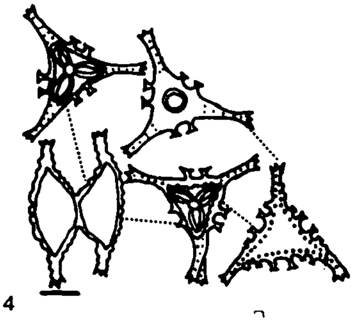

4

Plate I

(marker = 10 μm)

1. St. anatinum Cooke et Wills in Cooke 1881 (pl. 139, fig. 6)

2. St. anatinum f. hirsutum-vestitum Brook 1959a (pl. 8, fig. 2-4)

3. St. anatinum f. curtum-hirsutum-vestitum Brook 1959a (pl. 8, fig. 5)

4. St. anatinum f. pelagicum-glabrum-vestitum Brook 1959a (pl. 7, fig. 1)

5. St. anatinum f. longiradiatum-denticulatum-vestitum and longiradiatum-glabrum Brook 1959a (pl. 7, fig. 5)

6. St. anatinum f. denticulatum-tortum Brook 1959a (pl. 4, fig. 5)

7. St. vestitum var. distortum Wolle 1883 (pl. 27, fig. 15)

8. St. vestitum var. denudatum Nordstedt 1869 (pl. 4, fig. 40)

9. St. vestitum var. semivestitum W. West 1892b (pl. 9, fig. 38)

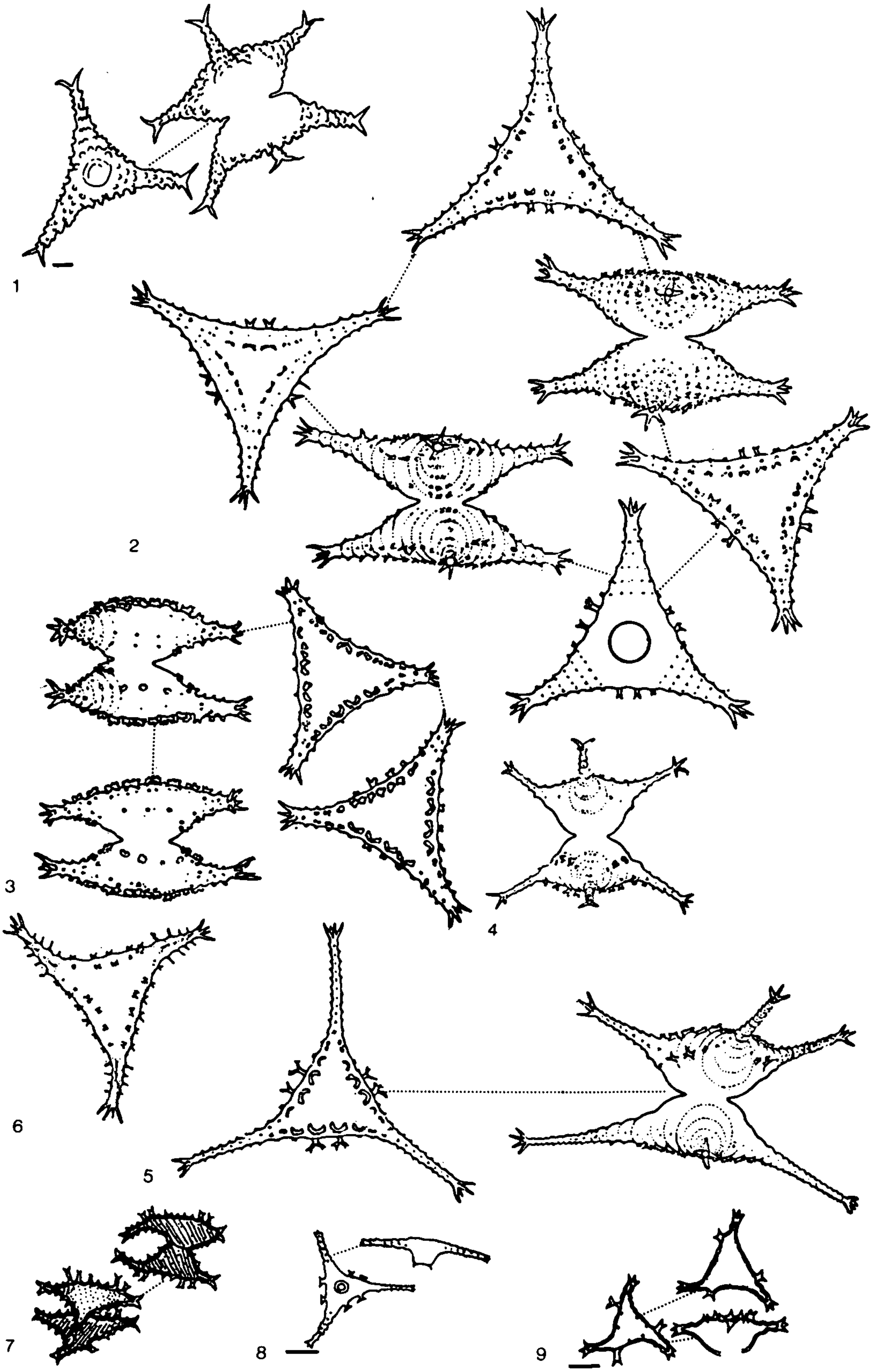
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Plate J

(marker = 10 μm)

1. St. vestitum var. subanatinum W. et G.S. West 1902b (pl. 1, fig. 28)

2. St. vestitum var. splendidum Grönblad 1920 (pl. 3, fig. 100-102) (= St. vestitum var. vestitum)

3. St. vestitum var. gymnocephalum Scott et Prescott 1961 (pl. 58, fig. 9)

4. St. vestitum var. cedercreutzii Croasdale in Croasdale et Grönblad 1964 (pl. 20, fig. 14; pl. 21, fig. 1-4) (= St. vestitum var. vestitum)

