

## A key to the sterile corticolous crustaceous lichens occurring in South Sweden.

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The determination of sterile lichens can be a difficult task, as lichen taxonomy is mainly built on characters taken from apothecia and spores. Yet a good deal of those lichens which are seldom or never found with apothecia can easily be recognized on other morphological characters. E. ACHARIUS, in the beginning of the 19th century, described several of them as proper species. In the 20's and 30's there arose an opposition against the Acharian taxonomy. K. F. W. WALLROTH and G. F. W. MEYER in Germany and E. FRIES in Sweden treated the majority of sterile lichens as monstrous forms of fertile species. These points of view were strengthened by the increasing knowledge of the morphology of apothecia and spores, which proved to be of fundamental importance for lichen taxonomy, and prevailed up to the end of the past century.

A reaction against these extreme views began with W. NYLANDER and E. VAINIO, both of whom regarded the organs of vegetative reproduction, mainly soredia and isidia, as important specific characters. About the turn of the century, *i.e.*, J. REINKE, O. V. DARBISHIRE and G. BITTER studied the morphology of the soredia, and succeeding lichenologists began to consider soredia and isidia to be of equal taxonomic interest as apothecia, thus, in many cases, returning to the same species concept as ACHARIUS. A valuable contribution to the morphology of the vegetative organs of reproduction was given by DU RIETZ (1924 p. 371), who classified the main types of soredia and isidia, proposed a consequent terminology and discussed their taxonomical importance.

An important help to the classification of sterile lichens has been provided by lichen chemistry. NYLANDER (1866 p. 198) found that the colour reactions given by potassium hydroxide and calcium

hypochlorite with certain lichens could be used as taxonomical characters. These reagents, as well as iodine solution and, in the last decades, paraphenylenediamine (ASAHINA 1934 p. 47), have been employed by most lichenologists. The taxonomical value of these chemical tests have been judged in different ways. An extreme tendency (*i.a.*, MÜLLER ARGOVIENSIS, hardly represented among modern lichenologists) did not ascribe any taxonomical value to chemical reactions. The other extreme, mainly represented by the leading men in the field of lichen chemistry, W. ZOPF and Y. ASAHINA, but also by a limited number of pure taxonomists, such as NYLANDER, and, in recent time, V. GYELNIK and V. RÄSÄNEN, consider a constant difference in the chemical constituents to be sufficient for specific segregation, even if there is no morphological difference. I agree with the majority of modern lichenologists who ascribe merely a subsidiary taxonomical value to lichen chemistry. Only when there is a correlation between chemical and morphological characters can the former be useful for the delimitation of species. With this reservation we must acknowledge the valuable aid offered by lichen chemistry, especially for the identification of fragmentary specimens and of sterile lichens. The use of »chemical characters» for the distinction of rather large groups of species in the following scheme does not mean to over-estimate the taxonomical value of lichen chemistry. It is a practical arrangement for the benefit of the beginner; the trained eye can in every case recognize the species on morphological characters.

The key that is given below is restricted to the sterile (or rather often sterile) crustaceous lichens reported as corticolous (or lignicolous) in South Sweden, *i.e.*, the provinces known as Götaland. A similar treatment of the sterile saxicolous species must be postponed to a future date. Sterile species or forms of larger foliose lichens, such as *Parmeliae* and *Physciae* (except the very small *Ph. elaeina*), have been excluded, as they are supposed to be well-known from elementary lichen floras. Also among the mere crustaceous lichens the choice has, in some cases, been somewhat subjective, *e.g.*, in the group containing species bearing pycnoconidia (nos. 31 a—36 b in the key). Some fertile species, whose apothecia can be mistaken for soredia (*i.a.*, *Pertusaria leptospora*, *P. multipuncta* and *Phlyctis agelaea*) have also been considered.

The scheme comprises 65 species. Two of them (*Lecidea Lightfootii* and *Pertusaria pulvereo-sulfurata*) must, however, be excluded from

the Swedish lichen flora, as the records of them have been stated to be incorrect. A similar key by ERICHSEN (1930 p. 230) from N.W. Germany listed 35 species. To some extent this increased number is due to the fact that our district contains more species than ERICHSEN's, but also to the extended knowledge of sterile lichens during the last two decades, mainly through the works of ERICHSEN. Yet I have a wider species concept than ERICHSEN. The study of the variation within a larger material has rendered it necessary to degrade several of his species, mainly within *Pertusaria*, to varieties or forms.

Nearly all species treated have at least some time been found fertile, so that it has been possible to place them in the system. They constitute no natural group: rather similar sterile lichens can belong to very different genera in the generally accepted ZAHLBRUCKNER system, which is based on the morphology of apothecia and spores. In some cases the material available does not allow a definitive judgement of the taxonomic rank. A number of species (some *Pertusariae*, the whole genus *Lepraria*) have never been found in a fertile state. Their generic arrangement must be provisional, as it is based on habitual similarity.

From a phytogeographical view-point, the majority of the species dealt with here are southern lowland plants. Propagation by means of soredia or isidia seems to be less frequent in northern or alpine districts. A list from Northern Sweden would probably not contain more than about 30 such species, according to our present knowledge. From an ecological view-point, we find a dominance of coniophilous species. It is evident that dust-impregnated habitats are more favourable to species spreading by means of soredia and isidia, than to those spreading by means of spores only.

The additional notes after the key contain no detailed descriptions. For such, I refer to the works quoted at each species. Only some short notes about the occurrence of apothecia and their morphology are given. Further, I have summed up the most useful chemical reactions for each species, particularly as, in many cases, the literature does not contain such data. It must be asserted that these reactions give only fragmentary hints of the chemical composition of the lichen thallus. For detailed information about lichen chemistry and its taxonomical significance reference must be made to the works of, *ia.*, ZOPF, ASAHINA, DES ABBAYES and LAMB.

The morphological terminology agrees with DES ABBAYES (1951) and, as to soredia and isidia, mainly with DU RIETZ (1924).

## Abbreviations.

Ap.=apothecia. Py.=pycnidia. Py.-con.=pycnoconidia. So.=soredia. Th.=thallus.

K=potassium hydroxide. C=calcium hypochlorite.

KC=these reagents used one after the other. P=paraphenylenediamine.

The signs  $\dagger$ ,  $\pm$  etc. after the reagents indicate a positive or negative reaction of cortex (superior sign) and medulla (inferior sign). In some cases, when cortex and medulla are less distinctly limited, the statement considers the whole thallus, e.g., K+ instead of  $K_{\dagger}^{+}$ . (+) means an indistinct reaction.

## Key to the species.

- 1 a. Thallus crustaceous only in the centre, at the circumference with distinct, corticate lobes (visible in the binocular), sometimes with distinct squamules.
  - 2 a. Th. deep yellow—orange.
    - 3 a. Th. K+ dark red.
      - 4 a. Lobes coralloid, sorediate, somewhat ascendent.
 

*Xanthoria candelaria*
      - 4 b. Lobes  $\pm$  appressed, sorediate in the margin, often broader than in the preceding sp., colour often darker yellow.
 

*Xanthoria fallax*
      - 3 b. Th. K—,
 

*Candelaria concolor*
  - 2 b. Th.  $\pm$  grey (often brownish-, greenish- or yellowish-grey).
    - 5 a. Th. squamulose.
      - 6 a. Th. C+ red; squamules grey or brownish above, whitish and sorediate beneath.
 

*Lecidea scalaris*
      - 6 b. Th. C— (or sometimes yellowish).
        - 7 a. Th. covered with coralloid isidia emerging from the edges of the squamules.
 

*Parmeliella corallinoides*
        - 7 b. Th. not isidiate.
          - 8 a. Squamules not appressed, greyish above, whitish beneath, at least sometimes forming cups or tubes (podetia).
 

*Cladonia* spp. (young stages)
          - 8 b. Squamules appressed, without podetia.
            - 9 a. Squamules crowded, brownish, not sorediate.
 

*Toninia caradocensis*
            - 9 b. Squamules scattered, glaucous—greyish, rounded, with a thickened sorediate margin.
 

*Normandina pulchella*
  - 5 b. Th.  $\pm$  continuous, lobate at the circumference.
    - 10 a. Th. covered with isidial so. in the centre.
      - 11 a. Th. whitish grey, K+ yellow. — Mainly on coniferous trees.
 

*Parmeliopsis aleurites*
      - 11 b. Th. brownish grey; K—, — Mainly on deciduous trees, especially *Populus tremula*.
 

*Pannaria ptyrea*
    - 10 b. Th. sorediate, without isidia.

- 12 a. Th. yellowish, K—, *Parmeliopsis ambigua*  
 12 b. Th. grey.  
 13 a. Cortex K+ yellow.  
 14 a. Marginal lobes free; so. maculiform. *Parmeliopsis hyperopta*  
 14 b. Marginal lobes appressed, pruinose; so. maculiform—diffuse in the centre. *Buellia canescens*  
 13 b. Cortex K—; marginal lobes closely appressed; so. maculiform. *Physcia elaeina*
- 1 b. Th. quite crustaceous, without corticate lobes in the circumference, nor with distinct squamules.  
 15 a. Th. (at least so.) C+ red or orange.  
 16 a. Th. thin, yellowish, quite dissolved into so.  
 17 a. Th. light yellowish green; so. diffuse or sometimes maculiform. *Lecanora expallens*  
 17 b. Th. pale brownish yellow, often limited by a dark hypothallus; so. diffuse. *Lecidea querneae*  
 16 b. Th. thicker, distinctly corticate (at least in the circumference), generally sorediate.  
 18 a. Cortex yellowish. Th. with verruciform isidia, generally mingled with sorediate verrucae. *Pertusaria lutescens*  
 18 b. Cortex light grey—dark grey, not yellowish.  
 19 a. So. well delimited; no isidia.  
 20 a. So. large (mostly exceeding 0.5 mm. diam.),  $\pm$  convex.  
 21 a. So. greyish white, K—,  
 22 a. Th. areolate; so. somewhat constricted at the base. *Pertusaria lactea* f. *faginea*  
 22 b. Th. not areolate; so. not constricted at the base. *Pertusaria hemisphaerica*  
 21 b. So. with a yellowish, dirty brownish (or reddish) tinge, K+ yellow. *Ochrolechia androgyna*  
 20 b. So. small (not or rarely reaching 0.5 mm. diam.), plane.  
 23 a. So. c. 0.4—0.5 mm. diam.; soredial granules c. 0.05—0.1 mm. diam. *Ochrolechia arborea*  
 23 b. So. mostly c. 0.2—0.4 mm. diam.; soredial granules c. 0.02—0.03 mm. diam. *Lecidea flexuosa*
- 19 b. Soredia mainly diffuse.  
 24 a. Th.  $\pm$  light grey, isidiate; isidia soon developing into whitish grey or faintly greenish grey so. *Ochrolechia subviridis*  
 24 b. Th. dark grey, without isidia; so. first roundish, soon confluent, dirty brownish or yellowish grey. *Pertusaria sordidogrisea*
- 15 b. Th. C—,  
 25 a. Th. distinctly yellow (not sulphur-grey).  
 26 a. K+ distinctly red.  
 27 a. Th. with maculiform so.  
 28 a. So. rounded, with a reddish or brownish tinge. *Caloplaca microphyllina*

- 28 b. So. rounded—confluent, bright (citrine) yellow.  
*Caloplaca chrysophthalma*
- 27 b. Th. with isidial so. *Caloplaca herbidella*
- 27 c. Th. almost quite dissolved into diffuse so. *Caloplaca phlogina*
- 26 b. Th. K— (or faintly red).
- 29 a. Th. quite dissolved into minute leprose so., K+ faintly red.  
*Lepraria candelaris*
- 29 b. Th. consisting of small granules, K—.
- 30 a. Granules c. 0.2 mm. diam., forming a continuous crust.  
*Candelariella vitellina*
- 30 b. Granules ca. 0.1 mm diam., scattered. *Candelariella xanthostigma*
- 25 b. Th. lighter or darker grey (also white-grey, brownish grey or sulphur-grey) or almost absent.
- 31 a. Py. numerous.
- 32 a. Py. black, not pruinose.
- 33 a. Py.-con. curved,  $5-7 \times 1-2 \mu$ . — Mainly on smooth bark.  
*Opegrapha rufescens*
- 33 b. Py.-con. straight. — Mainly on coarse bark or lignum.
- 34 a. Py. (0.2—)0.3(—0.6) mm. diam., plane or convex, rugose; py.-con.  $2-3 \times 1 \mu$ .  
*Catillaria graniformis*
- 34 b. Py. 0.1—0.2 mm. diam., »punctiform»; py.-con. 4.5—6  $\mu$  long.
- 35 a. Py.-con. 1—2  $\mu$  broad; th. P—.  
*Arthonia byssacea*
- 35 b. Py.-con. 0.5—1  $\mu$  broad; th. P+ orange.  
*Arthonia cinereopruinosa*
- 32 b. Py. covered with a white pruina (at least in young stages; sometimes disappearing on old py., revealing a brownish surface).
- 36 a. Py. 0.2—0.3 mm. diam.; py.-con.  $12-20 \times 2.5-4 \mu$ ; th. pulverulent.  
*Lecanactis abietina*
- 36 b. Py. 0.1—0.2 mm. diam.; py.-con.  $3-3.5 \times 1 \mu$ ; th. smooth.  
*Opegrapha fuscella*
- 31 b. Py. few or quite lacking.
- 37 a. Th. whitish, pulverulent, with numerous brownish abortive apothecia.  
*Lecanactis amylacea*
- 37 b. Th. of varying colour; no abortive apothecia.
- 38 a. No distinct contiguous cortex present; th. quite dissolved into minute granules or squamules, diffuse so. or coralloid isidia.
- 39 a. Th. surrounded by a distinct white hypothallus.  
*Haematomma coccineum*
- 39 b. Hypothallus blackish or lacking.
- 40 a. Th. sorediate; isidia and squamules lacking.
- 41 a. Most so. distinctly delimited, round or ovoid, partly  $\pm$  confluent, K+ yellow  $\rightarrow$  orange. *Xylographa spilomatica*
- 41 b. So. diffuse, K— (or impurely yellow).
- 42 a. Th. glaucous grey—whitish grey; no thalline lobes.
- 43 a. Granules forming a contiguous crust; no hypothallus.
- 44 a. Granules »leprose» (i.e., dissolved into a fibrillose or arachnoid texture). — Mainly on rough bark (in the crevices).  
*Lepraria aeruginosa*

- 44 b. Granules not leprose. — Mainly on twigs and needles of *Picea*.  
*Catillaria Bouteillei*
- 43 b. Granules scattered in the circumference, in the centre  $\pm$  confluent forming a crust of diffuse so.; blackish hypothallus often visible.  
*Lecidea Nylanderii*
- 42 b. Th. sulphur-grey,  $\pm$  leprose—arachnoid, with indistinct, non-corticate thalline lobes.  
*Crocynia membranacea*
- 40 b. Th. not soresciate.
- 45 a. Th. vivid green when moist, irregularly erose or composed of appressed greenish grey squamules.  
*Caloplaca obscurella*
- 45 b. Th. not changing colour when moist, nor erose or squamulate.
- 46 a. Th. composed of minute,  $\pm$  conglomerate, dark grey (greenish—brownish) corticate granules.  
*Catillaria prasina*
- 46 b. Th. composed of coralloid, ash-grey—sulphur-grey isidia.  
*Caloplaca herbidella*
- 38 b. Th. with a distinct contiguous cortex, at least visible in the circumference.
- 47 a. Th. (at least so., when present) K+ yellow, changing to red within a minute.
- 48 a. Th. with papillate or cylindrical isidia, sometimes developing into so.  
*Pertusaria coccodes*
- 48 b. Th. without isidia.
- 49 a. Th. with so. or soresciate apothecia; cortex light grey—ash-grey.
- 50 a. Th. with real so.
- 51 a. So. whitish grey (or sometimes reddish), K+ yellow  $\rightarrow$  orange  $\rightarrow$  red,  $\pm$  limited or later confluent to large diffuse efflorescences.  
*Phlyctis argena*
- 51 b. So. brown—brownish grey, K+ (indistinctly yellow  $\rightarrow$ ) red, as young  $\pm$  prominent and limited, later confluent.  
*Lepraria decolorans*
- 50 b. Real so. lacking; apothecia roundish, erose, surrounded by a prominent whitish pulverulent margin, thus giving the impression of so.  
*Phlyctis agelaea*
- 49 b. Th. without so.; cortex blackish or bluish grey.  
*Rinodina colobina*
- 47 b. Th. (at least so.) immediately K+ yellow, not changing to red. (*Vide* also 47 c).
- 52 a. Th. covered with low papillate isidia, soon bursting into so.  
*Pertusaria coccodes* var. *coronata*
- 52 b. Th. soresciate, without isidia.
- 53 a. Almost the whole th. covered with  $\pm$  diffuse so.
- 54 a. Soredial granules c. 0.05—0.1 mm. diam.
- 55 a. So. yellowish grey—whitish grey, K+ intensely yellow, after some day changing to reddish.  
*Haematomma elatinum*
- 55 b. So. brownish grey, K+ (brownish) yellow, not changing to reddish.  
*Catillaria pulverea*

- 54 b. Soredial granules c. 0.02 mm. diam. (hardly visible as granules to the naked-eye), sulphur-yellow.  
*Pertusaria pulvereo-sulphurata*
- 53 b. So. distinctly delimited (at least the majority of them).
- 56 a. Fertile verrucae sorediate in the margins, often quite pulverulent giving the impression of real so. *Pertusaria leptospora*
- 56 b. So. not containing apothecia.
- 57 a. Th. rather distinctly delimited, often with dark hypothallus lines; so. greenish grey (at least in a fresh state).  
*Buellia griseovirens*
- 57 b. Th. indistinctly delimited (no hypothallus lines); so. whitish or yellowish grey.
- 58 a. So. scattered, plane or convex, dissolved into rather coarse (c. 0.05—0.08 mm. diam.) granules. *Lecanora maculata*
- 58 b. So. dense (often touching each other, hence angular), plane or slightly concave, dissolved into very fine (c. 0.03 mm. diam.) granules. *Lecanora impudens*
- 47 c. Th. K— (sometimes very slowly changing to brownish or reddish).
- 59 a. Th. KC+ violet (medulla and soredia); taste bitter.
- 60 a. Th. with greyish, corticate, sterile verrucae, as a rule mingled with white-pruinose, fertile verrucae. *Pertusaria amara* f. *stelsvicensis*
- 60 b. No corticate verrucae; th. sorediate.
- 61 a. Th. with well delimited so. *Pertusaria amara*
- 61 b. Th. with diffuse so. *Pertusaria amara* f. *pulvinata*
- 59 b. Th. KC—; no bitter taste.
- 62 a. So. ± distinctly delimited, roundish.
- 63 a. »Soredia» in reality being fertile verrucae, i.e., containing apothecia covered with a sorediate margin. *Pertusaria multipuncta*
- 63 b. Fertile sorediate verrucae lacking (or extremely rare).
- 64 a. Th. distinctly delimited, margin often zonate (containing at least one pale and one dark line). *Pertusaria globulifera*
- 64 b. Th. not distinctly delimited.
- 65 a. Cortex with a yellowish tinge; so. small (c:a 1 mm. diam.). — Coniophobic, mainly on coniferous trees.  
*Ochrolechia alboflavescens*
- 65 b. Cortex whitish grey—ash-grey (not yellowish); so. large (often more than 2 mm. diam.). — Coniophilous, mainly on deciduous trees. *Pertusaria globulifera* var. *discoidea*
- 62 b. So. ± diffuse.
- 66 a. So. greenish grey or yellowish grey, P+ yellow → red.  
*Lecidea efflorescens*
- 66 b. So. whitish grey or faintly brownish grey, P—.
- 67 a. Th. covered with granulate isidia (0.2—0.5 mm. diam.), some of which become ± dissolved into so. (soredial granules 0.1—0.2 mm. diam.); margin of th. often zonate.  
*Pertusaria globulifera* var. *Henrici*
- 67 b. No real isidia present; soredial granules 0.02—0.1 mm. diam.; no zonate margin.