5, 6. St. vestitum var. vestitum, clone HC 151; cells in vertical view showing spine pattern

7. St. inflexum Brébisson 1856 (pl. 1, fig. 25)

8. St. brachycerum Brébisson 1856 (pl. 1, fig. 24) (= St. inflexum var. inflexum)

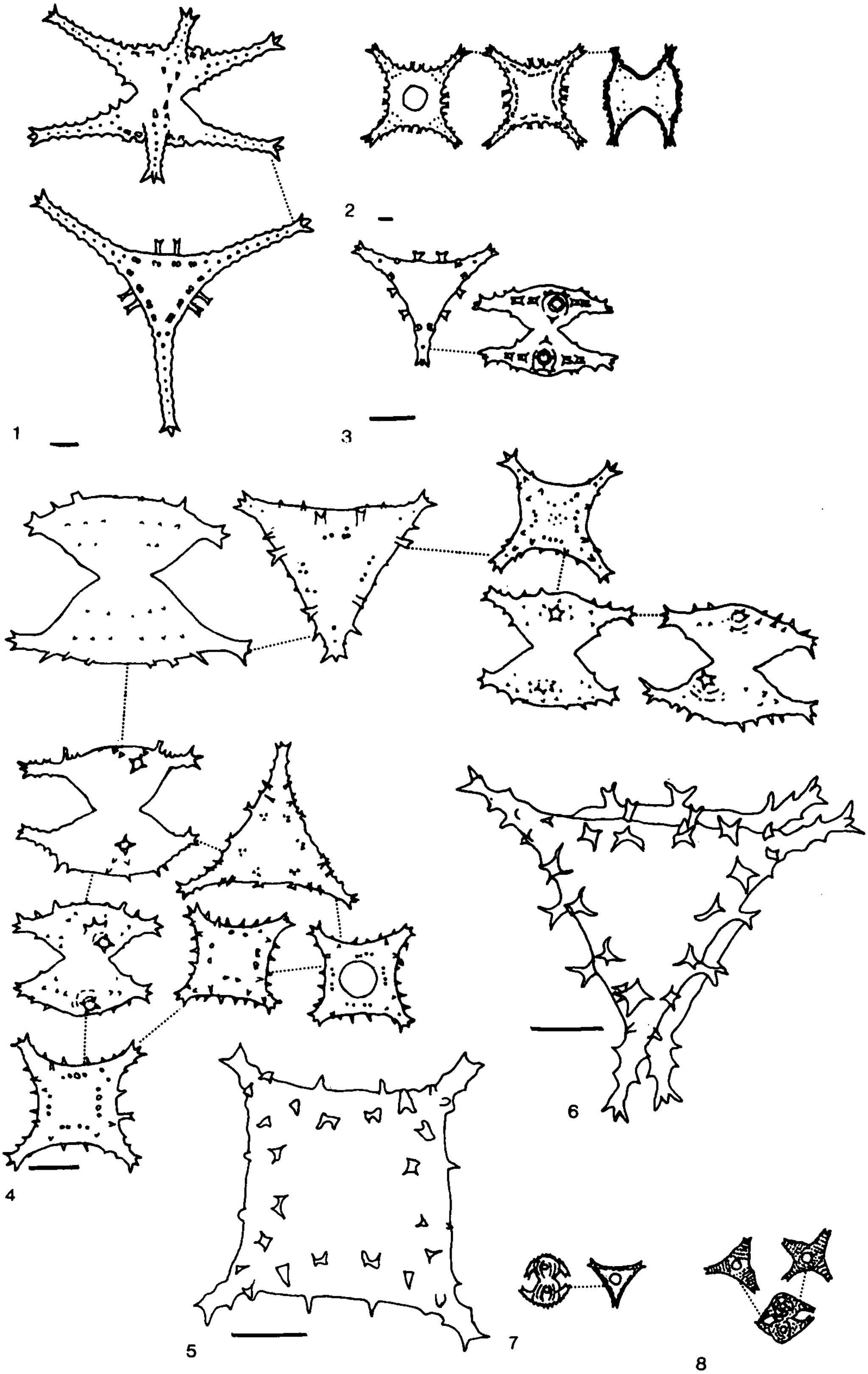
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Plate K

(marker = 10 μm)

1. St. brachycerum in Brook 1959 (pl. 29, fig. 1-8) A. Brébisson's material B. Brook's records

2. St. cyrtocerum Brébisson ex Ralfs 1848 (pl. 22, fig. 10)

3. St. tetracerum (Kützing) Ralfs 1848 (pl. 23, fig. 7)

4. St. tetracerum var. undulatum W. et G.S. West 1895b (pl. 9, fig. 6)

5. St. tetracerum var. validum W. et G.S. West 1897c (pl. 6, fig. 25)

6. St. tetracerum var. evolutum W. and G.S. West 1905a (pl. 2, fig. 31)

7. St. tetracerum var. trigranulatum W. et G.S. West 1907 (pl. 15, fig. 19)

8. St. tetracerum f. biradiata Borge 1925 (pl. 1, fig. 23) (= St. tetracerum var. tetracerum)

9. St. tetracerum f. Borge 1936 (pl. 3, fig. 57) (= St. tetracerum var. tetracerum)

10. St. tetracerum var. subexcavatum Grönblad 1921 in Bourrelly 1961 (pl. 22, fig. 3

11. St. tetracerum var. evolutum f. minor Irénée-Marie 1957 (fig. 24)

12. St. paradoxum Meyen var. osceolense Wolle f. biradiata Georgewitsch 1910 (fig. 6)

13. St. tetracerum var. maximum Messikommer 1966 (pl. 1, fig. 16)

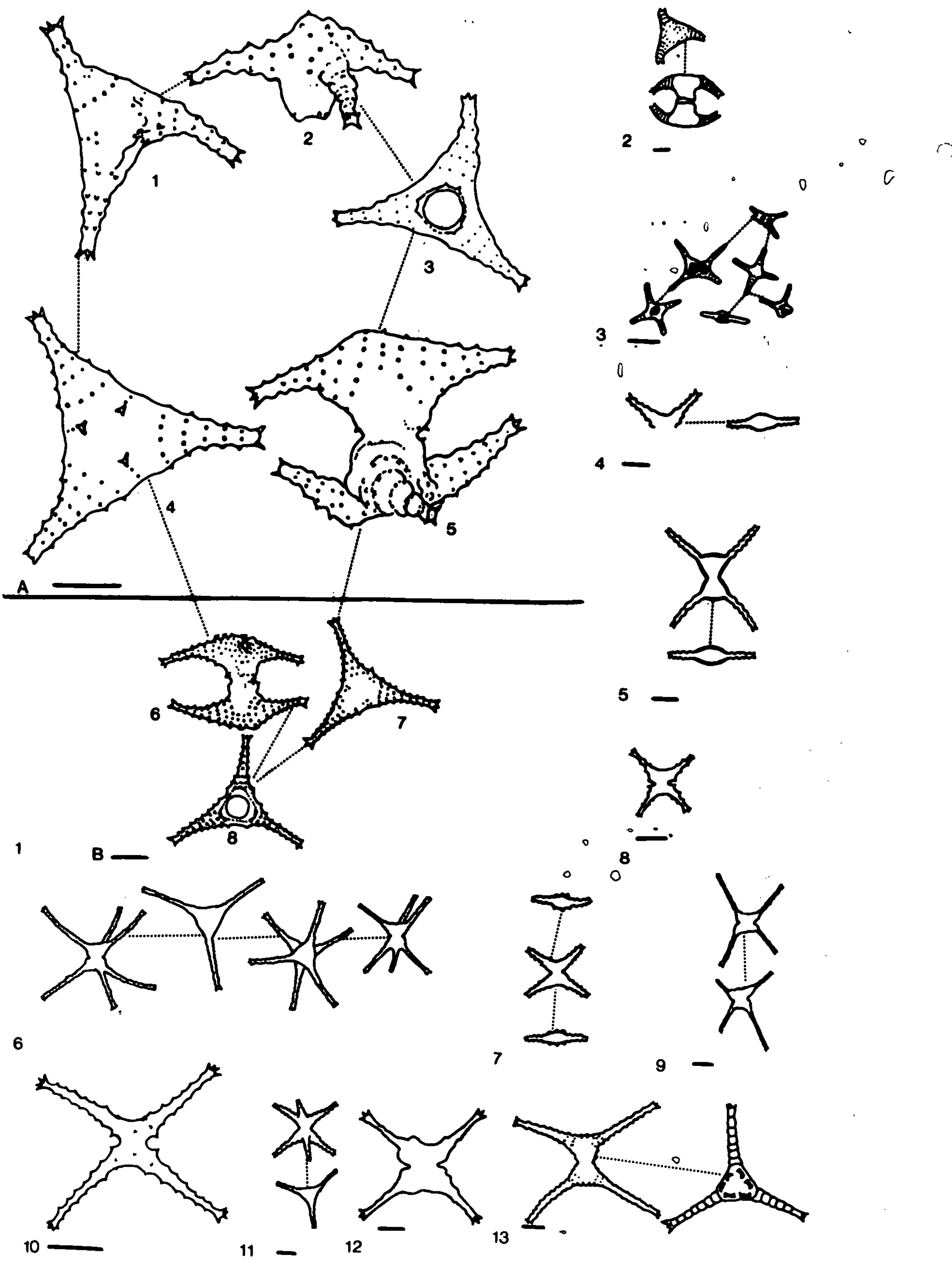
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Plate L

(marker = 10 μm)