- 68 a. Granules c. 0.02—0.03 mm. diam. *Lecidea Lightfootii*  
 68 b. Granules exceeding 0.04 mm. diam.  
 69 a. Th. thin, effuse, almost wholly covered with diffuse, whitish grey so.;  
 granules c. 0.05—0.07 mm. diam. *Ochrolechia microstictoides*  
 69 b. Th. rather thick, determinate (sometimes with a pale margin), at least  
 in the circumference with some determinate so., in the centre covered  
 with diffuse, brownish grey so.; granules c. 0.08—0.12 mm. diam.  
*Pertusaria leprarioides*

### Additional notes.

*Arthonia byssacea* (Weig.) Ach. — ALMQUIST 1880 p. 25. REDINGER 1937—38 p. 25. ALMBORN 1948 p. 198.

Rare, on coarse bark of old trees, mainly oaks. Known only from five Swedish stations, not collected in the present century.

React.: K $\ddagger$  impurely yellow, C=, KC=, P=. — Ap. not frequent, semi-globose, immarginate; disc blackish covered with a whitish pruina.

*A. cinereopruinosa* Schaer. — ALMQUIST l.c. p. 26. REDINGER l.c. p. 87. Rare, mainly on coarse bark of old trees.

React.: K $\ddagger$  impurely yellow, C=, KC=, P $\ddagger$  yellow  $\rightarrow$  orange. — Ap. not frequent, roundish, plane or slightly convex, immarginate; disc blackish covered with a bluish grey pruina.

*A. decolorans* (Turn. & Borr.) Erichs., vide *Lepraria* L.

*B. canescens* (Dicks.) De Not. — TH. FRIES 1874 p. 587. ALMBORN 1948 p. 173 (map).

On rough bark of old deciduous trees. Known only from two Swedish stations, both in Skåne.

React.: K $\ddagger$  yellow  $\rightarrow$  brownish, C=, KC=, P= ( $\rightarrow$  yellowish). — Ap. unknown from Sweden, black, plane; margin thin — disappearing.

*B. farinosa* Malme, vide *Pertusaria leprarioides*.

*B. griseovirens* (Turn. & Borr.) n.c. — Syn. *Variolaria griseovirens* Turn. & Borr. TURNER & BORRER 1839 p. 54 (descr.). Cf. A. L. SMITH 1918 p. 361 (sub *Pertusaria faqinea*). Icon.: J. E. SMITH, English Botany (1812) tab. 2400. *Buellia betulina* (Hepp) Th. Fr. TH. FRIES 1874 p. 610. *Rhizocarpon betulinum* Hepp (1862).

The syntypes of *Variolaria griseovirens* in the British Museum (Natural History), London, examined by me are sterile, but their identity with *Buellia betulina* is quite evident. As names given to sterile (or 'imperfect') states of lichens are valid if otherwise in conformity with

the rules of nomenclature, the well-known epithet *betulina* must be replaced by *griseovirens*.

React.:  $K^{(+)}$  yellow  $\rightarrow$  brownish,  $C=$ ,  $KC=$ ,  $P\mp$  yellow  $\rightarrow$  orange. — Ap. rather frequent, black, concave(—plane); margin thick, prominent.

*Caloplaca chrysothalma* Degel. — DEGELIUS 1944 p. 56.

On old deciduous trees. Probably overlooked; previously known from Öland and Gotland (DEGELIUS l.c.). An unpublished station: U p p l a n d, Ö. Ryd: in the avenue between the church and Rydboholm, on *Fraxinus*, leg. S. AHLNER.

React.: K and  $KC\mp$  dark violet-red,  $C—$  (or orange),  $P=$ . — Ap. rather rare, (brownish—)orange yellow; margin thick, yellow.

*C. herbidella* (Nyl.) H. Magn. — MAGNUSSON 1932 p. 430, 1944 p. 30. Not unfrequent though hitherto overlooked.

React.: K and  $KC+$  dark violet-red (pale forms —),  $C—$  or (+) orange,  $P(+)$  orange. — Ap. rather rare, dark orange; margin thick, flexuose.

*C. microphyllina* (Tuck.) Hasse. — DEGELIUS 1939 p. 186, 1940 p. 142.

Rare (or overlooked), on coarse bark of old trees. Known only from B o h u s l ä n, Skaftö (DEGELIUS l.c.) and S k å n e, Torekov: Hallands Väderö, on *Quercus* and also on rocks (ALMBORN, unpublished).

React.: K and  $KC+$  dark violet-red,  $C—$ ,  $P—$  (soredia orange). — Ap. unknown from Sweden, minute, dark orange; margin orange—greyish, crenulate.

*C. obscurella* (Lahm) Th. Fr. — TH. FRIES 1871 p. 182. HELLBOM 1871 p. 91.

Rare, on deciduous trees in eutrophiated situations.

React.:  $K=$ ,  $C=$ ,  $KC=$ ,  $P=$ . — Ap. not unfrequent, minute, brownish—blackish; margin grey—pale brown, soon disappearing.

*C. phlogina* (Ach.) Flag. — DEGELIUS 1944 p. 57.

Not unfrequent, though rather overlooked, on coarse bark.

React.:  $K+$  dark violet-red,  $C—$  (or orange),  $P—$  ( $\rightarrow$ orange). — Ap. rather rare, yellow; margin thin,  $\pm$  granular.

*Candelaria concolor* (Dicks.) Arn. — HILLMANN 1936 p. 20.

Frequent on eutrophiated bark.

React.:  $K—$ ,  $C—$ ,  $KC—$ ,  $P—$ . — Ap. rather rare, yellow or brownish; margin entire or granulate—sorediate.

*Candelariella vitellina* (Ehrh.) Müll. Arg. — TH. FRIES 1871 p. 188. Frequent in wood in eutrophiated situations, also on bark of old trees. React.: K—, C—, KC—, P—. — Ap. rather frequent, yellow; margin entire or granular.

*C. xanthostigma* (Pers.) Lettau. — TH. FRIES l.c. (pro var.), MAGNUS-SON 1935 p. 122.

Frequent on eutrophiated bark.

React.: as in *C. vitellina*. — Ap. rather rare, minute.

*Catillaria Bouteillei* (Desm.) Zahlbr. — VAINIO 1934 p. 441. DEGELIUS 1944 b p. 23.

Not unfrequent (though hitherto overlooked), mainly on twigs and needles of *Picea* in the outskirts of forests.

React.: K— (or impurely yellow), C—, KC—, P—. — Ap. rather common, yellowish—carneous; margin paler, thin or crenate.

*C. graniformis* (Hag.) Vain. — VAINIO 1934 p. 450. — Syn. *C. Ehrhartiana* (Ach.) Th. Fr. TH. FRIES 1874 p. 570.

Not unfrequent on wood, also on coarse bark, mainly of old oaks.

React.: K<sup>+</sup> yellow, C=, KC=, P=. — Ap. pale—yellow; margin often flexuose.

The name *C. Ehrhartiana* generally used by Swedish and Central European lichenologists must be replaced by *C. graniformis*, as *Lichen graniformis* Hagen (1782), though referring to the spermogoniferous state only, is the valid specific epithet. Cf. the analogous case concerning *Opegrapha fuscella* (ALMBORN 1948 p. 137) and the discussion by HYLANDER (in LANJOUW 1950 p. 162).

*C. prasina* (Fr.) Th. Fr. — TH. FRIES 1874 p. 572. VAINIO 1934 p. 466.

Rather frequent on wood and old bark.

React.: K—, C—, KC—, P—. — Ap. not unfrequent, minute, convex, immarginate, yellow brown—dark brown or blackish.

*C. pulverea* (Borr.) Lettau. — LINDAU 1923 p. 87. A. L. SMITH 1926 p. 134. — Syn. *Pertusaria miniescens* Erichs. (sec. holotype in herb. ERICHSEN, Hamburg, and isotype in herb. A. H. MAGNUS-SON, Gothenburg). ERICHSEN 1938 p. 111. MAGNUS-SON 1942 p. 16.

On old trees, oaks, etc., in woods. Known from some few stations in Bohuslän and Västergötland, but probably overlooked.

React.: K and KC<sup>+</sup> yellow, C=, P<sup>+</sup> yellow → orange → cinnabar. — Ap. probably rather rare, plane (—concave), black; margin thin, persistent, greyish black.

*Crocynia membranacea* (Dicks.) Zahlbr. — Syn. *C. lanuginosa* (Ach.) Hue. *Psoroma lanuginosum* (Ach.) Müll. Arg. (pro p.), LINDAU 1923 p. 150. ANDERS 1928 p. 33. *Lepraria cinereosulphurea* Flk. pro max. p.

Frequent on rough bark, especially overgrowing mosses, also on rocks.

React.: K and KC(+) impurely yellow, C—, P+ pink—brick-red. — Ap. unknown.

*Haematomma coccineum* (Dicks.) Kbr. — TH. FRIES 1871 p. 297.

Rather frequent on old trees, mainly *Quercus* and *Fagus*.

React.: K and KC(+) impurely yellow, C—, P+ yellow. — Ap. not unfrequent, blood-red or reddish brown; margin thick, sorediate.

The species contains several well-separated colour varieties. They are never confluent, though often growing together. Apparently they are genotypically different (not age stages; not due to different illumination), but as there are no other morphological differences than the colour, they cannot retain the rank of species.

var. *coccineum*. — Syn. *H. coccineum* sensu ang. ERICHSEN (1928—) 1930 p. 6. *H. coccineum* var. *ochroleucum* (Neck.) Th. Fr. TH. FRIES l.c. Th. sulphur-yellow.

var. *fuscocinereum* n. var.<sup>1</sup> Th. brownish grey.

var. *porphyrium* (Pers.) Th. Fr. TH. FRIES l.c. — Syn. *H. leiphaeum* (Ach.) Zopf. ERICHSEN l.c. Th. whitish grey.

*H. elatinum* (Ach.) Mass. — TH. FRIES 1871 p. 299. HÖEG 1923 p. 144.

Probably rare (or overlooked) in S. Sweden (more frequent in N. Sweden). Mainly on coniferous trees and *Betula*.

React.: K $\bar{+}$  yellow, C=, KC=, P $\bar{+}$  yellow  $\rightarrow$  orange  $\rightarrow$  cinnabar. — Ap. not very common, reddish brown; margin soon disappearing.

*Lecanactis abietina* (Ach.) Kbr. — LETTAU 1932 p. 30.

Frequent, mainly on coniferous trees, also on old deciduous trees (*Quercus*, *Fagus*, *Alnus*, etc.).

React.: K—, C— (top of pycnidia C+ red), KC—, P+ yellowish. — Ap. not unfrequent, black, covered with a thick, whitish—pale yellowish pruina; margin prominent, concolorous.

*L. amylacea* (Ehrh.) Arn. — LETTAU 1932 p. 35. ALMBORN 1948 p. 31 (map).

Rather rare, mainly on old oaks, especially on the northern sides.

<sup>1</sup> *Thallus fuscocinereus*. — Type locality: Sweden, Skåne, Torekov: Hallands Väderö, on *Fagus*, leg. O. ALMBORN, 1950. Holotype in herb. Lund.

React.: K and KC— (or impurely yellow), C—, P+ yellowish. — Ap. often abortive, but sometimes well developed, black, white-pruinose; margin thin or disappearing.

*Lecanora expallens* Ach. — MAGNUSSON 1927 p. 125. — Syn. *Lecidea soraliata* Vain. VAINIO 1934 p. 401.

Very frequent on all kinds of trees in not too illuminated situations.

React.: K+ yellow, C and KC+ orange → rose-red, P— (or darker yellow). — Ap. not unfrequent (though inconspicuous), pale yellowish; margin sorediate, at length disappearing.

*L. impudens* Degel. — DEGELIUS 1944 p. 50. — Syn. *Pertusaria farinacea* H. Magn. MAGNUSSON 1942 p. 15.

Probably not unfrequent, though hitherto overlooked, on different kinds of bark, especially *Fraxinus*.

React.: K<sup>(+)</sup> yellow, C=, KC=, P<sup>(+)</sup> citrine yellow. — Ap. rare, urceolate—plane, red-brown; margin thick, entire(—crenulate), persistent.

*L. maculata* (Erichs.) n.c. — Syn. see below.

Frequent, mainly on deciduous trees in woods.

React.: K and KC<sup>+</sup> yellow, C=, P<sup>(-)</sup> yellow, orange or cinnabarine. — Ap. rare, plane, brownish; margin thick, ± crenulate, persistent.

The discovery of typical lecanorine apothecia in several Swedish specimens renders it necessary to transfer *Pertusaria maculata* to *Lecanora*, quite as has been the case with the related species *L. impudens* (syn. *P. farinacea*). Both these species belong to the *L. subfusca* group.

*L. maculata* is a variable species:

f. *maculata*. — Syn. *Pertusaria maculata* Erichs. ERICHSEN 1936 p. 646 (descr.). *P. sublutescens* Malme in Lich. suec. exs. No. 868 (1923, nomen solum, non *P. sublutescens* Zahlbr. 1925). *P. chloropolia* Erichs. var. *planiuscula* H. Magn. MAGNUSSON 1942 p. 14. Soredia plane, delimited, c. 0.5 mm. diam., whitish—yellowish grey.

f. *chloropolia* (Erichs.) n.c. — Syn. *Pertusaria chloropolia* Erichs. ERICHSEN 1936 p. 645 (descr.) and 1940 p. 42. MAGNUSSON 1937 p. 131 and 1942 p. 14 (excl. var.). *P. chloropolia* f. *cana* Erichs. ERICHSEN 1936 p. 646. Soredia convex, ± delimited, c. 1 mm. diam., as a rule more distinctly sulphur-grey.

These forms may look rather characteristic in their extremes, but they are combined with numerous transitional stages. ERICHSEN and MAGNUSSON used the P reaction of the soredia as a line of demarcation

between *maculata* and *chloropolia*. In fact there is no correlation between this reaction and the morphological characters.

A detailed revision of this group will appear in a work in preparation.

*Lecidea efflorescens* (Hedl.) Erichs. — ERICHSEN 1932 p. 83. VAINIO 1934 p. 403. — Syn. *L. (Biatora) helvola* (Koerb.) Th. Fr. f. *efflorescens* Hedl. HEDLUND 1892 p. 126. MAGNUSSON 1927 p. 126.

Not unfrequent (though hitherto overlooked), often on *Quercus*.

React.: K=, C=, KC=, P $\bar{+}$  brick-red. — Ap. rather frequent, plane—semiglobose, pale reddish—brownish; margin disappearing.

*L. flexuosa* (Fr.) Nyl. — TH. FRIES 1874 p. 444. LYNGE in VAINIO 1934 p. 343. — Syn. *Biatora flexuosa* Fr.

Rather frequent on wood or on decaying bark of old trees.

React.: K $\bar{+}$  impurely yellow, C and KC $\bar{+}$  rose-red, P=. — Ap. rather frequent, plane, blackish; margin thin, often flexuose.

[*L. Lightfootii* (Sm.) Ach. — VAINIO 1934 p. 315. — Syn. *Catillaria Lightfootii* Oliv.

Not yet known from Sweden. The records by MAGNUSSON (1942 p. 13, Magn. exs. 338) from Bohuslän, Stenkyrka do not belong here. The exs. is *Lecidea flexuosa*.

In Central and Western Europe preferring smooth bark, often *Betula*.

React.: K=, C=, KC=, P=. — Ap. not unfrequent, dark brown or black; margin thin, persistent.]

*L. Nylanderi* (Anzi) Th. Fr. — TH. FRIES 1874 p. 462. VAINIO 1934 p. 201. — Syn. *Biatora Nylanderi* Anzi.

Not unfrequent, mainly on coniferous trees and *Betula* or on lignum.

React.: K=, C=, KC=, P=. — Ap. rather rare, brown or blackish often conglomerate; margin pale, flexuose, persistent.

*L. querneae* (Dicks.) Ach. — TH. FRIES 1874 p. 425. VAINIO 1934 p. 67. — Syn. *Biatora querneae* Fr.

Rather frequent, mainly on deciduous trees, in not too illuminated situations.

React.: K+ impurely yellow, C+ orange, KC+ dark orange, P— or darker yellow. — Ap. not unfrequent, brown or reddish brown; margin disappearing.

*L. scalaris* Ach. — VAINIO 1934 p. 44. — Syn. *L. ostreata* (Hoffm.) Schaer. TH. FRIES 1874 p. 414.

Frequent on rough bark, especially of *Pinus*, also on wood.

React.: K and KC=, C $\pm$  rose-red, P=. — Ap. not unfrequent, blackish, slightly pruinose; margin thin, at length pruinose.