1. St. tetracerum var. cameloides Florin 1957 (pl. 29, fig. 5-8)

2. Didymocladon furcigerus Ralfs 1848 (pl. 23, fig. 12) (= St. furcigerum var. furcigerum)

3. St. furcigerum var. reductum W. et G.S. West 1906 (pl. 11, fig. 12) (= St. furcigerum var. furcigerum)

4. St. armigerum Brébisson 1856 (pl. 1, fig. 22) (= St. furcigerum f. armigerum)

5. St. furcigerum var. armigerum f. gracillinum Smith 1924 (pl. 83, fig. 8-11) (= St. furcigerum f. armigerum)

6. St. pseudofurcigerum Reinsch 1867b (pl. 23C I, fig. 1-4) (= St. furcigerum var. pseudofurcigerum)

7. St. furcigerum var. crassum Schröder 1897 (pl. 4, fig. 6) (= St. furcigerum var. montanum)

8. St. hantzschii Reinsch 1867 (pl. 22 D II, fig. 1-6) (= St. senarium var. senarium)

9. St. senarium var. alpinum f. tatrica Raciborski 1885 (pl. 3, fig. 7) (= St. monticulosum var. bifarium)

450A

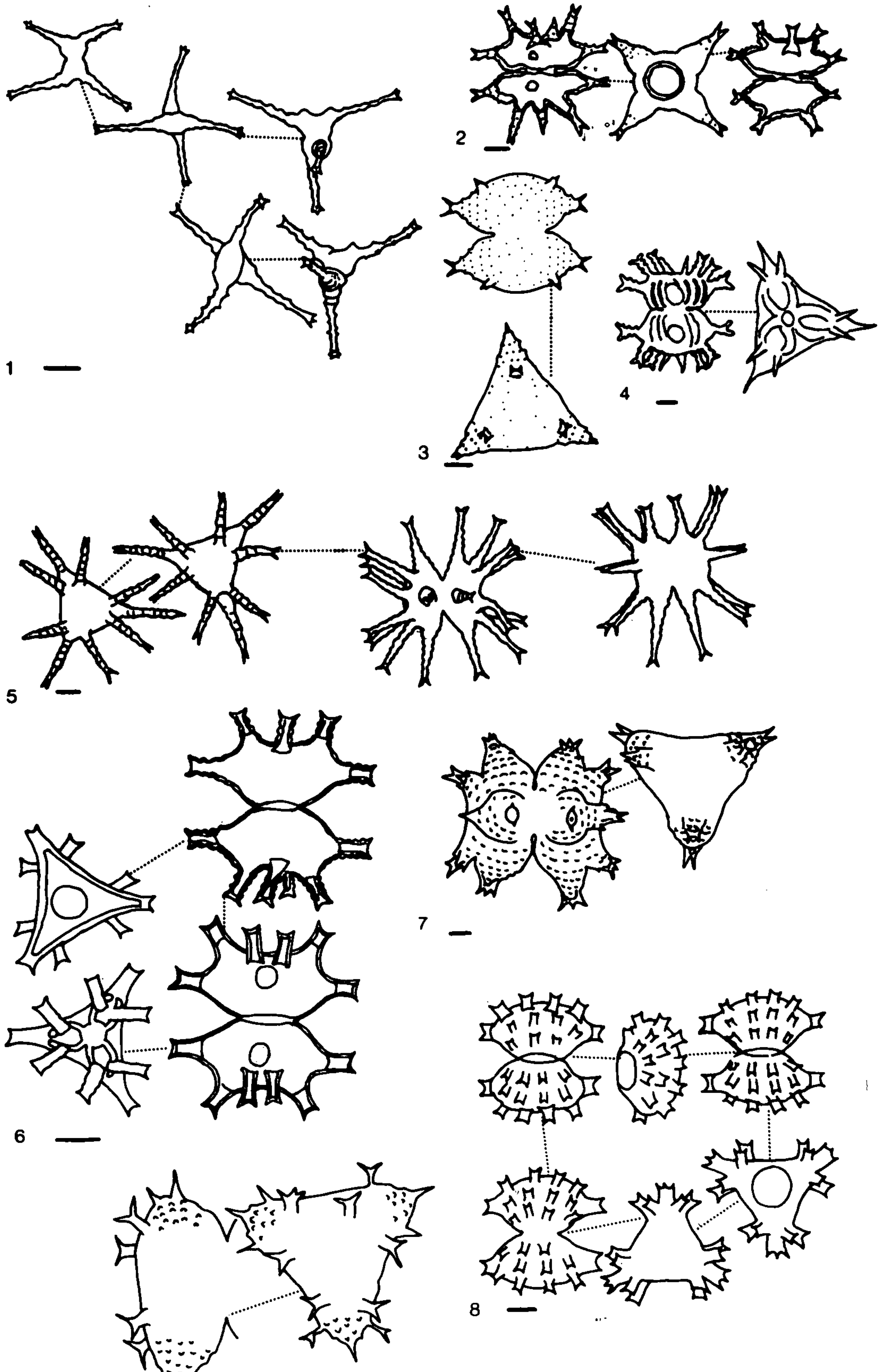

Plate M

(marker = 10 μm)

1. St. montanum Raciborski 1885 (pl. 12, fig. 11) (= St. furcigerum var. montanum)

2. St. senarium var. nigrae-silvae Schmidle 1893 (pl. 28, fig. 19) (= St. subavicula var. nigrae-silvae)

3. St. senarium var. pseudowallichii Grönblad 1920 (pl. 2, fig. 20-23; pl. 5, fig. 51-53)

4. St. hantzschii var. cornutum Turner 1892 (pl. 15, fig. 23) (= St. senarium var. senarium)

5, 6. St. tohopekaligense var. nonanum (Turner) Schmidle 1898

5. sensu Hughes 1950 (pl. 3, fig. 8)

6. sensu Irénée-Marie 1939 (pl. 55, fig. 13)

7. St. tohopekaligense f. minus (Turner) Scott et Prescott 1961 sensu Hinode 1971 (fig. X:12)

8. St. furcatum var. iyaense Hinode 1962 (pl. III, fig. 98, 99)

9. St. spinosum Ralfs 1848 (pl. 22, fig. 8) (a= zygotes)

10. St. renardii Reinsch 1867b (pl. 23, fig. AI) (= St. furcatum var. furcatum)

11. St. grallatorium var. forcipigerum Lagerheim 1885 (pl. 27, fig. 27)

12. St. grallatorium var. forcipigerum f. longispinum Irénée-Marie 1952a (pl. 7, fig. 9) (= St. grallatorium var. forcipigerum)

13. St. grallatorium Nordstedt 1869 (pl. 4, fig. 52)

451A

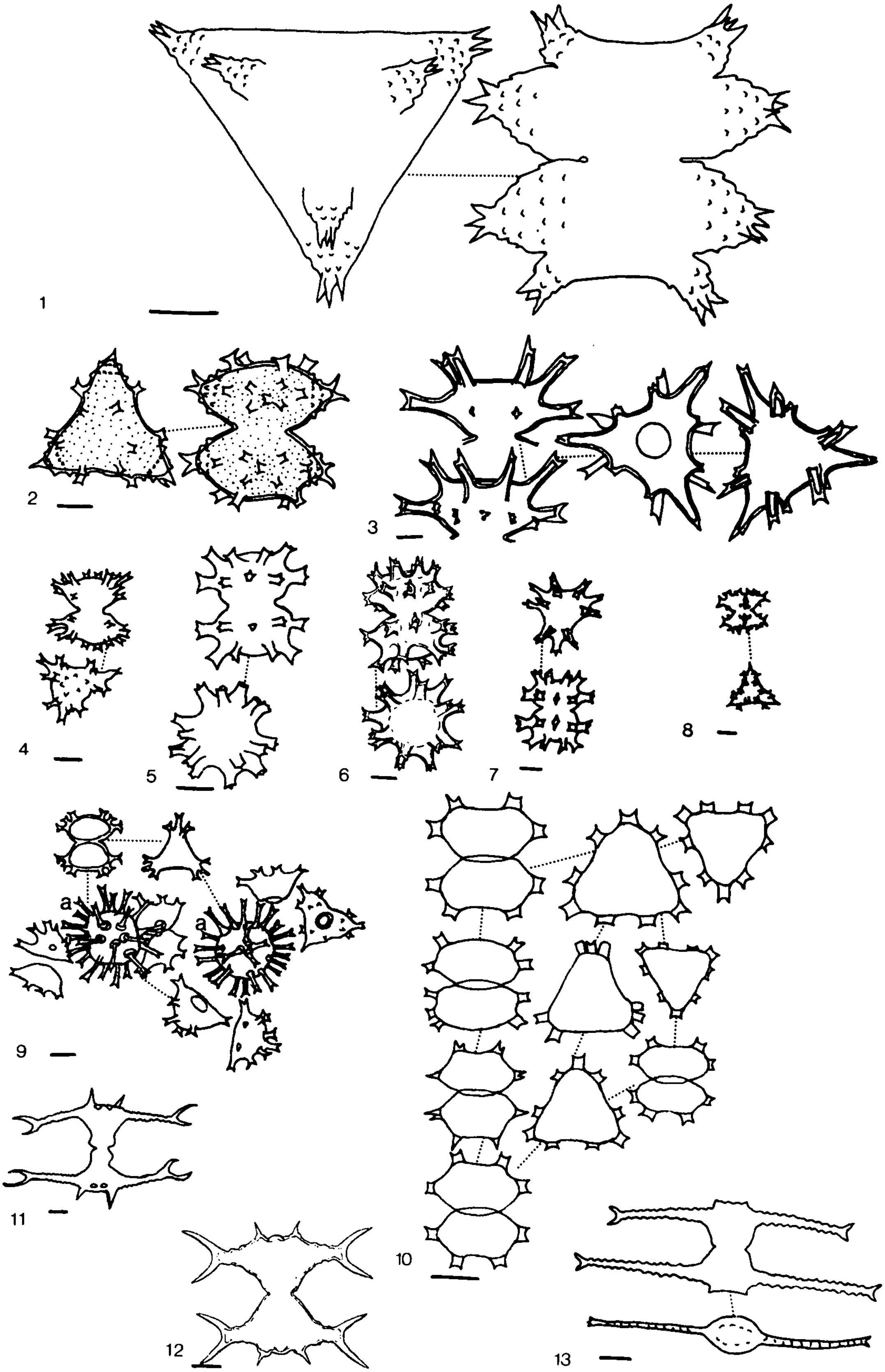

Plate N

(marker = 10 μm)

1. _St._ _grallatorium_ var. _forcipigerum_, Jacobs Lake 26-VII-80

2. _St._ _arachne_ Ralfs 1848 (pl. 23, fig. 6)

2. _St._ _arachne_ in Ralfs 1845 (pl. 11, fig. 6)

4. _St._ _arachnoides_ W. West 1892a (pl. 24, fig. 4) (= _St._ _arachne_ var. _arachne_)

5. _St._ _arachne_ var. _curvatum_ W. et G.S. West 1903 (pl. 18, fig. 9)

6. _St._ _gyrans_ Johnson 1894 (pl. 211, fig. 4) (= _St._ _arachne_ var. _gyrans_)

7. _St._ _arachne_ var. _sumatranum_ Scott et Prescott 1961 (pl. 59, fig. 7)

8. _St._ _ophiura_ var. _pentacerum_ Wolle 1882 (pl. 13, fig. 5)(= _St._ _pentacerum_ var. _pentacerum_)

9. _St._ _arachne_ var. _basiornatum_ Capdevielle et Couté 1980 (pl. 1, fig. 1-4)

10. _St._ _ophiura_ f. _nonaradiata_ W. West 1890(pl. 5, fig. 15)