*L. scraliata* Vain., vide *Lecanora expallens*.

*Lepraria aeruginosa* (Wigg.) Sm. — LINDAU 1923 p. 235. ANDERS 1928 p. 209. — Syn. *L. glauccella* (Flk.) Nyl.

Very frequent, mainly in the crevices of rough bark preferring shaded exposition.

React.: K— or impurely yellow, C— KC—, P—, slowly + yellow ( $\rightarrow$ cinnabar). — Ap. unknown.

*L. candelaris* (L.) Fr. — Syn. *L. flava* (Schreb.) Ach. LINDAU l.c. ANDERS l.c.

Frequent on coarse bark of old trees, especially oaks.

React.: K(+) faintly red, C—, KC—, P+ brown-red  $\rightarrow$  orange ( $\rightarrow$ cinnabar). — Ap. unknown.

*L. decolorans* (Turn. et Borr.) Almb. (1948 p. 127). — Syn. *Arthonia impolita* (Ehrh.) Borr. var. *decolorans* Redinger (1937—1938 p. 96). *A. decolorans* Erichs. (1936 b p. 11, 1940 b p. 311). MAGNUSSON 1942 p. 4.

Rather frequent in the crevices of coarse bark, mainly old oaks.

React.: K=, brownish colour of soredia changing to red. C= (not red as stated by ERICHSEN and REDINGER), P=. — Ap. unknown.

*Normandina pulchella* (Borr.) Nyl. — DEGELIUS 1935 p. 99 (map). AHLNER 1942 p. 81 (map). HASSELROT 1948 p. 185.

Rare, mainly in oceanic districts, on deciduous trees, as a rule growing upon bryophytes or other lichens.

React.: K=, C=, KC=, P=. — Perithecia rare (or overlooked), very minute, globose, immersed, superior part visible as dark points.

*Ochrolechia alboflavescens* (Wulf.) Zahlbr. — RÄSÄNEN 1939 p. 61.

Rare (or overlooked; previously not specifically distinguished from *O. pallescens*), mainly on coniferous trees in the N. parts of the district.

React.: K=, C=, KC=, P= (soredia slowly yellow  $\rightarrow$  red-brown). — Ap. rather rare,  $\pm$  urceolate, yellowish—pink, white-pruinose; thalline margin thick, wrinkled—crenulate, persistent.

*O. androgyna* (Hoffm.) Arn. — ALMBORN 1948 p. 76. — Syn. *O. sub-tartarea* (Nyl.) Mass.

Frequent, mainly on rough bark of deciduous trees.

React.: K $\mp$  yellow, C and KC $\mp$  rose-red, P= (soredia slowly yellow  $\rightarrow$

orange). — Ap. rather rare,  $\pm$  urceolate, brownish or yellowish red, not pruinose; thalline margin thick, entire, often sorediate.

f. *roseosorediosa* (Gyeln.) Erichs. ERICHSEN 1944 p. 31. — Syn. *O. roseosorediosa* GYELNIK (1930 p. 391); cf. ERICHSEN 1937 p. 108. Soredia larger than in the type with a pink or red-brown colour. Not rare together with the type. Apparently a growth state with a very slight taxonomic value.

*O. arborea* (Kreyer) n.c. — Syn. *Pertusaria arborea* (Kreyer) Zahlbr. ERICHSEN 1936 p. 545. DEGELIUS 1936 p. 74. ALMBORN 1942 p. 395. *P. myriosora* Erichs. ERICHSEN 1938 p. 113.

Rare (or overlooked), on deciduous trees. At present known from five Swedish stations.

React.: K $\pm$  yellow (not always distinct), C and KC $\ddagger$  rose-red, P= (or faintly yellow). — Ap. very rare (not known from Sweden), plane, reddish, not pruinose; thalline margin rather thin, entire, persistent.

The discovery of apothecia in Russian specimens necessitates the transference of the species to *Ochrolechia*. A detailed treatment of the species will appear in a forthcoming paper.

*O. microstictoides* Räs. — RÄSÄNEN 1936 p. 26. Cf. ERICHSEN 1940 p. 50. Exs. Lich. Fenn. exs. No. 226. Lichenotheca fennica No. 107. — Syn. *Pertusaria silvatica* H. Magn. (pro p.), MAGNUSSON 1942 p. 16. *P. leprarioides* Erichs. var. *silvatica* (H. Magn.) Almb. (pro p.) ALMBORN 1942 p. 397.

Frequent, mainly on wood-trees (non-eutrophiated bark).

React.: K=, C=, KC=, P= (or slowly brown). — Ap. rare, (somewhat urceolate —) plane, light brown, not pruinose; thalline margin thick, granular—sorediate, persistent.

*O. subviridis* (Höeg) Erichs. — ERICHSEN 1942 p. 146. — Syn. *Pertusaria s.* Höeg. HÖEG 1923 p. 150. ERICHSEN 1936 p. 546. ALMBORN 1948 p. 77 (map). *Ochrolechia bahusiensis* H. Magn. (at least pro p.), MAGNUSSON 1927 p. 115. Magn. exs. 4. Cf. ERICHSEN (1928—) 1930 p. 2.

Rather frequent, mainly in the S.W. districts, often on somewhat eutrophiated bark.

React.: K=, C and KC $\ddagger$  rose-red, P=. — Ap. very rare, somewhat concave, light brown, not pruinose; thalline margin thick, granular—sorediate, persistent.

*Opegrapha fuscella* (Fr.) Almb. — ALMBORN 1948 p. 137 (map). — Syn. *O. hapaleoides* Nyl. REDINGER 1937—1938 p. 352.



Rather rare (known from Skåne, Blekinge and Öland), on shaded trunks of old trees, especially *Ulmus*.

React.: K=, later yellowish, C=, KC=, P=. — Ap. rather frequent, elongate, branched or sometimes stellate; disc narrow.

*O. rufescens* Pers. — Syn. *O. herpetica* (Ach.) Ach. ALMQUIST 1869 p. 20. REDINGER l.c. p. 343.

Frequent, mainly on smooth bark.

React.: K=, C=, KC=, P=. — Ap. as a rule frequent, innate, oval or linear, simple or branched, straight or curved; disc black, variable in width; margins rounded and inflexed.

As emphasized by REDINGER the difference in the curvature of the pycnoconidia is too slight to allow a specific separation of *O. herpetica* and *O. rufescens*. The type specimens agree perfectly. The valid epithet of the species is *O. rufescens* Pers. (1794), which is earlier than *Lichen herpeticus* Ach. (1798).

*Pannaria pityrea* (DC.) Degel. — DEGELIUS 1935 p. 105 (map). — Syn. *P. coeruleobadia* (Schleich.) Mass. *P. lanuginosa* (Hoffm.?) Szat. GYELNIK 1940 p. 241.

Rather rare on deciduous trees, mainly *Populus tremula*, preferring oceanic districts.

React.: K=, C=, KC=, P=. — Ap. rare, yellowish red; thalline margin granular—sorediate.

*Parmeliella corallinoides* (Hoffm.) Zahlbr. — GYELNIK 1940 p. 180. — Syn. *Pannaria triptophylla* (Ach.) Arn.

Rather frequent on deciduous trees in woods.

React.: K=, C=, KC=, P=. — Ap. not unfrequent, plane—convex, dark brown; margin paler, red-brown.

*Parmeliopsis aleurites* (Ach.) Nyl. — Syn. *Cetraria aleurites* Th. Fr. *P. pallescens* (Hoffm.) Zahlbr. HILLMANN 1936 p. 36.

Not unfrequent, mainly on coniferous trees, especially *Pinus*, also on wood.

React.: K<sup>+</sup> yellow, C=, KC=, P=. — Ap. not very common, reddish brown; margin granular—sorediate.

*P. ambigua* (Wulf.) Nyl. — HILLMANN 1936 p. 27.

Frequent, on all kinds of bark and on wood.

React.: K= (or impurely yellowish), C=, KC=, P=. — Ap. not frequent, dark red-brown; margin thin, entire or crenulate, sometimes sorediate.

*P. hyperopta* (Ach.) Arn. — HILLMANN 1936 p. 31.

Not unfrequent (rare in the southernmost districts), preferring coniferous trees, often near the ground, also on wood.

React.: K ± yellow, C=, KC=, P=. — Ap. not frequent, brownish, nitidous; margin thin or granular—sorediate.

*Pertusaria amara* (Ach.) Nyl. — HÖEG 1923 p. 152. ERICHSEN 1936 p. 560.

Frequent on different kinds of bark, mainly in rather illuminated situations.

React.: K= (or slowly brownish—reddish), C=, KC± violet-red, P= (or soredia slowly orange—cinnabarine). — Ap. rare, in semiglobose sorediate verrucae; disc immersed, pale reddish, at first covered by a whitish pruina.

ERICHSEN described some species from this form-circle, which, in my opinion, cannot retain the rank of proper species:

f. *pulvinata* (Erichs.) Almb. (1948 p. 76). — Syn. *P. pulvinata* Erichs. (1936 p. 573). Soredia ± diffuse.

f. *slesvicensis* (Erichs.) n.c. — Syn. *P. slesvicensis* Erichs. ERICHSEN 1934 p. 391, 1936 p. 555. ALMBORN 1939 p. 778, 1948 p. 208. Th. papillate, not or little sorediate, ap. frequent. This form can give the impression of a proper species, but transitional stages — »var. *intermedia*» Erichs. (1940 p. 38) — occur often together with it.

*P. arborea* (Kreyer) Zahlbr., vide *Ochrolechia a.*

*P. chloropolia* Erichs., vide *Lecanora maculata* f.

*P. coccodes* (Ach.) Nyl.

Frequent, mainly on rather rough bark, somewhat coniophilous.

React.: K ± yellow, often changing to red (cf. below). C=, KC= (or yellowish), P= (or yellowish). — Ap. rare, in semiglobose verrucae; disc immersed, minute, dark.

Owing to the numerous transitional types occurring, *P. coccodes* and related species, sensu ERICHSEN, had, in my opinion, better be treated as varieties of a collective species:

var. *coccodes*. — Syn. *P. coccodes* (Ach.) Nyl. sensu ang. HÖEG 1923 p. 166 (excl. f.). ERICHSEN 1936 p. 351. Th. dark or light grey, forming granular sorediate isidia, K ± yellow → red.

var. *coronata* (Ach.) n.c. — Syn. *P. coronata* (Ach.) Th. Fr. HÖEG 1923 p. 165. ERICHSEN 1936 p. 394. Th. yellowish grey, forming granular sorediate isidia; K ± yellow.

var. *isidiifera* (Erichs.) n.c. — Syn. *P. isidiifera* Erichs. ERICHSEN 1936 p. 399. Th. grey, forming granular—cylindrical, non-sorediate isidia, K<sup>+</sup> yellow.

var. *phymatodes* (Ach.) n.c. — Syn. *P. phymatodes* (Ach.) Erichs. ERICHSEN 1936 p. 361. *P. coccodes* f. *bacillosa* Nyl. HÖEG l.c. Th. grey (often dark), forming granular—cylindrical (sometimes branched), glomerate, non-sorediate isidia; K<sup>+</sup> yellow → red.

*P. coronata* (Ach.) Th. Fr., vide *P. coccodes* var.

*P. discoidea* (Pers.) Malme, vide *P. globulifera* var.

*P. globulifera* (Turn.) Mass.

Frequent, mainly on deciduous trees in open situations, somewhat coniophilous.

React.: K=, C=, KC=, P=. — Ap. very rare, in  $\pm$  sorediate verrucae; disc immersed, reddish—brown, pruinose.

*P. globulifera* is also a polymorphous species including several varieties ranked as species by ERICHSEN:

var. *globulifera*. — Syn. *P. globulifera* (Turn.) Mass. sensu ang. HÖEG 1923 p. 155 (excl. f.). ERICHSEN 1936 p. 654. Margin of th. containing zones of dark and pale lines; soredia c. 2 mm. diam.

var. *discoidea* (Pers.) n.c. — Syn. *P. discoidea* (Pers.) Malme. ERICHSEN 1936 p. 664. *P. scutellata* Hue. HÖEG 1923 p. 157. Margin not or indistinctly zonate; th. more whitish; soredia large (reaching 6 mm. diam.).

var. *Henrici* (Harm.) n.c. — Syn. *P. Henrici* (Harm.) Erichs. ERICHSEN 1936 p. 671. *P. globulifera* f. *isidiata* Höeg. HÖEG 1923 p. 155. Margin  $\pm$  zonate; th. granular—isidiate, isidia partly dissolved into diffuse soredia.

*P. hemisphaerica* (Flk.) Erichs. — ERICHSEN 1936 p. 541. ALMBORN 1948 p. 65 (map). — Syn. *P. speciosa* Höeg. HÖEG 1923 p. 147.

Rather frequent, mainly in the S.W. districts, preferring old trees in woods.

React.: K=, C and KC<sup>+</sup> dark red, P=. — Ap. unknown.

*P. Henrici* (Harm.) Erichs., vide *P. globulifera* var.

*P. isidiifera* Erichs., vide *P. coccodes* var.

*P. lactea* (L.) Arn. — Mainly a saxicolous species sometimes occurring in a somewhat aberrant corticolous form: f. *faginea* Erichs. ERICHSEN 1936 p. 535.

Rather rare, on deciduous trees.

React.: K=, C and KC $\bar{=}$  rose-red, P=. Ap. very rare (only known from the saxicolous form), in sorediate verrucae; disc immersed, brownish—pink,  $\pm$  white pruinose.

*P. leprarioides* Erichs. — ERICHSEN 1936 p. 678. MAGNUSSEN 1942 p. 15. ALMBORN 1942 p. 396. Magn. exs. No. 352. — Syn. *P. incolorata* Erichs. (in herb.; nomen solum). *P. silvatica* H. Magn. (pro p.) MAGNUSSEN 1942 p. 16. *P. Henrici* (Harm.) Erichs. var. *sepincola* Erichs. ERICHSEN 1929 p. 114, 1936 p. 675, 1940 p. 50. — *Buellia farinosa* Malme (MALME 1923 p. 374) is a *P. leprarioides* affected by the fungus *Leciographa inspersa* (Flk.) Rehm, sec. a holotype in herb. Stockholm. The epithet *farinosa* cannot be used for the present species being a nomen confusum.

Frequent, mainly on eutrophiated bark (near roads, etc.).

React.: K=, C=, KC=, P=. — Ap. very rare, in almost wholly sorediate, semiglobose verrucae; disc immersed, minute, pale brownish.

*P. leptospora* Nitschke. — ERICHSEN 1936 p. 611, ALMBORN 1948 p. 163 (map).

Some stations, mainly on *Fagus* and *Quercus*, in Skåne, W. Småland, Halland and Bohuslän.

React.: K and KC $\dagger$  yellowish, later brownish, C=, P $\dagger$  orange. — Ap. always present, in conic—semiglobose sorediate verrucae; disc plane, yellowish—reddish brown, not pruinose.

*P. lutescens* (Hoffm.) Lamy. — HÖEG 1923 p. 160. ERICHSEN 1936 p. 648.

Frequent, mainly on deciduous trees, in woods.

React.: K= (or yellowish), C and K $\dagger$  orange, P=. — Ap. rare, immersed in sorediate verrucae; disc minute, blackish brown.

*P. maculata* Erichs., vide *Lecanora m.*

*P. miniescens* Erichs., vide *Catillaria pulvereae*.

*P. multipuncta* (Turn.) Nyl. — HÖEG 1923 p. 145. ERICHSEN 1936 p. 605. ALMBORN 1948 p. 167.

Rare in S. Sweden (more frequent in N. Sweden), mainly on *Alnus* and *Betula*.

React.: K=, C=, KC=, P=. — Ap. always present, in rather flat sorediate verrucae; disc plane, greyish—black, usually pruinose.

*P. myriosora* Erichs., vide *Ochrolechia arborea*.

*P. phymatodes* (Ach.) Erichs., vide *P. coccodes* var.

[*P. pulvereo-sulfurata* Harm. — ERICHSEN 1936 p. 679.

A dubious species. A comparison with an isotype (from France, Cheniménil, leg. Harmand) in herb. Hamburg has revealed that the two Swedish records of *P. pulvereo-sulfurata* are not correct. The type is a plant somewhat similar to *Haematomma elatinum* though it has much finer soredia. The specimen from Bohuslän, N. Skaftö (DEGELIUS 1939 p. 151) is young and not determinable with certainty. It is granular—verrucose with very slightly developed soredia, which are not so finely pulverulent as in the HARMAND specimen. Moreover, it has a distinct white hypothallus. Probably it belongs to *Haematomma coccineum*. The record Halland, Hasslöv (ALMBORN 1942 p. 399) refers to a young *P. lutescens*.

React. (in the isotype): K and KC $\frac{+}{-}$  yellow, later brownish, C=, P=. — Ap. unknown.]

*P. pulvinata* Erichs., vide *P. amara* f.

*P. silvatica* H. Magn., vide *Ochrolechia microstictoides*.

*P. slesvicensis* Erichs., vide *P. amara* f.

*P. sordidogrisea* Erichs. — ERICHSEN 1940 p. 32. MAGNUSSON 1942 p. 17. ALMBORN 1942 p. 399.

Rare (or overlooked), on coarse bark in eutrophiated situations. Known from some stations in Skåne, Blekinge, Halland, Bohuslän and Västergötland.

React.: K and KC= (or soredia yellowish), C $\frac{+}{-}$  red, P=. — Ap. unknown.

*P. subviridis* Höeg., vide *Ochrolechia s.*

*Phlyctis agelaea* (Ach.) Flot. — HÖEG 1923 p. 173.

Not unfrequent, mainly on smooth bark, often on *Fraxinus*, *Sorbus aucuparia*, etc.

React.: K  $\left\{ \begin{array}{l} - \text{ or impurely brown-red} \\ + \text{ yellow} \rightarrow \text{orange} \rightarrow \text{rust-red, C=, KC=, P}\frac{+}{-} \text{ yellow, soredia} \rightarrow \text{orange.} \end{array} \right.$  — Ap. always present, in sorediate verrucae; disc blackish, grey- or white-pruinose.

*Phl. argena* (Ach.) Flot. — HÖEG 1923 p. 174.

Very frequent on different kinds of bark, mostly in somewhat shaded situations.