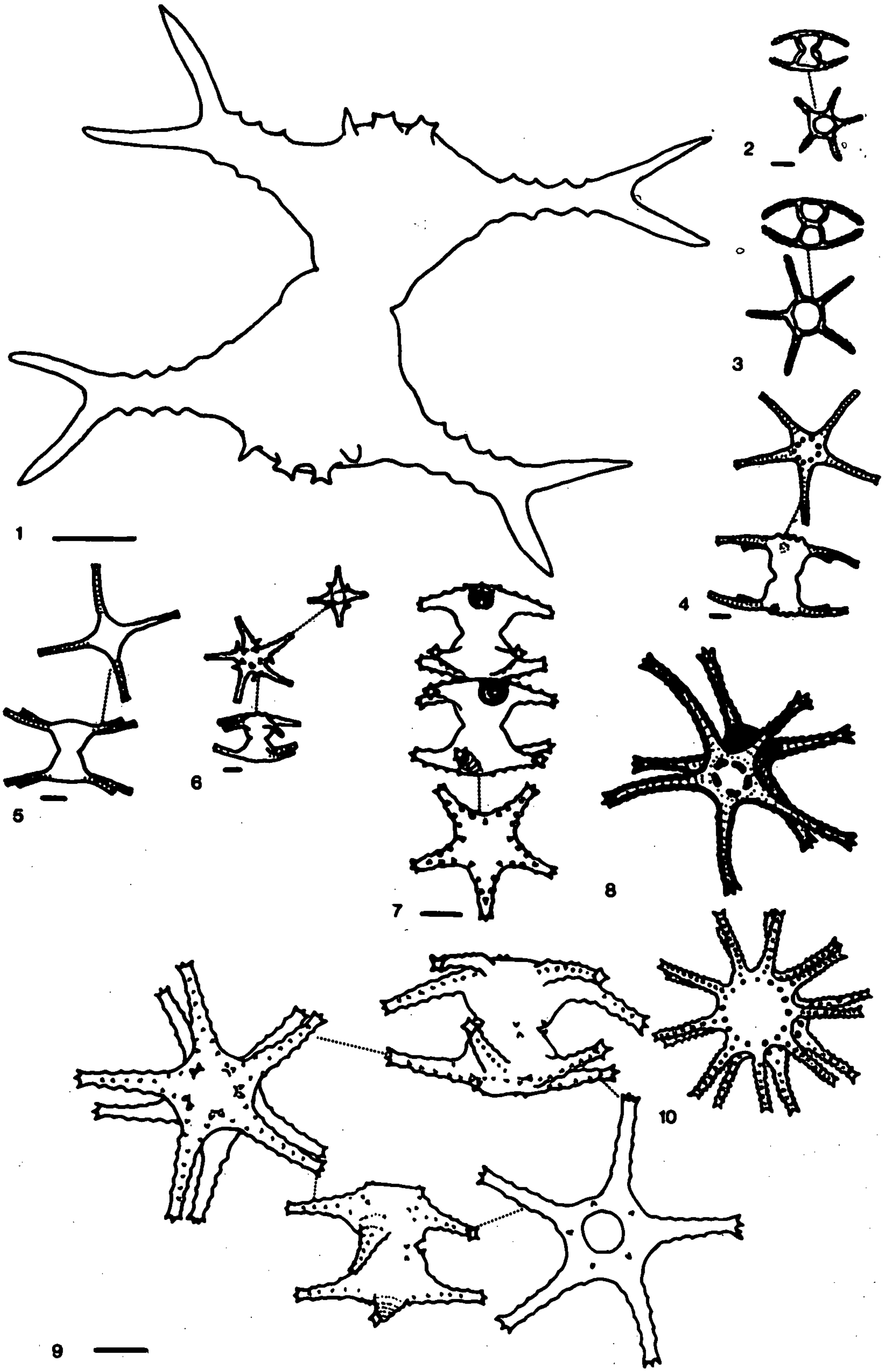
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Plate O

(marker = 10 μm)

1. St. ophiura var. longiradiatum Scott 1950 (pl. 2, fig. 1-6) (a= zygote)

2. St. senarium (Ehrenberg) Ralfs in West et al. 1923 (pl. 156, fig. 3)

3. Std. dejectus forma β Croasdale 1957 (pl. 2, fig. 28) (= Std. dejectus var. dejectus)

4. Std. dejectus var. dejectus, clone HC 306; cell in front view showing variation in angular spines

5. St. dejectum var. subglabrum Grönblad 1920 (pl. 3, fig. 105, 106)

6. St. arachne var. basiornatum f. pseudogyrans Capdevielle et Couté 1980 (pl. 1, fig. 5-8)

7. St. pentacerum (Wolle) Smith 1922 (pl. 12, fig. 19-22)

8. Std. dejectus forma α Croasdale (fig. 27)

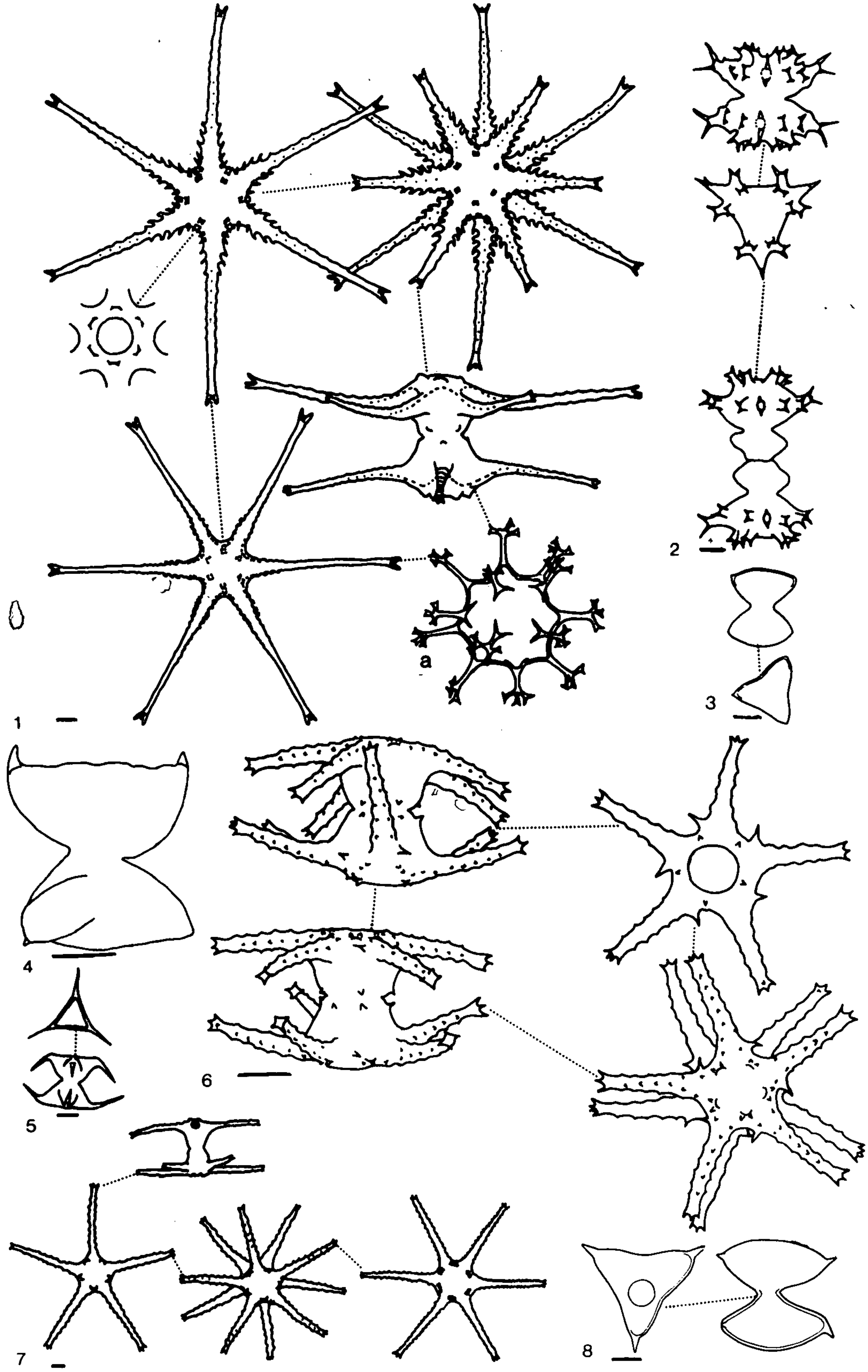
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Plate P