React.: K<sup>+</sup> yellow→orange→rust-red, C=, KC=, P<sup>±</sup> yellow, soredia→orange. — Ap. rather rare, in sorediate verrucae; disc blackish, white-pruinose.

f. *erythrosora* (Erichs.) n.c. — Syn. *Phl. erythrosora* Erichs. ERICHSEN 1939 p. 75. ALMBORN 1939 p. 773. MAGNUSSON 1942 p. 17. Soredia more distinctly delimited, rounded, pink. This form is very characteristic in its extremes but it is connected with the type through numerous transitions.

*Physcia elaeina* (Sm.) A. L. Sm. — DU RIETZ 1923 p. 87. MAGNUSSON 1935 p. 123. — Syn. *Ph. adglutinata* (Flk.) Nyl.

Rare (or perhaps overlooked); only two Swedish stations known: G o t l a n d, Visby (on *Abies*) and B o h u s l ä n, Solberga (on *Ulmus*), both in dust-impregnated situations.

React.: K=, C=, KC=, P=. — Ap. very rare (unknown from Sweden), minute, blackish brown; margin entire.

*Rinodina colobina* (Ach.) Th. Fr. — MALME 1915 p. 253. DU RIETZ 1923 p. 86. MAGNUSSON 1947 p. 319.

Not unfrequent (though often overlooked), at the base of deciduous trees in eutrophiated situations.

React.: K<sup>±</sup> yellow→red, C=, KC=, P=. — Ap. usually scarce, ± plane, black; margin thick, prominent, grey.

*Toninia caradocensis* (Leight.) Lahm. — MAGNUSSON 1927 p. 120. ALMBORN 1948 p. 206.

Rare (or perhaps overlooked; only some stations in Bohuslän and Västergötland known), especially on coniferous trees and *Betula*, also on wood.

React.: K=, C and KC± yellowish (or orange), P=. — Ap. scarce, black; margin usually flexuose.

*Xanthoria candelaria* (L.) Arn. — DU RIETZ 1921 p. 185. HILLMANN 1935 p. 23.

Frequent, on eutrophiated bark.

React.: K and KC± dark violet-red, C± pale reddish. P=. — Ap. not very unfrequent, yellow; margin entire or somewhat sorediate.

*X. fallax* (Hepp) Arn. — DU RIETZ l.c. — Syn. *X. substellaris* (Ach.) Vain. HILLMANN l.c. p. 28.

Rather frequent, on eutrophiated bark.

React.: as in *X. candelaria*. — Ap. rather rare, orange-yellow; margin often sorediate.

*Xylographa spilomatica* (Anzi) Th. Fr. — TH. FRIES 1874 p. 639.  
REDINGER 1937—1938 p. 207.

Mainly on wood, rarely on living bark. Rare in S. Sweden (not unfrequent in N. and Central Sweden).

React.: K and KC<sup>+</sup> citrine yellow → orange, C=, P<sup>+</sup> yellowish—brown. — Ap. sometimes frequent, sometimes quite lacking, elliptical; disc concave, reddish brown; margin thin, darker brown.

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## Evolutionary studies on the shape of the cell and of the chloroplast in desmids.

By EINAR TEILING.

»A modern biologist is no longer satisfied with the terse statement of CUVIER, according to whom the task of an investigator is to 'nommer, classer, et décrire'. He wishes to know something about the causes which make an individual what it is, and which make different individuals similar in some respects and different in others.»

T. DOBZHANSKY: Genetics and the origin of species.

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### 1. Introduction. Basic morphological types.

When, more than a century ago, MENEGHINI and RALFS first produced order and system into the bewildering multiplicity of the desmids then known, the three main types *elongate*, *compressed*, and *angular* were used as important characters of the cell shape. Though these types, among themselves, exhibit so many points of agreement that the desmids *sensu stricto* stand out as an extremely clearly delimited taxon,

very little investigation has been made of the forces which have been active in the formation of these very different types.

The present author (1950) has submitted a theory that the compressed, *i.e.* biradiate, desmids are derived from angular, *i.e.* pluriradiate ones, and that the latter are descendants of short, circular ancestors and, further, that this evolution has been induced by an ecological factor, namely light.

Apart from some small genera with laminated chloroplast, there is one character occurring in the vast majority of the desmids, *viz.* the radiate chloroplast. This common feature is, in certain cases, not immediately visible but a comparative morphological examination reveals its surprising constancy.

The author (1950) has shown how the chloroplast of the anguloradiate (compressed and angular) desmids, being the majority of the placoderms, probably have arisen from a primitive radiate chloroplast which functioned in ancestral desmids, circular *a vertice*. The radial enlargement of the radiate lamellae of the chloroplast favoured greater photosynthesis and connected with this there occurred a corresponding change of the cell-wall so that the primitive short-cylindrical shape evolved into an angular one, each angle containing the outgrown distal part of a lamella of the chloroplast. An extreme radial enlargement has given rise to the long processes characteristic of many *Staurastrum*. Among these pluriradiate desmids there has, during their evolution, occurred a reduction of the angles and this evolutionary path, common and very important within the animal as well as the vegetable kingdom, has gradually given rise to quadriradiate, triradiate and biradiate forms.<sup>1</sup> The last represent the end-stage and is characteristic of the majority of the placoderm desmids, *Cosmarium*, *Euastrum*, *Micrasterias* etc. The trend of reduction is to be comprehended as a further result of selection performed by the light factor; it gives the chlorophyll a better exposition to light. Indeed, the compressed biradiate end-stage is an equivalent to the flattened or leaf-like shape of the photosynthetic organs of the multicellular green plants.

It is now my intention to submit my view of the part played by light-ecological agents in the phylogeny of the desmid chloroplast as well as the connecting causative formation of the shape of the desmid cell. Finally a consequent summary of the chloroplast of the desmid genera is given in accordance with the more adequate terminology which I have used here.

<sup>1</sup> In culture KALLIO (1951) has produced uniradiate facies of *Micrasterias*.

## 2. Historical survey.

In the beginning of desmidiology, when there were only primitive microscopes, the external morphology was the sole descriptive character. Later on, better microscopes made it possible to complete the diagnoses of the rapidly increasing number of species with internal characters. The chloroplast, its shape, position and number of pyrenoids became over-emphasized and were given a too great part both in taxonomy and biosystematy. This was done on the assumption that these characters are constant and specific, but without sufficient knowledge of the structure of the chloroplast; for instance the concepts of axile and parietal were comprehended as contrasting characters.

The first scientist who devoted special attention to these subjects was LÜTKEMÜLLER (1893 and 1895). His papers, however, did not succeed in stimulating research in this direction until NELLIE CARTER in 1919 and 1920 published a comprehensive, objective examination, founded on good methods, of numerous desmid species belonging to the more important genera. This standard-work is still our most important source of knowledge on this subject. I am glad to express a sincere estimation of this excellent work which has, to a large extent, been the basis on which I have worked.

GAY (1884, p. 16) seems to have been the first who summarized the contemporary knowledge and devised a system of chloroplast types. It is quite artificial; the axil »chloroleucites en plaques» contain the type of *Mougeotia* as well as the type of *Micrasterias*. 53 years later, the system of CZURDA is constructed similarly. He (1937, p. 55) distinguished six types: 1. Plattenförmige. 2. Morgenstern- bis rippenwalzenförmige, Beispiele: *Zygnema*, *Cylindrocystis*, *Penium*. 3. Chromophoren, welche um ein zentral gelagertes Pyrenoid flache, den Zellenraumverhältnissen angepasste Lappen oder entsprechend angeordnete kurze Leisten führen, Beispiel: *Cosmarium*. 4. Flächig ausgebildete Chromatophoren mit zahlreichen, gleichmässig verteilten Pyrenoiden, Beispiel: *Micrasterias*. 5. Unregelmässig verlaufende, ungefähr bandförmige Chromatophoren mit einreihig angeordneten Pyrenoiden, Beispiel: *Pleurotaenium*. 6. Schraubenbandförmige, dabei ebene oder rinnenförmige, an der Wand verteilte Chromatophoren mit mehreren, verschieden grossen Pyrenoiden, Beispiel: *Spirotaenia*, *Spirogyra*. FRITSCH (1935) has given a short survey of the desmid chloroplast from a morphological point of view.

### 3. The chloroplast.

In the following a chloroplast is defined as a chlorophyllous organel of the desmid protoplast. This simple definition must be used because it is often impossible to decide whether the visible green parts are isolated or joined at the basis of the semicell. Sometimes the word chloroplast must be used in a collective sense signifying the total mass of the chlorophyll of a semicell not considering shape or parts.

The chloroplast is irritable and contractile, several factors cause changes of its volume, shape and consistency. It is difficult, sometimes impossible, to examine living chloroplasts of complicated structure and preserving liquids often change the details. The research method of fixing, staining, and cutting, so successfully performed by N. CARTER, is very intricate and time-consuming and thus has been avoided by later scientists. The culture of desmids is difficult and often gives rise to degenerative and teratological forms. CZURDA emphasizes that the chloroplast degenerates in culture especially because of a lack of carbon dioxide as well as through changes in other ecological conditions, which are in many cases unavoidable.

The main features of the chloroplast show an evident constancy when, by means of comparative studies, their phylogenetical evolution is followed. Certain parts of primitive character, *viz.* the lamellae especially of the furcoid chloroplast may be distinguished in their development through the genera. As in all comparative morphology, it is a *conditio sine qua non* to distinguish between homologous and analogous details and features in order to avoid the sources of error dependant on biological convergency. These points of view have hardly been used in desmidiological research, as will be shown hereafter.

A great many descriptive desmidiologists have mentioned and sometimes also figured the chloroplasts. Most of the figures, however, must be examined critically for they often conceal sources of errors. The three-dimensional structure is difficult to comprehend and the investigator is seldom artist enough to give a quite clear figure even when it is correctly understood. The most valuable informations may be obtained from the works of G. S. WEST, GRÖNBLAD, and SKUJA but others also, *e.g.* DELPONTE and NORDSTEDT, have given reasonably good figures. Dr. GRÖNBLAD is worthy of a special recognition in this respect and I am likewise much obliged to him communicating to me valuable drawings of chloroplasts. It should be extremely valuable for our science if the active desmidiologists devoted their attention to the

chloroplast, this organel being in many cases variable and our knowledge of it very incomplete. A figure *a fronte* is often of little or no value, it must be combined with figures *a vertice* in optical sections.

#### 4. Terminology.

Since the following investigation discusses a subject, previously dealt with in more general terms, it is necessary to define the terms used. Some of them were created by TEILING (1950) and are as yet little known, others must be newly created.

*Omniradiata* is the term for a cell circular *a vertice* if the isodiametry is primitive. Certain desmids having the same shape, however, are derived from bi- or triradiate, (perhaps also from pluriradiate) angular cells, and such are called *pseudo-omniradiata*. In many cases this latter form seems to be constant; in other cases a broad oval form occurs either as variation of the pseudo-omniradiate species, in other species this character constitutes a definite form and may conveniently be called *quasi-omniradiata*. The angular and compressed cells are termed *angulo-radiata* and may be bi-, tri-, quadri-, quinque-radiate and so on. The most remarkable difference within this series is the one between biradiate and pluriradiate (*i.e.* more than two). This difference has been frequently used in biosystematy and also in taxonomy, the terms *sensu* CAMP 1951.

The old concepts axile and parietal have not been defined nor can they be; they are relative. As axile has been meant a chloroplast having most of its chlorophyll round the vertical axis where the pyrenoids normally are situated; the parietal chloroplast has the greater part of its green mass and the pyrenoids in the distal parts of the semicell. Neither of the terms says anything about shape or structure. Even the axile chloroplast may have most of its photosynthetically active parts in a parietal position, *e.g.* in certain *Staurastrum* it is axile in structure and parietal in function. In order to satisfy the need of a term for transitional forms GRÖNBLAD (1924, p. 11) has proposed the term *pseudo-parietal*. Axile and parietal may be used in a general sense in order to indicate the average distribution of the pyrenoids but never in order to indicate a biosystematical character.

The axile types of chloroplast may conveniently be divided into *monocentric*, *dicentric*, and *tetracentric*. The monocentric chloroplast, containing one or more central pyrenoids is the most frequent type of the stellate chloroplasts in small angulo-radiate

desmids, the *Cosmaroids* and the *Staurastroids* for instance, and in most of the elongated desmids, e.g. *Penium* and *Closterium*. In the latter the term monocentric would more correctly be replaced by *monaxil*; the long axis usually contains a row of pyrenoids. The dicentric type occurs in rather large biradiate desmids, e.g. *Cosmaria* and *Euastra*, the mass of chlorophyll is divided in two parts each of them containing one (group of) pyrenoid(s). Tetracentric means the stage where the chloroplast is divided into four parts each with one (group of) pyrenoid(s). The location of the pyrenoids in the ends of the ramified chloroplast represents a separate type, called *pericentric*.

The parietal chloroplast *sensu stricto* is very rare. It consists of several parts, plates or ribbons, or, exceptionally, of one tubular part which as well as the pyrenoids have a parietal position without or with a reduced axile part. It has evolved from ancestral axile form (G. S. WEST 1916) in diverse ways and represents the results of a general trend to parietal position of the chlorophyll, a position most favourable to photosynthetic activity. This neglected point of view is, as far as I can find for the first time submitted by JACOBSEN as early as in 1874 and strongly stressed by ELFVING (1889). The parietal chloroplast *sensu stricto*, being an adaptation of an organel fairly easily influenced by evolutionary agents, has developed in diverse manners and at various stages of the evolution. Thus, it has proved necessary to use new terms in order to keep the different concepts separate. These are defined below and enumerated on page 284.

Expedient reasons speak in favour of a terminological diversity between the primitive stellate chloroplast of the saccoderm and lower placoderm genera (*Penium* and *Closterium*), it is called *stelloid*, and on the other side the stellate chloroplast of the placoderm tribus *Cosmarieae* which is called *furcoid*. Both consist of an axile core with pyrenoid(s) and a number of longitudinally radiating lamellae. The lamellae of the furcoid type have their free edges longitudinally divided into *semilamellae* and in its advanced forms there are longitudinal secondary *ridges (cristae)* from the basis of the lamellae. In many cases these ridges play a dominant rôle in the structural development of the chloroplast.

## 5. Leading lines of the evolution of the desmid shape and chloroplast.

As in other green plants, light has been the most important factor in the evolution of the desmids and the morphological changes for

obtaining a maximal exposition to light discerned among the higher plants, are also relevant for the desmid morphology, *i.e.* enlargement and favourable disposition of the chlorophyll and phototaxis, features modified according to the unicellular organisation. The methods are as follows:

1. enlargement of the chloroplast
  - a) in apical direction,
  - b) in radial direction.
2. placing the chlorophyll in a more exposed position, by means of
  - a) transferring the chlorophyll from axile to parietal position,
  - b) transferring the cellwall close to the chloroplast.

Besides these main methods, a favourable exposition may be attained by development of ridges, papillae and marginal extensions.

Because of the morphological agreement between the shape of the cell and the contour of the chloroplast the methods mentioned above correspond to the basic shapes of the cell as follows:

1. a) elongate cells,
  - b) angular and inflated cells,
2. a) large cells,
  - b) compressed cells and angular cells with hollow processes.

The final shape of the desmids is in most cases the result of combinations of several of these basic features.

## 6. The stelloid chloroplast.

As the phylogenetical ancestral forms of the desmids one must imagine forms with a short stelloid chloroplast. Of their descendants those forms have proved most successful which have a more effective chloroplast. From this point of view it is possible to eliminate the subsequent morphological changes and distinguish a probable prototype, *viz.* the stelloid type shortly characterized above. Actually, it is possible to derive the chloroplasts of all desmids from this prototype.

The stelloid chloroplast occurs in the saccoderms and the lower placoderms, *viz.* the tribus *Penieae* and *Closterieae*. In the higher placoderms with a permanent fissure of division, *viz.* the tribus *Cosmarieae*, the stelloid chloroplast is represented in *Docidium*, *Pleurotaenium*, and the little primitive group of omniradiate and more or less elongated desmids, here called the *Clevei*-section of *Cosmarium*, dealt with later.

The stelloid chloroplast has enlarged its surface by means of vertical elongation, the course can be followed in the series: *Cylindrocystis*,



*Spirotaenia*, *Netrium*, *Penium*, *Closterium*, the *Clevei*-section, and *Docidium-Pleurotaenium*. The number of the lamellae is variable, normally 6—8, but it may be increased to about the double in large forms but also reduced to two in desmids with laminate chloroplast, *viz.* the saccoderm small genera *Mesotaenium*, *Ancylonema*, and *Roya* and the placoderm genus *Groenbladia* nov. gen. (pag. 275).

In smaller forms of the following types there is one axile pyrenoid. With increasing elongation the pyrenoids increase in number or, in certain cases, in length. With increasing thickness of the cell the pyrenoids migrate to the peripheral region of the chloroplast. Parietal chloroplast occurs in *Spirotaenia* and *Pleurotaenium* (taenioparietal) and *Closterium* (holoparietal).

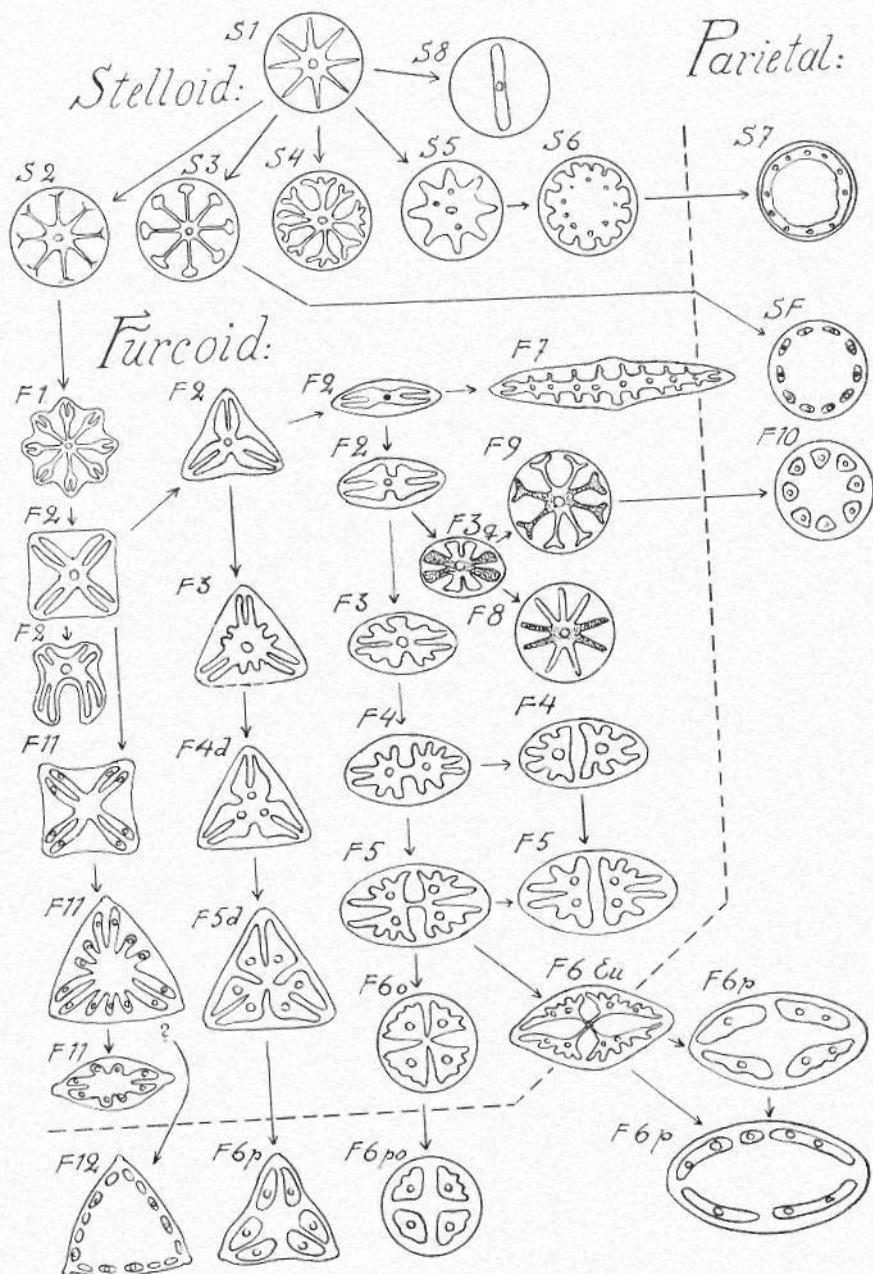
Type S 1. (fig. 1) is the primitive simple stelloid chloroplast with entire lamellae characteristic of *Penium* and the *Clevei*-section of *Cosmarium*.

Type S 2. has incised lamellae and the lappets being usually more or less bent aside. It occurs in *Cylindrocystis* and *Netrium*. In the schematic survey of these types (fig. 1) and their relations this type is apprehended as a typologically connecting link between the pure stelloid and the furcoid chloroplast.

Type S 3. has the edges of the lamellae thickened or transversally flattened sometimes to such a degree that only these parts, similar to ribbons, are visible which gave rise to the opinion that *Spirotaenia* possessed parietal chloroplasts. This was corrected by LÜTKEMÜLLER (1895) who stated that the chloroplast of certain species (the subgenus *Polytaeniae*) is axile and stellate with extended edges of the lamellae and axile pyrenoids. LÜTKEMÜLLER (1893) also examined *Pleurotaenium minutum* (RALFS) DELP. (by him called *Docidium baculum*), where he found transitorial forms from the primitive stelloid chloroplast developing in the direction of a parietal one, in which there had occurred a migration of the pyrenoids from axile to parietal position. These examples show how the taenio-parietal chloroplast has evolved from a stelloid type, nearest to S 3; the flattened edges of the lamellae have been the seat of the chlorophyll and the pyrenoids and the proximal parts and the core have disappeared, thus forming the

Type SF. *Spirotaenia* (subgenus *Monotaeniae*) and *Pleurotaenium* both belong partly to this type. Of the latter some species have a stelloid chloroplast (GRÖNBLAD 1924) but most of the genus represent an advanced type of taenioparietal chloroplasts. Irregularities of the ribbons, for instance the polygonal plates occurring in several species, *e.g.* *coronatum* and *ovatum*, depend on an original anastomosis of the lamellae, such as is known to occur in *Docidium*, *Spirotaenia* and *Closterium*.

The types S 4—S 7 are confined to *Closterium*. Its richness in diversity in the structure of the chloroplasts is impossible to concentrate into a few types, all the more the variation within the species is great, especially in the large species. The chloroplast of *Closterium* is in its evolution not to be compared with the cylindrical stelloid chloroplasts, where the development of the basal and the apical parts is uniform. On the other hand, the light-ecological condi-



tions for the conical chloroplast are very different in the thick basal and the slender apical parts, especially in the case of the large species. The smaller *Closteria* possess a simple chloroplast according to type S 1, as do the apical part of the chloroplast of the large species.

S 4. In this type the core is rather reduced in thickness (fig. 23), especially in the slender parts of the chloroplast to such an extent that adjacent lamellae seem to be attached on longitudinal elevations (N. CARTER 1919 a, t. 15: 29, 32, 41, 42). The basal parts of the core are thicker and cylindrical and the section of the chloroplast appears as type S 6. Examples are: *Cl. regulare*, *costatum* (fig. 23), and *striolatum* (N. CARTER 1919 a, t. 15: 30, 34, 43).

S 5. Here the median part of the chloroplast show a thickened core bearing a fairly large number of lamellae; a transverse section gives the figure of a cog-wheel with triangular, staff-like or rounded cogs. This applies also to the attenuate apical parts even where the lamellae of the median part are simple with the edges acute, thickened or parietally extended, or split up in longitudinal strips.

Type S 6. has the core and the lamellae more thickened (N. CARTER, 1919 a, t. 15: 46), a stage towards the parietal position of the chlorophyll accompanied by an augmentation and parietal position of the pyrenoids, *Cl. laterale* (GRÖNBLAD 1945, t. 1: 11).

Type S 7. This trend has culminated in this type found in *Closterium Ehrenbergii* of which drawings have been kindly sent me by Dr. GRÖNBLAD (fig. 25). The chloroplast consists of a conical layer with scattered pyrenoids. This type of parietal chloroplast differs both in genesis and structure from other parietal chloroplasts. Consequently it must be distinguished by a special term: *holo-parietal*.

Normally the chloroplast of *Closterium Ehrenbergii* belongs to type S 6 often showing a beginning desorganisation of the axile part of the core and parietal pyrenoids.

Type S 8. The laminate chloroplast in the desmids will be dealt with separately.

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Fig. 1. Series of stelloid chloroplasts: S 1—S 6 diverse stelloid, S 7 holo-parietal, S 8 laminate. SF taenio-parietal. Furcoid chloroplasts: F 1 primitive, F 2 quadri-, tri-, and biradiate monocentric, F 3 tri- and biradiate monocentric with ridges, F 3 q biradiate with ridges in quasi-omniradiate cell, F 4 dicentric, F 4 d dicentricoid, F 5 tetracentric, F 5 d tetracentricoid, F 6 Eu tetracentric stage of *Euastrum*-type, F 6 p biradiate sector-parietal, F 6 o tetracentric in pseudo-omniradiate cell, F 6 po sector-parietal in pseudo-omniradiate cell, F 6 p bi-, and triradiate sector-parietal, F 7 discoid (biradiate), F 8 pseudo-stelloid, F 9 pseudo-stelloid with flattened edges, (in the figures of F 3 q, F 8 and F 9 the primary semilamellae are dotted), F 10 limbo-parietal, F 11 tetra-, tri-, and biradiate pericentric, F 12 limbo-parietal derivation of the pericentric type. — The interrupted line indicates the limit between the concepts axile and parietal chloroplast. The arrows indicate the paths of evolution presented in this paper and the small circles represent pyrenoids. — S 7 is drawn after drawings of GRÖNBLAD, F 12 is the result of a construction. The other figures are somewhat simplified copies after figures selected in the desmid literature.

## 7. The laminate chloroplast.

The laminate chloroplast occurs in cylindrical cells and consists of one, rarely two, axile plates with one or several axile pyrenoids, according to the length of the chloroplast. Sometimes it consists of 3—6 longitudinal lamellae which indicates that the typical laminate chloroplast consists of two lamellae joined in an axile core where the pyrenoids are situated. It represents an end-stage of reduction, a path of evolution more common amongst desmids having a furcoid chloroplast. The desmids with a laminate chloroplast are small and often rare and thus not so well known. A comparison of the known cases, however, shows that the derivation of the laminate from the stelloid chloroplast, as described above, is most probable. Genera with laminate chloroplast are the saccoderm genera *Mesotaenium*, *Ancylonema*, *Roya* and the placoderm new genus *Groenbladia* (p. 275).

In this connection another kind of laminate chloroplast may be mentioned, viz. the one of *Micrasterias* spp. which must be derived from furcoid ancestors. It possesses the furcoid edges of the two lamellae and the frontal ridges characteristic for the furcoid chloroplast. Secondary ridges are not found on stelloid chloroplasts.

*Mesotaenium* possesses ordinarily a laminate chloroplast but DE BARY (1858, p. 31) emphasized that some of the cells of *M. Braunii* contain »drei, selten sogar vierstrahligen Chlorophyllkörper, aus 3 oder 4 Längsplatten bestehend» (shown in t. 1:1, 3, 4). *Ancylonema* has an axile laminate chloroplast but is suggested by NORDSTEDT to have the chloroplast in parietal and oblique position (WILLE 1890, fig. 6 B). In *Roya* which ordinarily contains a laminate chloroplast, there sometimes occurs a stelloid chloroplast with four lamellae, according to GRÖNBLAD (1935, p. 3, f 1—4). The same occurs in *Gonatozygon* which usually has a laminate chloroplast. Already in 1858 DE BARY drew *G. monotaenium* with a stelloid chloroplast consisting of three lamellae and GRÖNBLAD (1948, p. 9, fig. 1) has found chloroplasts with four and even six lamellae.

RACIBORSKI, the inventor of *Hyalotheca neglecta*, has not mentioned the chloroplast at all in his diagnosis (1895, p. 31) nor have the WESTS (1897) but later G. S. WEST (1898) has figured a laminate chloroplast without any comment, remarking, however, on »a considerable variation in the pyrenoids». In Monograph V, WEST and N. CARTER described the »chloroplast axile, one in each semicell, typically with a single central pyrenoid in each, and plate-like, so that when viewed from the

edge it seems very narrow, just as in *Mougeotia*. Even here the significance of this peculiar chloroplast is neglected, though it is admitted that these »chloroplast are rather unusual for the genus *Hyalotheca*, although chloroplasts of this type occur, amongst other Desmidiaceae, in the genus *Mesotaenium*.

Probably, RACIBORSKI placed his new species in *Hyalotheca* on the basis of the shape of the cell: cylindrical or slightly barrel-shaped, often with a slight isthmusfurrow, always visible because of its lack of pores. These characteristics, however, are insignificant, occurring in other placoderm genera. *Hyalotheca* is clearly pseudo-omniradiate; in *H. dissiliens* there are forms with two or three small prominences on the cellwall, indicating bi-, and triradiate *facies* (TEILING 1950, p. 307). According to the shape of the cell the chloroplast is pseudo-stelloid, in *dissiliens* stated with varying number of lamellae and ridges, 6 (BOURRELLY 1946, fig. 24—25), 7 (WEST's Monograph V, t. 161: 19), 8 (IRÉNÉE-MARIE 1939, t. 62: 2), 9 (ACTON 1916, t. 8: 1) and 10 (TAYLOR 1935, t. 49: 16).

The chloroplast of *neglecta* is described as axile and laminate by all authors who have dealt with it. It consists of one axile, thin plate, often somewhat incised in the middle, but sometimes there are two (incipient division of the cell?), the pyrenoids are two or, in longer cells, four. Of especial interest is GRÖNBLAD's statement of triradiate chloroplasts (1921, p. 64). This quite agrees with the variation of the chloroplasts of *Mesotaenium*, *Roya*, and *Gonatozygon*, and it is thus most probable that *neglecta* has a stelloid chloroplast, ordinarily reduced to two opposite lamellae. This chloroplast places *neglecta* in an isolated position without any connection to *Hyalotheca* and all known placoderm genera and makes it necessary to establish a separate genus for *neglecta* and some desmids, classified as varieties of *H. indica*, which also possess an axile laminate chloroplast.

According to the true omniradiate cells, the slight isthmus furrow and the stelloid chloroplast, its taxonomic position may be among the primitive genera of the tribus *Cosmarieae*, represented by the *Clevei*-section.

### *Groenbladia*, n. gen.

Cellulae cylindriformes vel leviter doliformes, saepe isthmo leviter constricto; filamenta breviter formantes, muco amplo circumdata. Membrana tenuis poris in circulos transversales — interdum sparsis cir-

culis singulis utrimque ad isthmum — ordinatis, praeter in area ipsius isthmi. Massa chlorophyllacea in utraque cellula laminis axilibus singulis — vel interdum lamellis tribus e centro radiantibus; nucleis amylaceis singulis vel binis. Zygosporae globosae vel citrifformes(?), membrana glabra.

*G. neglecta* (RACIBORSKI) n. comb.

*G. fennica* (GRÖNBLAD) n. comb. Synonyms: *Hyalotheca indica* f. *fennica* GRÖNBLAD (1921, p. 64, t. 6: 11), *H. indica* v. *sparsipunctata* GRÖNBLAD (1920, p. 84, t. 4: 32—33).

Dr. GRÖNBLAD has, *in litt.*, communicated that the forms of *H. indica*, described by him, only with some hesitation may be classed among TURNER'S *H. indica*. This species is very insufficiently described; the chloroplast is not mentioned and the dotted outlines of the chloroplast (from material fixed in alcohol 30 years earlier) give no clear idea of its shape. That is why TURNER'S *H. indica* must be regarded as a dubious species and it can not be taken into consideration in a question concerning the chloroplast.

### 8. The furcoid chloroplast.

The second method of increasing the surface exposed to light is by enlargement in the radial direction. This is realized only in genera belonging to the tribus *Cosmarieae* LÜTKEM., a circumstance which, as will be shown later, is due to the permanent fissure of the cell-division and the consequently fixed organisation of the isthmus.

The radiate extension of the lamellae is connected with corresponding inflations of the cell-wall in which the distal parts of the grown out lamellae are situated thus forming the angular shape of the semicell. A further enlargement of the lamellae has entered in the longitudinal bipartition of their distal edges. This makes the lamellae *a vertice* like forks, hence the term furcoid. This bipartition can be so complete that the two parts of the lamella form fictitious double lamellae. As these halves of a lamella are important concepts in the discussion of the phylogeny they will be termed *semilamellae*. In this respect the semilamellae must be kept separate from the laterally protruding secondary ridges (or *cristae*) so very common, especially among the biradiate desmids, and not infrequently forming the main part of the chloroplast. These two concepts are not homologous and in particular because of their analogous changes in the complicated development of the large biradiate desmids it is necessary to keep them separate, an aim often

very difficult and indeed sometimes impossible to obtain. The primary lamellae alone correspond to the radiate structure of the angular desmids, secondary ridges only exceptionally correspond to small processes of the cell-wall, always on the frontal parts, fig. 15, 16, 17.

The trend for the enlargement of the edges of the stelloid chloroplast previously dealt with, is a general and more effective feature of the angulo-radiate desmid's: the forked lamellae. This type is, however, confined to genera of the tribus *Cosmarieae*; the exceptions are the *Clevei*-section of *Cosmarium* and *Docidium* and *Pleurotaenium*. In certain genera the basal parts of the lamellae, often enlarged by secondary ridges, form the preponderant part of the chloroplast, for instance in the most flattened species of *Micrasterias*, but even in several of these species the forks of the two lamellae are still visible.

The evolution of the furcoid chloroplast can be followed gradually and the most prominent types are distinguished as follows.

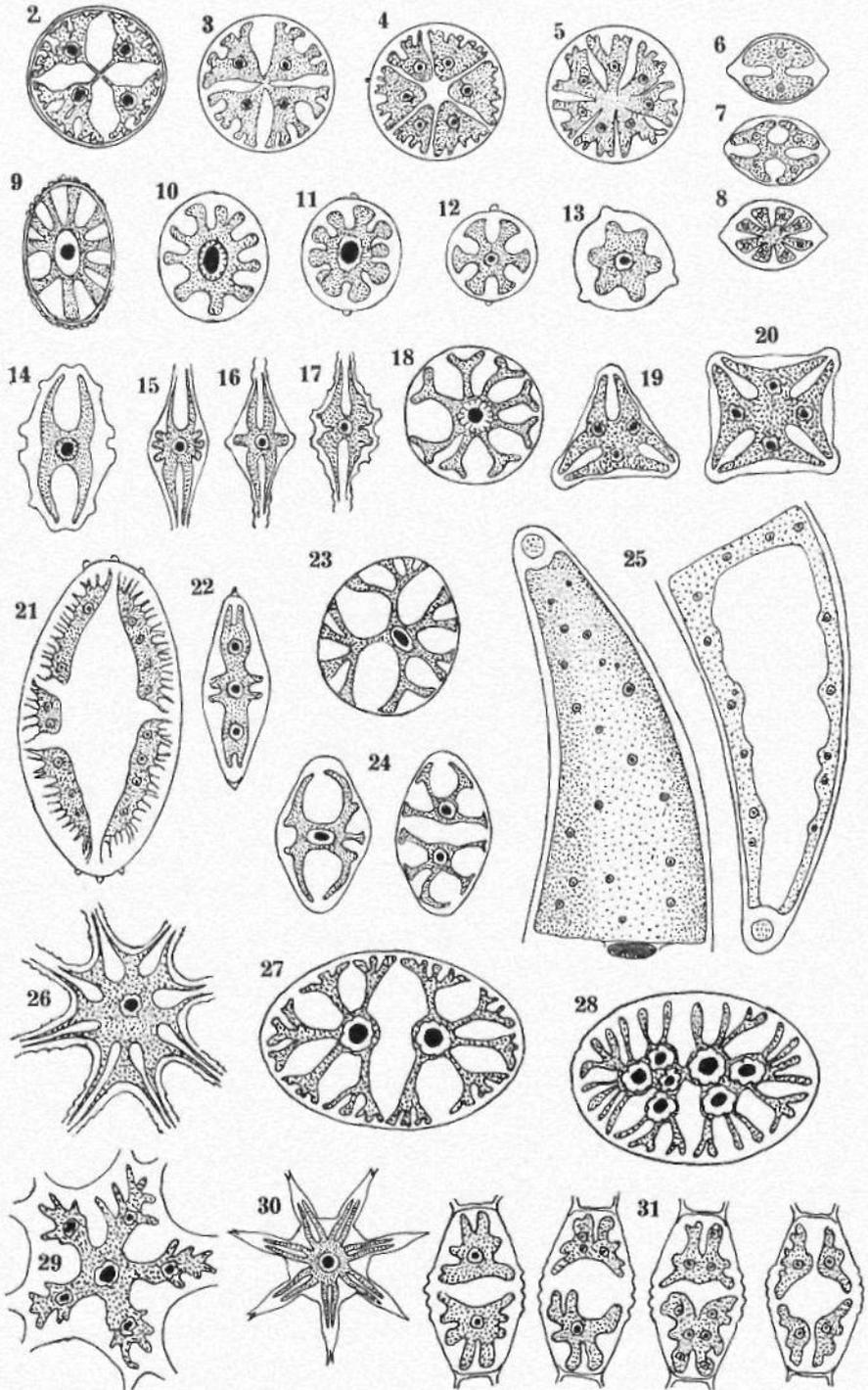
Type F 1. The primitive furcoid chloroplast is found among the pluriradiate *Staurastrum*, the best examples in species with well developed processes, fig. 26, 30.