(marker = 10 μm)

1. St. dejectum var. inflatum W. West 1892a (pl. 22, fig. 11) (= Std. patens f. inflatus)

2. Std. dejectus var. dejectus, clone HC 306; cell in front view showing variation in angular spines

3. St. pentacerum var. hexacerum Irénée-Marie 1957 (pl. 2, fig. 18) (= St. pentacerum var. pentacerum)

4. Std. dejectus var. dejectus, clone HC 340; cell in front view showing variation in angular spines

5. Std. dejectus var. borealis Croasdale 1965 (pl. 7, fig. 4-7)

6. Std. dejectus var. dejectus, clone HC 340; cell in front view showing variation in angular spines

7. St. ophiura var. perornatum Grönblad 1945 (fig. 241)

8. St. ophiura Lundell 1871 (pl. 4, fig. 7)

9. St. ophiura var. tetracerum Wolle 1882 (pl. 13, fig. 4) (= St. pentacerum var. pentacerum)

10. St. mucronatum var. delicatulum G.S. West 1905 in G.S. West 1909 (= Std. mucronatus var. delicatulus)

11. St. mucronatum var. subtriangulare W. et G.S. West 1903 (pl. 17, fig. 11) (= Std. mucronatus var. subtriangularis)

12. St. dickiei var. parallelum Nordstedt 1888 (pl. 4, fig. 15) (= Std. mucronatus var. parallelus)

13. St. mucronatum var. debaryanum Turner 1892 (pl. 16, fig. 20)

14. St. pentacerum f. obesum Smith 1922 (pl. 13, fig. 1, 2)

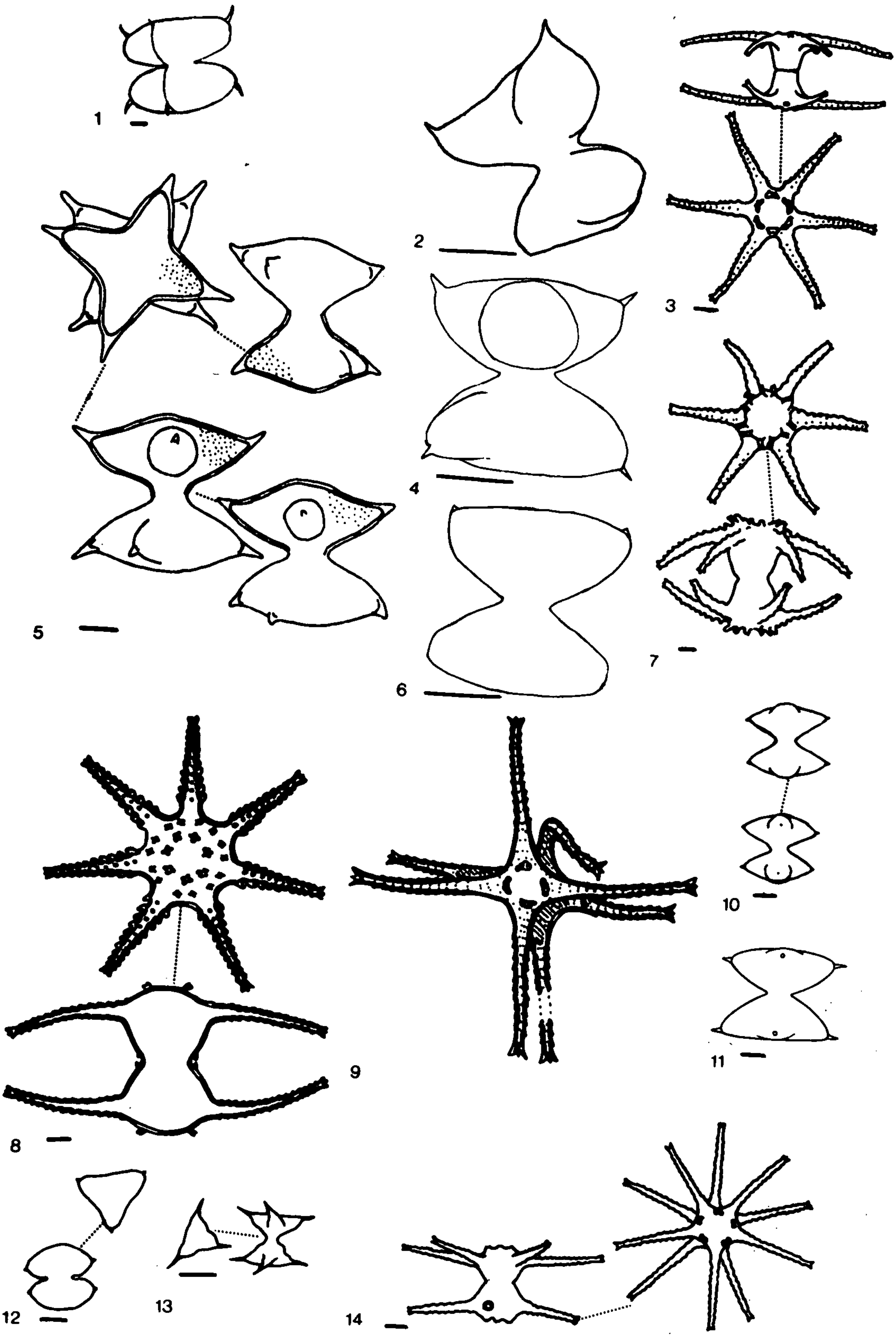
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Plate Q