Type F 2. In short-branched triradiate and thin biradiate desmids of »normal» size, about 20—30  $\mu$ , the lamellae are entirely divided up in two halves and the core with the axile pyrenoid forms a robust central part of the chloroplast. In broad and thin species secondary pyrenoids appear in the long semilamellae.

Type F 3. In convex-sided triradiate and thicker biradiate desmids secondary ridges appear from the core, more or less filling up the interspace between the core and the cell-wall. These three types are monocentric.

Type F 4. In larger forms of biradiate and also, though very rarely, in triradiate desmids there appears a bi-, or tripartition of the core and the pyrenoid. The axis is reduced to an intermediate connecting part or lacking. When present, it is, as a rule, without a pyrenoid. This is the *dicentric* type, occurring in many biradiate species of *Cosmarium*. The pluriradiate desmids of this type show a corresponding partition of the chloroplast and the pyrenoid. These modifications of the dicentric type in pluriradiate chloroplasts may conveniently be termed *dicentricoid*, F 4 d, e.g. *Staurastrum anatinum* and *sexangulare*, *Desmidium Swartzii* (fig. 19, 20).

Type F 5. This *tetracentric* type represents an interstage from the dicentric F 4 and F 6. The two pyrenoids of F 4 are divided into four but the connecting axile part of the chloroplast remains or is lacking in a manner quite analogous to the dicentric type and like this one occurring mainly in large species of *Cosmarium* and *Xanthidium*, often in the same species as does the following type. Among the triradiate desmids there are very few species large enough to make this type possible; it is, in a certain degree, recorded from *Staurastrum Sebaldi* var. *altum* (N. CARTER) where, however,





the axial pyrenoid may remain. According to the type F 4, the corresponding modifications in pluriradiate chloroplasts may be termed *tetracentricoid*, F 5 d.

Type F 6 represents the final stage of this line of evolution. The parts of the dicentric chloroplast are each divided into two, or sometimes more. The connecting axile part is retained or lacking, probably varying in the same species. Each of the parts contains one or, usually, several pyrenoids; this type is the most pronounced *tetracentric* stage of the primary axile chloroplast. For this kind of parietal chloroplast I propose the term *sector-parietal*.

In *Euastrum* there is, especially in the large, most elongated species, a cross-shaped connection with the reduced primary pyrenoid in the middle of the cross; the axility is still left but rudimentary; functionally the chloroplast is a parietal one. This stage may correspond closest to the concept pseudoparietal. In most cases this connection has disappeared and the tetracentric type shows at least four isolated cushion-shaped parts. Each part is, phylogenetically, an enlarged semilamella often with secondary protuberances. With increasing size of the cell the number of pyrenoids increases and subsequently there may appear further partitions of the plates, F 6 p.

The types F 4—F 6 occur in large biradiate desmids where the ratio of thickness to breadth is fairly large, about 1 : 2 or more, and appear in the order of numbers with increasing magnitude of the cell. They are very scarce among triradiate desmids and not found in forms of higher radiation.

The more the largeness of the cell increases, the more the ridges increase in importance; they become branched in front view and their edges become ramified in parietal direction, forming a dense confusion of irregularly arranged edges and fringes. The di- or tetracentric type is maintained (fig. 2); the pyrenoids are still »axile» covered by a thin layer of chlorophyll, e.g. *Cosmarium Ralfsii*, *biretum*, *pachydermum* (fig. 27), *ochthodes*, *tetraophthalmum*, *reniforme* (N. CARTER 1920 a, t. 33, 34). The variable *Cosmarium Brebissonii* shows diverse aspects: true tetracentric chloroplasts, desorganisation of the centres according to the increasing number of pyrenoids (fig. 28) and also true sector-parietal chloroplasts.

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Fig. 2—5: *Cosmarium pseudoconnatum*, fig. 6—8: *Desmidium Grevillei*, fig. 9: *Cosmarium speciosum*, fig. 10: *C. cucurbita*, fig. 11: *Hyalotheca dissiliens* var. *hians*, fig. 12: *Desmidium quadratum*, fig. 13: *Hyalotheca dissiliens* facies *tridentula*, fig. 14: *Euastrum lapponicum*, fig. 15: *Staurastrum Johnsonii* var. *perpendicularatum*, fig. 16: *St. natator* var. *Boldtii*, fig. 17: *St. dimazum*, fig. 18: *Tetmemorus Brebissonii*, fig. 19, 20: *Desmidium Swartzii*, fig. 21: *Cosmarium Askenasyi*, fig. 22: *Micrasterias pinnatifida*, fig. 23: *Closterium costatum*, fig. 24: *Euastrum bidentatum* (two figs), fig. 25: *Closterium Ehrenbergii* (two figs), fig. 26: *Staurastrum ophiura*, fig. 27: *Cosmarium pachydermum*, fig. 28: *C. Brebissonii*, fig. 29: *Staurastrum brasiliense* var. *Lundelli*, fig. 30: *St. subnudibrachiatum*, fig. 31: *Xanthidium Brebissonii*, series of four figs. (Fig. 2 after a drawing of LÜTREMÜLLER, 4, 5, 25 after drawings of GRÖNBLAD, fig. 3, 9, 10, 18, 21, 22—24, 26—29, 31 after N. CARTER, fig. 14—17 after GRÖNBLAD, fig. 19, 20 after WEST, fig. 6 after IRÉNÉE-MARIE, fig. 7 after DE BARY, fig. 11 after WM. R. TAYLOR, fig. 12 after NORDSTEDT and fig. 30 after BORGE.)

Type F 7. In *Micrasterias* the more flattened species have developed in an other way. The thickening and partition has not been possible to such an extent as in the genera mentioned above. On the contrary, the chloroplast has been enlarged in the two opposite radiale directions. The forked edges of the two actual lamellae are in most cases small or rudimentary but their persistence is a witness of the origin from true furcoid ancestral forms. The extended lamellae bear ridges, in thicker species these are rather high and may reach the cell-wall; in the extreme flattened species they are but low strips. Owing to the wide extension and laciniation of the chloroplast the number of pyrenoids is often very great, up to about one hundred (N. CARTER).

This type must be comprehended as an organel analogous to the platelike organs for photosynthesis of the higher plants: leaves, cladophylls and the like. It unites the primitive axile chloroplast with the general trend to parietal position. It must be emphasized that this one, in its origin, is quite different to other parietal chloroplasts which are the results of a transport of the chlorophyll to the cell-wall. In the case of the flattened *Micrasterias* spp. the parietal position is the result of an inverse evolution.

Type F 11, the *pericentric* chloroplast, is the result of a somewhat peculiar mode of evolution in the arrangement of the chlorophyll and the pyrenoids. Typologically it may be derived from F 2 and F 3 and is characterized by radiating processes, semilamellae and ridges which have pyrenoids in the thickened distal parts. In *Desmidium laticeps* fac *quadriradiatum* (the upper fig.) the processes consist of the semilamellae, in fac *biradiatum* (the lowest fig.) there are also secondary ridges, confirmed by a drawing of W. B. WITTRÖCK, now in my possession. This type has also been found in *Desmidium Grevillei* and *Staurodesmus tumidus*. The chloroplast of *Desmidium Grevillei* is by IRÉNÉE-MARIE figured as dicentric (fig. 6), by DE BARY as tetracentric (fig. 7), and by GRÖNBLAD as type F 11, fig. 8. N. CARTER's figure of *Std. tumidus* (1920 b, t. 15: 47—48) is drawn a fronte and shows strips of chlorophyll rich in pyrenoids giving the impression of a taenio-parietal chloroplast. A drawing kindly sent to me by Dr. GRÖNBLAD completes the exterior in giving a section of the semi-cell (the centre fig.). It shows an axile chloroplast with dense processes (semilamellae and ridges) with thickened parietal ends. This does not prevent both statements being correct. In accordance with the general trend of atrophying the central part in large desmids where the chlorophyll has been displaced to the periphery, there may occur species having a chloroplast of type F 11 with variations containing a pronounced parietal chloroplast F 12. Such variations are recorded in *Std. grandis*, see p. 285. Possibly the chloroplast of *Std. longispinus* belongs to the same type.

The series of evolution from monocentric to sector-parietal chloroplast within the triradiate desmids corresponds exactly to the evolution in biradiate cells. The existing difference depends on the diversity of the structure of the cells.

In biradiate oval desmids the enlargement of the lamellae extends in two opposite directions with sufficient room for a rich development of

ridges and increasing enlargement of the chloroplast, leading to a bipartition of the latter. By further enlargement the trend towards a parietal position leads to an other bipartition into four isolated parts, consequently each of the thus formed sector-parietal chloroplasts consists of one more or less metamorphosed semilamella.

In triradiate semicells the lamellae extend in three directions and the angles do not give space enough for an enlargement with ridges like the one in biradiate desmids. On the contrary, especially among *Staurastrum* and *Staurodesmus* the space available for the lamellae is a tapering, and often fairly long process with a narrow end which possibly may not be quite filled up by chlorophyll. From the objective figures of N. CARTER one must suspect a certain degree of contraction of the chloroplast caused by the fixing agent. Only in *Streptonema* the processes possess a bulge in the tip where the lamellae develop the semilamellae. In the long-spined *Staurodesmi* the ends of the processes are too narrow for the lamellae, they become solid in the adult cells. Some *Staurastrum* possess branches on the angles where parts of the chloroplast enter, e.g. *sexangulare* and the *Arctiscon*-section. In *St. brasiliensis* var. *Lundelli*, pentagonal with broad angles, the distal parts of the lamellae are ridged (fig. 29).

Only in bulged semicells, e.g. *Staurodesmus Dickei* the dicentricoid chloroplast has developed into a shape identical with the one of dicentric biradiate semicells, and tetracentricoid chloroplast is recorded, e.g. *St. Sebaldi*. The further evolution in the few existing large triradiate semicells has taken other paths. The type represented by *Std. tumidus* has already been dealt with. The development of the tetracentricoid triradiate type to sector-parietal has occurred through the disappearance of the axile part, and the semilamellae have thus been separated to form six parietal chloroplasts, F 6 p. The homology with the sector-parietal chloroplast, derived from the tetracentric ridged chloroplast, is evident. There are a few cases of this type known, in the plan, fig. 1, it is represented by *Std. ceratophorus* (GRÖNBLAD 1845, fig. 200). More cases are mentioned on p. 284. *Std. grandis* belongs in part to this type, it is dealt with on p. 285.

A corresponding development of a parietal chloroplast in large angular pluriradiate semicells of higher order is not known to me and the probability that there are such cases is fairly small; the multiangular shape seems to provide too little space, compare *Staurastrum arctiscon* and *brasiliense*, fig. 29 (N. CARTER 1920 b, t. 14, 15).

### 9. The pseudo-stelloid chloroplast.

The biradiate monocentric chloroplast of the type F 3 is typologically connected to the flattened discoid type F 7, but it also is the starting-point of secondarily stellate types. There are many desmids of very different taxonomic position in which the cells tend to circular shape *a vertice*, a series of the stages is shown in fig. 9—13. The broad oval forms are called *quasi-omniradiate*. In these the ridges have grown out to lamella-like plates. This is a special path of evolution, the vast majority of the biradiate desmids have maintained the oval shape. In these the lamella are still dominating and the ridges form small frontal outgrowth on them, viz. the types F 4—F 6. In pseudo-omniradiate cells, containing a chloroplast of the type F 8, the frontal ridges have grown out to the same size of the lamellae which are divided into semilamellae, giving the chloroplast *a vertice* a stellate shape, often scarcely separable from the true stelloid chloroplast, hence the term *pseudo-stelloid*. Two opposite pairs of the plates are semilamellae from the ancient biradiate chloroplast, and, consequently, they are not homologous with the other plates which are secondary ridges. This type is fairly common in *Cosmarium* (fig. 2—5) but also occurs in other genera.

The decisive difference between non-filamentous desmids with a true furcoid chloroplast and those bearing a pseudo-stelloid chloroplast, lies in the isthmus being smaller than the breadth of the cell and lying at the bottom of a wellmarked, often deep sinus. Several pseudo-omniradiate species show quasi-omniradiate variation and in some cases their biradiate origin is confirmed by the ornamentation of the cell, e.g. *Cosmarium Welwitschii*. In this connection it must be emphasized that the species of the *Clevei*-section are true omniradiate, see further p. 292.

TEILING (1950) gave the term pseudo-omniradiate for this kind of angularadiate desmids and the propriety of this concept is verified by the structure of the chloroplast. Pseudo-stelloid chloroplasts occur, besides in *Cosmarium*, in the pseudo-omniradiate species of *Desmidium* (fig. 12), *Bambusina*, and *Hyalotheca* (fig. 11, 13) and in the elongated basal part of *Tetmemorus* (fig. 18), *Triplloceras*, and *Ichtyocercus*.

The pseudo-stelloid chloroplast has, in several respects, followed a morphological evolution similar to that of the stelloid chloroplast. The radiating plates increase the surface of their edges in diverse ways. The genus *Tetmemorus* provides good examples, based on the careful investigations of N. CARTER. The smallest of the three species examined

by her, *T. laevis* has plates with toothed edges. In the larger *T. granulatum* the edges are roughened up and the filamentous parts are bent in all parietal directions similar to the type S 4, forming a dense nap (N. CARTER 1919 a, fig. 77). *T. Brebissonii*, of about the same thickness, has the edges transversely flattened, forming a kind of »pseudo-furcoid» chloroplast (N. CARTER, l.c.) fig. nostr. 18, so that the desmid, seen from the side, seems to contain ribbon-like chloroplasts. Actually, these edges sometimes lack the basal plate and form true parietal chloroplasts (N. CARTER 1920 b, p. 315). In other larger desmids, the axile part is atrophied and the edges have been developed into parietal laths analogous to the taenio-parietal chloroplasts, e.g. *Cosmarium prae grande* (GRÖNBLAD, in litt. c. icon.), *redimitum* (GRÖNBLAD 1945, fig. 138), *tesselatum* (LÜTKEMÜLLER 1893, and others).

In large bilateral *Cosmaria*, where the end-view is a broad oval, there are several species showing this kind of parietal chloroplast, e.g. *cucumis* (N. CARTER 1920 a, fig. 74), *deBaryi* (LÜTKEMÜLLER 1893 and others), *maculatum* (SKUJA 1949, t. 27: 17), *maculatifforme* (ibid. fig. 18).

This type of ribbon-shaped parietal chloroplasts has an origin quite different to the one of the taenio-parietal chloroplast. In the phylogenetic and taxonomical discussion these analogous but *not homologous* concepts must be kept separate, and consequently this type must be given a term to itself: *limbo-parietal*.

## 10. The parietal chloroplasts.

In the desmid terminology parietal refers to a position at or near the cellwall. In cells where the primitive axile chloroplast is large enough to prevent light from entering the central part in a degree sufficient for photosynthesis, the protoplast has displaced the chlorophyll to a more exposed position in the peripheral parts of the cell; the chloroplast trends to be parietal. In the varying shapes of the desmid cells this centrifugal trend has been embodied in different kinds of parietal chloroplasts, which can best be discriminated when examining the different ways in which they have been developed since their shape in certain cases is very similar.

As this is a phylogenetical process, still active, interstages occur and these are visible when comparing species at different stages of development, as well as when studying the variation within a species, sometimes within the same specimen, in dichotypical cells.

For these interstages GRÖNBLAD (1924, p. 11) has proposed the term

pseudoparietal. This term as well as the terms axile (axial), parietal and similar ought to be used exclusively in order to indicate the localisation within the semicell. In order to obtain an extensive knowledge of the chloroplast, definite unambiguous concepts and corresponding terms must be used; that is why I have proposed the terms applied to the concepts which concern the structure of the chloroplast which I have tried to analyse. I am well aware of the difficulties arising from the insufficient basis of facts known regarding the chloroplast, and, not least the natural reluctance of those desmidiologists who hitherto have concentrated their attention mainly to detailed describing of the external morphology and dimensions of the desmids. The anatomy of the desmids, however, has been neglected, thus every contribution ought to be accepted as an incitement to further investigations.

With reference to the preceding pages a survey is given of the different kinds of the parietal chloroplast, so far discerned.

A. In rounded elongated cells:

a. origin: the stelloid chloroplast in omniradiate cells.

1. *holoparietal*, developed from the peripheral part, forming a conical tube,

*e.g. Closterium Ehrenbergii p.p.*

2. *taenio-parietal*, developed from the thickened edges of the primitive lamellae,

*e.g. Spirotaenia (sectio Monotaeniae), Docidium-Pleurotaenium p.p., Cosmarium turgidum.*

b. origin: the furcoid chloroplast.

3. *limbo-parietal*, developed of the thickened edges of the semilamellae and the secondary ridges of a pseudo-stelloid chloroplast,

*e.g. Cosmarium cucumis, deBaryi, maculatum, maculatiforme, redimitum, praegrande, tessellatum.*

B. In angular cells:

4. *sector-parietal a)*, developed from the semilamellae in triradiate cells,

*e.g. Staurodesmus ceratophorus* (GRÖNBLAD 1945, fig. 200), *subgrandis* var. *aversus* (GRÖNBLAD 1935, fig. 284), *grandis p.p.* see p. 285.