(marker = 10 μm)

1. St. ophiura var. subcylindricum Borge 1913 (fig. 14)

2. St. ophiura var. coronatum Scott 1950 (pl. 1, fig. 1, 2)

3. St. coronulatum var. quebecense Irénée-Marie 1952a (pl. 6, fig. 20)

4. Std. mucronatus var. croasdaleae Teiling 1967 (pl. 18, fig. 14)

5. Std. mucronatus var. groenbladii Teiling 1967 (pl. 18, fig. 12)

6. St. pentacerum var. horridum Scott 1950 (pl. 1, fig. 3, 4)

455A

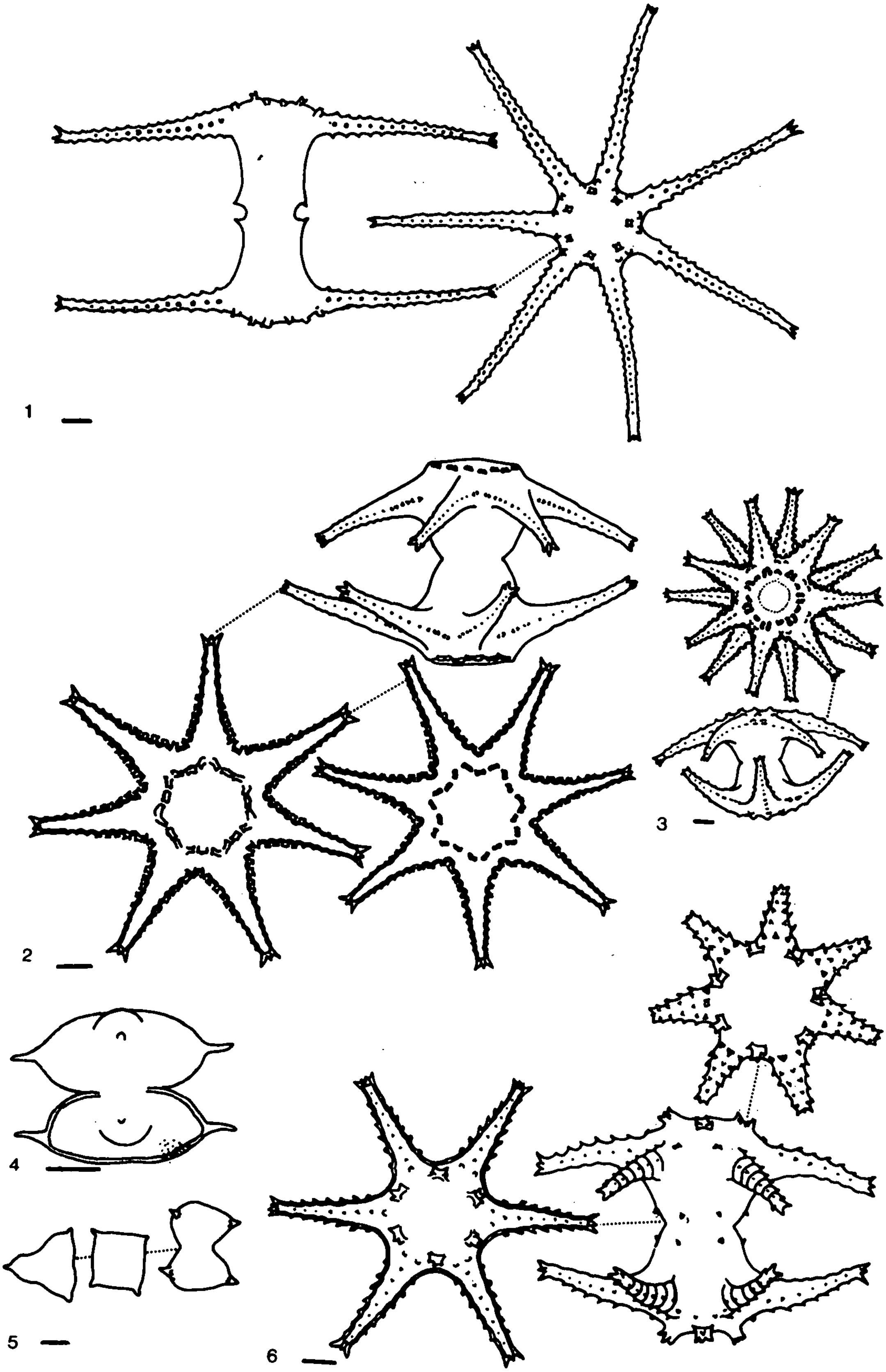

Plate R

(marker = 10 μm)

1, 2. Std. mucronatus var. delicatulus

1. Clone HC 79

2. Clone HC 173

3. St. dejectum Ralfs 1848 (pl. 20, fig. 5) (a= Std. mucronatus ; b= Std. dejectus ; c= conjugation; d= mature zygote)

4. St. apiculatum Brébisson 1856 (pl. 1, fig. 23) (= Std. dejectus var. dejectus)

5. St. dejectum var. patens Nordstedt 1888 (pl. 4, fig. 16) (= Std. patens var. patens)

6. St. mucronatum in Ralfs 1845 (pl. 10, fig. 5, 6) (a= Std. connatus ; b= Std. mucronatus ; c= conjugation; d= mature zygospore)

7. St. dejectum in West et al. 1923 (pl. 129, fig. 9-12)

8. Std. dejectus (Ralfs) Teiling 1954 in Teiling 1967 (pl. 9, fig. 1-4)

456A