5. — b), developed from the semilamellae and secondary ridges in biradiate cells according to the evolutionary series indicated by means of the types F 3—F 6,

*e.g. Cosmarium Brebissonii p.p., magnificum, ovale, controversum p.p., Askenasyi, splendidum, denticulatum, Ginzbergeri, tuddalense.*

C. In compressed cells:

6. *discoid*, developed of an elaborate monocentric furcoid chloroplast.

The discoid chloroplast of the most compressed species of *Micrasterias* may be considered as a parietal chloroplast *sensu lato*.

Being the result of an evolution, phylogenetical as well as ontogenetical, the interstages between axile and parietal *sensu stricto* may be common, a matter of occurrence which is worthy of examination. For instance: *Staurodesmus grandis*, often recorded as having parietal chloroplasts, seems to be variable in this respect. According to the WESTS' Monograph IV, p. 141, LÜTKEMÜLLER, on the basis of a great and varying material, has stated the chloroplast to be mainly axile, but also parietal, which probably means that the core with the axile pyrenoid has not been developed. N. CARTER (1920 b, p. 309) has found dichotypical cells of this species where the one semicell has an axial and the other a sector-parietal chloroplasts.

### 11. The importance of the isthmus.

Originally the term isthmus is referred to the marked constriction between the semicells in anguloradiate desmids, but in a wider sense, it is common to all desmids. The isthmus is a short transversal zone usually in the middle of the cell, characterized either by a minimum or a complete lack of chlorophyll (in most cases) and, with few exceptions, the presence of the nucleus. In some species the angular or compressed shape of the cell has modified its regularity but generally it is circular even in desmids with very complicated semicells. The desmidiologists who have given a thought to this fact have probably apprehended the circular shape as an axiom. According to the phylogenetical consequences of the theory of desmid radiation (TEILING 1950) the circular isthmus is a primitive feature derived from the omni-radiate ancestors.

The saccoderms have no semicells *sensu stricto*, i.e. two symmetrical halves of the cell with their walls joined together by the overlapping edges. True semicells with a connecting and limiting zone of the cell-wall where the cell-division takes place occur only in placoderm desmids. In *Penium* and *Closterium*, however, this is not permanent; after the division a new zone is formed in the wall of the younger semicell. In *Penium* it is often marked by a slight constriction.

The higher placoderms, tribus *Cosmarieae* LÜTKEM., have a permanent isthmus where the new semi-cells bud out by the division. In cylindrical forms, for instance *Docidium*, *Pleurotaenium*, *Bambusina*, the constriction of the isthmus is a shallow furrow and in certain cases visible only because of the lacking pores, but in angular and compressed

genera it is situated in the bottom of a more or less deep *sinus*, i.e. it is fenced round by the radially enlarged semicells.

The relation between the area of the transverse-section of the semicell and the area of the isthmus-hole is of a great importance in the formation of the daughter-chloroplast, that is why this exposition is necessary to comprehend the evolution of the chloroplast.

The cell-division of the saccoderm desmids takes place at the »internal» isthmus after the nuclei have moved to the middle of the daughter-chloroplast where a new internal isthmus is formed. Its position is marked by the nucleus and a gap in the chloroplast. The daughter-cells each contain half of the chloroplast of the mother-cell, thus, these halves form a direct continuation of the chloroplast formed at the germination of a zygosporangium (N. CARTER 1920 b). Almost the same procedure occurs in the lower placoderm genera *Penium* and *Closterium*; the half of the mother-chloroplast forms an internal isthmus at the place to which the daughter-nucleus has immigrated and completes its growth in the end cut-off after the division (LUTMAN and N. CARTER).

The relative simplicity of regeneration of the chloroplast after the division may be connected with the simplicity of its shape. The methods of making the stelloid chloroplast more effective are restricted to the enlargement of the edges of the lamellae by means of fringes, lappets or thickening; only in a few cases have true parietal chloroplasts been evolved.

The fairly unconstricted higher placoderms, *Docidium*, *Pleurotaenium* and the *Clevei*-section of *Cosmarium*, are in this respect of special interest. Unfortunately, there seems to be no information on the mechanics of their division but scattered references to the continuity of the taenio-parietal chloroplasts along the whole length of the cell, for instance *Cosmarium turgidum* and certain *Pleurotaenia*, indicate a similar procedure of direct outgrowth of the chloroplasts.

In *Tetmemorus* the regeneration of the chloroplast seems to follow the scheme of *Closterium* (N. CARTER 1920 b, t. XV: 60). In *Hyalotheca* the new chloroplast is formed by a simple division (ACTON 1916). Probably the same occurs in other desmids with cell-wide isthmus, for instance *Bambusina* and *Desmidium* spp.

The development of the new chloroplast occurs in a quite different manner in the *constricted* placoderm desmids. Here the formation of the new semicell takes place from a constant point of origin, the isthmus-zone. Because of the considerably smaller area of the isthmus-



hole it is impossible for the chloroplast to enter the new semi-cell in the manner of non-constricted desmids. That is why the new chloroplast must be rebuilt by rather amorphous elements of the mother-chloroplast intruding through the isthmus-hole. The daughter-semicell has reached a certain size when the chloroplast begins to be produced in it (N. CARTER 1920 b). Thus, the essential difference between the development of the slightly or not constricted and the constricted desmids is that the chloroplast of the former is a direct continuation of the mother-chloroplast, while the chloroplast of the latter must be built up *de novo*.

There seems to be no doubt that this development course is due to, and, in many cases has been to a great extent complicated by, the narrow communication of the isthmus-hole. In the angulo-radiate desmids of normal size the chloroplast has a monocentric and rather simple radiate structure and its rebuilding from migrating slabs of the mother-chloroplast can be carried out without far-reaching complications; each lamella sends a part and the rebuilding is a procedure of mere reorganisation. In the biradiate desmids of larger size with ditetracentric or sector-parietal chloroplasts, the rebuilding without any uniting central pyrenoid-bearing part may contain considerable possibilities for structural variations.

It is also significant that non-monocentric complicated chloroplasts are known in biradiate but only exceptionally in triradiate desmids. It should be of interest to compare the chloroplasts of bi- and triradiate *facies* of large desmids. I know only two cases. In *Cosmarium biretum* the biradiate *facies* has a typical bicentric chloroplast with parietally extended ridges (N. CARTER 1920 a, fig. 64—65). A drawing, kindly sent to me by Dr. GRÖNBLAD of *facies triquetrum* shows a rather simple triradiate dicentricoid chloroplast and in *C. cymatopleurum* the dicentric chloroplast (WEST, Monogr. III, p. 5) of the biradiate *facies* is in *fac. triquetrum* dicentricoid with some auxiliary pyrenoids (GRÖNBLAD 1952, fig. 1).

The variation in chloroplast structure is greater in the large biradiate desmids of the higher F-typus than in the smaller of type F 2 and F 3, and the conclusion seems inevitable that the necessity of rebuilding the chloroplast of every new semi-cell has been the conditioning factor which has made possible the richness in forms, all of which show the tendency for the chloroplast to be placed in the best position for the photosynthesis. N. CARTER emphasizes (1920 b, p. 315) the marked precedence taken by the distal parts of the mother-chloroplast over the

central parts during the transition to the daughter-semicell and the reconstruction of the new chloroplast. She also calls attention to the possibility that »very often the division of the chloroplast at the isthmus occurs before the axial part has entered the young semi-cell at all». She also gives examples, especially from *Euastrum* and allied *Micrasterias* spp., of a shortening and even lack of the axis. In this N. CARTER suggests a hypothesis of the origin of parietal chloroplasts.

This hypothesis, modified and completed, can be summarized as follows. The starting-point is the bi- (or tri-) radiate monocentric desmid, type F 2. With the enlargement of the semi-cell and of the chloroplast more pyrenoids are formed and located in the now more effective, *i.e.* distal, parts. Owing to this the primitive axile part with its pyrenoid decreases in importance (type F 4 and F 5) and disappears, type F 6. Consequently the distal parts, by their entrance in the new semicell, are independent; they possess their own pyrenoids, their photosynthetic activity can take place without the ever more insignificant and finally atrophied part. With increasing enlargement this evolution continues, giving rise to sector-parietal, and limbo-parietal chloroplasts, the vast majority of which occur in constricted desmids.

The persisting axile pyrenoid in type F 6 Eu especially in certain species of *Euastrum*, as stated by N. CARTER, may be considered rudimentary; this is probably due to the elongated apex, a shape favourable to the formation of elongated or of numerous pyrenoids. To judge from N. CARTER's figures this rudimentary pyrenoid is situated in the fairly narrow apical part where the conditions are like those of a smaller more primitive semi-cell.

## 12. Other forms of enlargement of the chloroplast.

Several cases have been described in which papillae occur on the outside of certain chloroplasts. LÜTKEMÜLLER (1893) carefully examined the hollow warts of *Cosmarium tessellatum* and found that the cavities of these warts were occupied by small protuberances from the surface of the chloroplast. The same author also found similar papillae in *Cosmarium Debaryi* and *turgidum*, which have a smooth cell-wall. BORGE (1903, t. 27) stated filiform papillae in *C. splendidum*. N. CARTER found papillae in *Cosmarium binum*, *ovale*, *Askenasyi* (fig. 21), *controversum*, *margaritifera*, *Xanthidium fasciculatum* and *armatum*, in several species of *Euastrum* and also in *Pleurotaenium*. She points

out that these papillae imply an advantageous increase in the surface exposed to light (1920 a, p. 267).

The accurate conformation between the papillae and the hollow bulges of the cellwall seems to be a mere matter of space; a result of the trend towards parietal position of the chlorophyll. In this respect some statements of GRÖNBLAD (1921) are illuminating. In *Staurastrum Johnsoni* with slightly inflated corpus of the cell the chloroplast bears three frontal ridges (fig. 15). In *St. dimazum* there are two papillae in the two hollow warts of the front (fig. 17), and in *St. Natator* var. *Boldtii* there is one papilla in the single hollow wart (fig. 16). The branches of the chloroplast in the upper processes of *St. sexangulare* and *Arctiscon* confirm this opinion.

The same function — more effective absorption of diffuse light — may be attributed to diverse parietally directed small parts of the chloroplast, such as the fringes and lappets of the edges, mentioned above in several saccoderm genera. Fringes either more or less branched, are recorded by N. CARTER in several *Cosmaria*, both in monocentric, e.g. *diplosporum* and *pseudopyramidatum*, but especially in larger bi- and tetracentric, e.g. *amoenum*, *pyramidatum*.

### 13. Combinations of elongation and radial expansion.

In the previous chapters I have shown that vertical elongation and radial expansion are Nature's methods of enlarging the desmid chloroplast by means of the cell-shape. Each of these ways is realised separately and thus can be clearly distinguished, even though in many cases they are intermixed in numerous combinations.

In the saccoderm and lower placoderm desmids elongation is the only way; this is due to the structure of the wall and the inconstancy of the situation of the isthmus. Among these, *Netrium* is the only genus having species of conspicuous width; this in itself involves a step towards radial enlargement of the cell. The simplicity of the structure appears in the great paucity of variation in morphological entities; even more this paucity is emphasized by the cell's incapability of forming any other sculpture than striae. Thus, there are few genera, most of them small, and, even in the largest genus, *Closterium*, the species differ mainly in dimensions, proportions and curvature.

By contrast, in the higher placoderm desmids, viz. the tribus *Cos-*

*marieae* LÜTKEMÜLLER,<sup>1</sup> which embraces all radially enlarged desmids, combinations of the two paths of evolution constitute an important factor in creating the enormous richness in forms.

In *Pleurotaenium* a good many of the species show a combination of the generic elongation and an omniradiate inflation, either over the whole semicell, for instance *ovatum*, *rotundatum*, *doliforme*, and *latum*, or zonally, for instance *nodosum*, and *Kayei*. A similar zonal inflation is also seen in *Docidium*. Together with the *Clevei*-section these two genera seem to be the true omniradiate placoderm desmids, thus forming a transitional group from the lower to the higher placoderms. Of interest in this respect may be mentioned the peculiar isthmal suture of certain species of *Pleurotaenium*.

The remaining elongated genera show important attributes of their evidently ancestral angulo-radiate character. *Tetmemorus* may be regarded as an elongated biradiate genus, often compared with *Euastrum*, owing to its having adapted a biradiate ridged chloroplast to a pseudo-furcoid one; by means of flattening the edges of the ridges, type F 9. *Triploceras* is no doubt of angulo-radiate origin, the apex being 2, 3, or 4-radiate while the elongated part is cylindrical having a ridged chloroplast. The *pileolatum*-group of *Staurastrum* has the same structure but the cylindrical part is fairly short. *Ichtyocercus* is, in its shape closely related to *Tetmemorus*; but the biradiate apex is more pronounced. *Triplastrum* has prismatical elongated triradiate semicells with a triradiate furcoid chloroplast with or without ridges.

In the other placoderm genera the elongation is less pronounced. In *Cosmarium* it is visible only when the length of the semicell is equal to, or greater than the breadth, for instance, in *annulatum*, *elegans* and similar, *ovale*, *pseudopyramidatum*, *anceps* and other. These examples have monocentric chloroplasts. There are also some dicentric *Cosmaria* which are somewhat elongated, e.g. *Thwaitesii* and *amoenum*. ROUBAL (1947, t. 7: 2) has in *amoenum* found chloroplasts of parietal type with two pyrenoids and so has GRÖNBLAD (*in litt. c. icon.*).

Many species of *Euastrum* represent a more or less pronounced

<sup>1</sup> It is to be regretted that L. chose this misleading name. The first four *tribus* of his system contain genera of staff-shaped and rather uniform, often elongated cells, two of the genera being monogeneric. This uniformity depends on the »wandering» isthmus, the most important character common to these *tribus*. *Tribus* 5 forms a strong contrast due principally to the constant isthmus which has caused the immense diversity of the most different shapes in a lot of genera for which the name *Cosmarieae* is not at all representative, *Radiatae* or something descriptive and yet nevertheless neutral, would be better.

degree of vertical elongation. Possibly, in accordance with this, the connection by means of bridges between the parts of the tetracentric chloroplast is more pronounced here than in those *Cosmaria* of the same type which are, however, not elongate.

Also in *Micrasterias* there are a few examples of vertical elongation, for instance in *muricata* and *americana*. The filiform cells of *Gonatozygon*, *Genicularia*, and *Groenbladia*, typify an elongation of this kind.

#### 14. Convergency, and some examples.

The trend towards a favourable exposition to light in the form of enlargement in apical and radial direction of the cell and parietal displacement of the chlorophyll has been active in varying degrees and at varying times during the evolution of the desmids, and is still active. Since these processes are carried out in unicellular organisms, they must in several cases lead to analogous forms which are not the results of homologous development: the development called convergency.

Actually, cases of convergency are not uncommon among the desmids and have been understood as identities or homologies, consequently they have led to misapprehensions. The stelloid and the pseudostelloid chloroplast, the taenio-parietal and the limbo-parietal chloroplast, the short-cylindrical shape of certain saccoderms and the similar shape of certain *Cosmaria*, the true omniradiate and the pseudo-omniradiate cells, the elongated cells of *Penium* and certain genera of the tribus *Cosmarieae* are examples of desmid convergency.

In the taxonomy of the desmids the last mentioned convergency has played an interesting part, being the special reason for the unsuccessful attempts made to unite the staff-shaped desmids with rounded ends in one genus. From a morphological point of view it was an bold act when NÄGELI (1849) erected the genus *Dysphinctium* with its subgenera *Actinotaenium*, *Calocylindrus* and *Dysphinctium*, well aware, as he was, that »diese Gattung ist eine künstliche» (p. 109). This genus is now rejected and the five (!) species on which it was founded, viz. *Regelianum* (= *curtum*), *annulatus*, *Cylindrus*, *striolatum* (= *tessellatum*), and *Meneghinianum* (= *connatum*), which are now included in *Cosmarium* except (*Penium*) *cylindrus*. *Dysphinctium*, probably because of its deceptive simplicity, was for half a century an acknowledged genus. DE TONI (1889) assigned to it 39 species, and other authors (e.g. KIRCHNER) have used *Calocylindrus* as a genus in a similar sense.

The legitimate idea of separating the desmids, circular *a vertice*, from the heterogenous crowd of *Cosmarium* requires to be carried through. The failure of NÄGELI's attempt is due to the heterogeneity of the circular desmids. Actually, there are several categories of these desmids. The first possess the primitive omniradiate cylindrical or fusiform shape characteristic of the saccoderms and a stelloid primitive chloroplast or certain types derived from it. The second category consists of the pseudo-omniradiate desmids derived from bi-, or triradiate angular placoderms with either the pseudostelloid chloroplast or a di-, or tetra-centric chloroplast. Both categories contain species with taenio-, or limbo-parietal chloroplasts.

The first category covers the *Clevei*-section. This group consists, firstly, of the species, previously reckoned to *Penium* and which were excluded by LÜTKEMÜLLER, in his revision (1905, p. 336) from this genus and provisionally reckoned to *Dysphinctium*; secondly, the species which were excluded by LÜTKEMÜLLER from *Cylindrocystis* (1913) and, lastly, several other species, described as *Cosmaria*. The members of the *Clevei*-section are all of a cylindrical or fusiform shape, more or less elongated with rounded or somewhat obtuse apex and a very shallow sinus at the isthmus. With a few exceptions they have a stelloid chloroplast with one pyrenoid, *e.g.* *inconspicuum*, *curtum*, *palangula*, *cucurbitinum*; the longer species have 2—3 pyrenoids, *e.g.* *Clevei*, *floridanum*, *elongatum* and *Taylori*, the last mentioned having a chloroplast with plicated and fringed edges of its lamellae. The largest species have a taenio-parietal chloroplast, *e.g.* *turgidum*.

No doubt the *Clevei*-group represent a natural and well delimited taxon for which the erecting of a separate genus is a matter of importance; its present place in *Cosmarium* is quite unnatural and fallacious. At present the foregoing outlines may suffice.

Contrary to the *Clevei*-section, the second category consists of rounded *Cosmaria* of a shape *a vertice* varying between broad-oval and circular; the latter is the true pseudoomniradiate shape, whilst for the broad-oval form the term *quasi-omniradiate* may be used. These *Cosmaria* are a heterogeneous group, comprising species with ornamented wall, *e.g.* *annulatum* and *elegantissimum*, or with smooth wall, elongate *e.g.* *gonioides* and *cucumis*, and globular, *e.g.* *moniliforme* and *pseudoconnatum*. Of these the *pseudoconnatum*-group is worthy of a short discussion because of the fairly detailed knowledge of the chloroplast.

The species of this group have semicells of almost globular to semi-globular shape united at a wide isthmus visible in a shallow isthmus-

furrow. The species which have a chloroplast sufficiently known to be compared are: *C. Wollei*, *subglobosum*, *pseudoconnatum*, *connatum*, *zonatum*, and *Westii*. The pseudoomniradiate character is verified by *C. globosum*, which is known in circular, oval (var. *compressum*) and triangular (var. *trigonum*) forms according to WILLE (1879, t. 13: 41, 42). *Cosmarium Wollei* (WEST and WEST) GRÖNBL. has a pseudostelloid chloroplast according to WEST (1907, t. 7: 10), which is confirmed by PLAYFAIR (1914, t. 3: 3) and by GRÖNBLAD (1947, t. 1: 9). The very similar *C. subglobosum* also has a pseudostelloid chloroplast according to NORDSTEDT (1878, t. 1: 13) and, above all, JOHNSON (1894, t. 211: 7).

The other species mentioned possess a more elaborate chloroplast. The most frequently depicted is *pseudoconnatum*. It usually contains a tetracentric chloroplast, the four parts of which are either separate or axially connected. NORDSTEDT, in his original diagnosis (1869, t. 3: 17), reports four sector-shaped chloroplasts possibly joined in the axis. This was also found by N. CARTER (1920 a, t. 10: 35, 36) with longitudinal ridges (fig. 3), also SKUJA (1849, t. 26: 18—20), BORGE, LEMMERMANN, IRÉNÉE-MARIE, FRITSCH and others. Fig. nostr. 2 is a copy of a drawing of LÜTKEMÜLLER's, belonging to the collection of the late professor NORDSTEDT. GRÖNBLAD (1924, t. 2: 51—56) found, besides specimens with this chloroplast, specimens with three lobes, each with one pyrenoid, specimens with one axile undivided chloroplast with three pyrenoids, and also specimens with three separate chloroplasts each with one pyrenoid. GRÖNBLAD has, further, in material from Louisiana (A. M. SCOTT coll.) found specimens with the normal four as well as specimens with one axile chloroplast split in seven parts (fig. 5), each with one pyrenoid, but also specimens with six sector-shaped parietal parts each with one pyrenoid (fig. 4) (*in litt. c. icon.*).

*Cosmarium connatum* and *Westii* have bicentric chloroplasts, their shape a vertice is oval and they must be considered as clearly biradiate. It seems almost inevitable to understand *C. pseudocannatum* as having received its somewhat peculiar tetracentric chloroplast owing to its omniradiate shape, since the larger but somewhat compressed *connatum* has remained bicentric. According to this the smaller species *Wollei* and *subglobosum* are monocentric and, according to their circular shape, pseudostelloid.

BERNARD (1908, fig. 108, 109, and 1909, fig. 54) has described *Cosmarium pseudoconnatum* var. *ellipsoideum* as having 8—10 parietal ribbons with 2—4 pyrenoids. The figures show typical taenio-parietal

ribbons extending from apex to apex with 6—8 pyrenoids. If this is a correct observation the actual desmid can not be *pseudoconnatum*; it is very unlikely that a tetracentric chloroplast can develop into a taenio-parietal one. In literature there are, however, several examples of misapprehended chloroplasts in which after a superficial examination only the ridges have been drawn; the drawer has seen the chloroplast as parietal ribbons and by his drawing he conveys this same error to the reader. The pyrenoids are often difficult to discern without staining and seem sometimes to have been drawn *ad libitum*.

### 15. Chloroplast and taxonomy.

In 1871, the beginning of research on the chloroplast caused LUNDELL to distinguish a separate subgenus in *Staurastrum*, viz. *Pleurenterium*, comprising *tumidum*, *grande*, *longispinum*, *brasiliense*, *sexcostatum*, and *mutilatum*. None of these species, whose structure is now correctly elucidated, possesses true parietal chloroplasts. According to the same principle he also distinguished *Pleurotaeniopsis* as a subgenus of *Cosmarium* with the species: *turgidum*, *de Baryi*, *Cucumis*, *ovale*, *striolatum*, *elegantissimum*, and *praegrande*. WILLE (1890) raised both *Pleurotaeniopsis* and *Pleurenterium* to the rank of genera. Earlier, LAGERHEIM (1887) had used the name *Pleurotaeniopsis* as a generic name for *cucumis*. BOLDT (1888) divided *Xanthidium* in two subgenera: *Euxanthidium* with a parietal and *Centreterium* with an axile chloroplast.

The attempts of LUNDELL and his followers to use the central or parietal location of the chlorophyll as generic characters have been abandoned, for good reasons. The centrifugal trend in the location of the chlorophyll is an evolutionary procedure connected with the enlargement of the semicell, especially in a radial direction. This trend occurs in every taxon which contains species of sufficient size and thus is of no taxonomic value, at least if there are intermediate forms. The fairly well examined genus *Euastrum* is a good example of the evolution of the chloroplast within a delimited genus.

The small and fairly thin *Eu. lapponicum* and *dubium* possess a monocentric chloroplast, while in the somewhat larger *bidentatum* (fig. 24) and *pectinatum* the chloroplast is mono- or bicentric. The largest of these relatively short *Euastra* is the bicentric *verrucosum*. N. CARTER (1919 a) has divided this genus into two groups, the one with one pyrenoid in an axile chloroplast and the other, comprising larger species, with numerous pyrenoids in the parietally advanced



parts of the chloroplast. She found no place for *verrucosum*, with its typical bicentric chloroplast very similar to that of certain large species of *Cosmarium*. In its short semicells it is quite different from other large and elongate *Euastra* examined; thus evolution has followed the same line as in semicells of these dimensions in other genera, e.g. *Cosmarium* and *Xanthidium*.

The second group of *Euastra* examined contains species of larger size and elongate shape. The smallest of these is *ansatum* which is monocentric with a doubled or elongated pyrenoid, (compare for instance *Netrium* and *Closterium*); while *sinuosum*, of the same breadth and thickness but shorter, is bi-(or tetra(?))-centric. The somewhat larger *cuneatum* is bi- or tetracentric. The rest of the species: *ampullaceum*, *affine*, *ventricosum*, *insigne*, *didelta*, *oblongum*, and *crassum* have numerous pyrenoids in tetracentric chloroplasts, most of them with thin crossing bridges between the parietal parts, the cross often has rudiments of the primitive axile pyrenoid, a type characteristic of *Euastrum*.

Similar typological series occur in other sufficiently extensive and delimited natural genera, for instance *Xanthidium* and *Micrasterias* as well as in the many intricately confluent, as yet not distinguished series of the *Cosmaria*. In *Staurastrum*, which is more primitive because of the persistent pluriradiation and the consequent general lack of space in the semicell-room, an evolution from axil to parietal position of the chlorophyll has not occurred. In the more advanced genus *Staurodesmus* where the bi- and triradiate facies dominate, this centrifugal evolution has occurred in a few species, e.g. *grandis* and *longispinus*.

## 16. Chloroplast and pyrenoids.

There is an evident correlation between the number and organisation of the pyrenoids and the size and structure of the chloroplast as was indicated already by GAY and emphasized by N. CARTER. This appears very clearly when comparing the short single pyrenoid of the stelloid chloroplast of *Cylindrocystis* with the rod-shaped one in *Netrium* or with the series of pyrenoids in a long *Closterium* or with the numerous pyrenoids (up to more than hundred, according to N. CARTER) in the largest and most flattened *Micrasterias* investigated. In this respect the units of stromastarch are considered as equal to pyrenoids (LUTMAN 1910, p. 253).

A more intensive comparison reveals that the relation is not a simple

mathematical ratio of pyrenoids to the mass of chlorophyll: moreover, the situation of the pyrenoids in relation to the disposition of the chlorophyll must be considered. In a primitive stellate chloroplast the central pyrenoid is capable of supplying the whole chloroplast. In an enlarged chloroplast which is divided into more or less separate parts, the more isolated parts need their own pyrenoids. Significant examples are, for instance, the variable chloroplast of *Desmidium Grevillei*, fig. 6—8, and the ribbon-like parietal chloroplasts, e.g. *Pleurotaenium* with its series of pyrenoids, each pyrenoid being exclusively restricted to a surrounding part of the ribbon and quite independent of adjacent ribbons.

In the discussion and the figure of the types of the chloroplasts (fig. 1) it is possible to follow the phylogenetical evolution of the chloroplast and the increasing number of the pyrenoids. The more the semicell increases, the more the chloroplast changes its structure, placing the chlorophyll in parietal position; this is accompanied by an accelerated increase in the number of pyrenoids, and by their taking up a more advantageous position.

It must be noted that the pyrenoid does not exceed a rather small size. Instead of growing larger it divides into two or more pyrenoids, grouped closely together. This circumstance is in most cases not observed because it is visible almost exclusively in stained specimens, but seems to occur fairly often. N. CARTER has given several examples of it. The giant pyrenoids, rarely recorded, e.g. *Cosmarium bengalicum* (SKUJA 1949, t. 25: 12) possibly consist of multiplied pyrenoids. They may be caused by an increased photosynthetic capacity and do not influence the types mono-, di-, and tetracentric, which are founded on the structure of the chloroplast, though the number and, above all, the position of the pyrenoids are significant and in most cases characteristic.

Earlier, the difference between 1 or 2 and 2 or 4 pyrenoids, was considered as constituting specific characters and in some cases this is still so, e.g. *Cosmarium connatum* in contrast to *pseudconnatum* and *amoenum* in contrast to *pseudamoenum*, but the number of the pyrenoids is not decisive in itself, it is only a convenient indicator of the mono-, di-, and tetracentric chloroplasts. The distinguishing of similar forms as separate species is often a matter of individual approach and, in this case an extensive knowledge of the variation of the types is necessary. Apart from the elongate or elaborate chloroplasts with numerous pyrenoids in varying number, the chloroplasts containing 1, 2 or 4 pyrenoids seem to be very constant. There are, however,

variations, and these are of two kinds. The first comprises variations in the structure of the chloroplast which involves changes of the number of the pyrenoids, the other comprises the varying number of the pyrenoids in an invaried chloroplast.

The first case occurs in desmids where the chloroplast is in transition from monocentric to dicentric, e.g. *Euastrum bidentatum* (N. CARTER 1919 a, l. 16: 53, 54), *Cosmarium benedictinum* (DUCELLIER 1919, p. 119), *C. subcucumis* (N. CARTER 1935, f. 10, 11), or from dicentric to tetracentric, e.g. *Xanthidium Brebissoni*, fig. 31, and *Cosmarium pseudoconnatum*. Special cases of this variation show the dichotypical (TEILING 1948, p. 17 and 1950, p. 325) specimens. G. S. WEST (1916, p. 365), in a critical examination of the taxonomical character of the chloroplast, mentioned that «it is by no means uncommon to find axile chloroplast in one semicell and parietal chloroplast in the other semicell of the same individual». Here must be noted that WEST used the terms axile and parietal in a much more definite sense as contrary types than does the present author. In Monograph II t. 60: 4 a specimen of *Cosmarium subcucumis* is figured, the semicells of which show varying stages of parietal disposition of the chlorophyll.

The transition from triradiate to biradiate chloroplast and *vice versa* in *janus* specimens (TEILING 1950) common in *Staurastrum* and *Staurodesmus*, are examples of a type of variation within the simple monocentric furcoid chloroplast.

In the second case the variation in monocentric chloroplasts has been dealt with by LÜTKEMÜLLER, N. CARTER and DUCELLIER. The former examined specimens with supernumerary pyrenoids of *Cosmarium pyramidatum*, *pseudopyramidatum*, *botrytis*, *pseudobotrytis*, *Staurodesmus convergens*, and *Staurastrum echinatum*. DUCELLIER examined (1917) *Cosmarium vexatum*, *subprotumidum*, *conspersum*, and *pyramidatum*, and (1919) *benedictinum*.

The biradiate desmids of type F 2 are, as a rule, small. There are, however, desmids of considerable breadth but with little thickness which have maintained the simple biradiate type F 2. In the elongated lobes of the forked lamellae there are developed several *accessory* pyrenoids. An example is *Cosmarium chondroides*, the chloroplast of which G. S. WEST (1909, p. 62, t. 4: 9, 10) erroneously described as broad parietal bands. N. CARTER (1920 a, p. 273) found in stained specimens a biradiate axile chloroplast with one central and 1—2 pyrenoids in each of the four lobes. Considering the fact that this desmid is 72—78  $\mu$  broad, accessory pyrenoids are necessary. Further, BORGE (1903, t. 5:

22) figured *Spondylosium pulchrum* var. *inflatum* with a frontal row of pyrenoids in the elongated narrow lobes of the biradiate chloroplast. Later (1925, t. 4: 16) he found the same in var. *brasiliense*. The species of *Spondylosium* are small; in *moniliferum*, *nitens* and *Luetkemulleri* the chloroplast is recorded as bi- or triradiate with one axile pyrenoid. *Sp. pulchrum* is one of the few broad species; hence the formation of accessory pyrenoids.

IRÉNÉE-MARIE (1951, t. 1: 9) has given illuminating figures of the chloroplast of a desmid, labelled *Staurastrum brevispinum* var. *inerme* WILLE. It shows a typical triradiate chloroplast of type F 2 in which the lobes of the forked lamellae contain 1—4 auxiliary pyrenoids just as in *Std. grandis* as it is figured by N. CARTER (1920 b. t. 15: 40—42). Also in large pluriradiate *Staurastrum* auxiliary pyrenoids occur, e.g. *St. brasiliense* var. *Lundelli*. By a comparison of the desmid with auxiliary pyrenoids it is apparent that these pyrenoids are necessary when the cell is more than 50  $\mu$  broad.

### 17. The chloroplast and the size of the cell.

In 1874, JACOBSEN emphasized that the »chlorophyll est toujours disposée de manière à étaler la surface la plus grande possible à l'action la plus direct de la lumière». He also held that the principle of radiate disposition of the chlorophyll is common to all desmids but appears in very different aspects in relation to the shape and the dimensions of the cell, and is, moreover, in certain cases difficult to discern. Exceptions may occur, e.g. *Spirotaenia*. It must be pointed out that JACOBSEN was one of the pioneers of the Darwinism in Denmark and the Danish translator of »The Origin of Species». His ideas of the desmid chloroplast are, seen against the background of the very poor contemporary knowledge, to be regarded as results of intuition, more than results of a scientific synthesis of known facts.

Fifteen years later, the Finnish physiologist and desmidiologist ELFVING (1889) published a little paper which, since it is written in Swedish, has been neglected. The author criticized the method originated by LUNDELL and also used by BOLDT and GAY of using the chloroplast as a basis of taxonomy. He considered the axile chloroplast of the smaller desmids sufficient for photosynthesis because it could be entirely penetrated by light, but, in larger cells, the chlorophyll must be placed in an extended peripheral position in order to be able to absorb sufficient light. He gave a list with the dimensions of the larger

*Cosmaria*, *Staurastrum* and *Xanthidia* with more or less parietal chloroplasts. From this he deduced the relationship between the size of the cell and the tendency to a parietal position of the chlorophyll.

ELFVING's points of view are fundamental to the understanding of the metamorphosis of the chloroplast. When comparing desmids of varying shape it is striking how exactly the chloroplast makes the greatest possible use of the space available in the distal parts. Thus it is reasonable to consider the cell shape as the primary deciding factor in the development of the chloroplast. This is not correct; both the chloroplast and the cell-shape are the results of the activity of the protoplast, but it may be used as a convenient mode of expression.

The size of desmids covers a wide range, from small *Cosmaria* of about 9  $\mu$  in length to gigantic *Pleurotaenia* of more than 1000  $\mu$ . A comparison between desmids of diverse size shows that there is an evident, often definite connection between the size and the structure of the chloroplast. In analysis it is convenient to deal with two kinds of size: on the one hand the length of the elongate desmids, most of them containing the stelloid chloroplast and parietal forms of it, and, on the other hand, the largeness of the angulo-radiate desmids containing the furcoid chloroplast and its derivatives. In both cases the small desmids are confined to those with an axile monocentric chloroplast.

A statistical survey of the 177 monocentric species of *Cosmarium* in WEST's Monograph shows that about 65 % do not exceed a length of 40  $\mu$  and about 92 % do not exceed 50  $\mu$ . In *Staurastrum*, *Staurodesmus* about 76 % do not exceed 50  $\mu$ . Several of those longer than 50  $\mu$  are recorded as having ridges. Of the 74 *Cosmaria* with a more elaborate chloroplast only 15 % do not exceed 50  $\mu$ , and about 15 % exceed 100  $\mu$ , 70 % measure between 50 and 100  $\mu$ . The figures, of course, are only approximations because of the common absence of, or inexactitude in, the records of the number of the pyrenoids, but they have value in showing that about 50  $\mu$  is the average maximum length of the monocentric species of these genera, at least in the ecological conditions of the English area.

The small angulo-radiate genera, *Cosmocladium*, *Oocardium*, *Sphaerosozoma*, *Onychonema*, *Spondylosium*, *Hyalotheca*, *Phymatodocis*, and *Bambusina*, have fairly short cells of about 20–30  $\mu$ , only in a few cases exceeding 30  $\mu$ ; measurements from WEST's Monograph. All of these possess monocentric chloroplasts. In other genera, where the majority of species with di- and tetra-centric and parietal chloroplasts occur, the dimensions are greater. In *Euastrum* the monocentric species

scarcely exceed 70  $\mu$ , while species with the normal tetracentric chloroplast can reach more than 200  $\mu$  in length, e.g. *crassum* and *oblongum*. The length, however, is no adequate index of the size: it contains only one factor of the volume. Elongate desmids have their volume mainly in the vertical direction, while in angular forms the lateral and frontal parts make up much of the volume. Thus, in comparison with the elongate *Euastrum*, the genera *Cosmarium*, *Staurastrum*, and *Xanthidium* may not be able to reach any more considerable length. In the WEST's Monograph the parietal *Xanthidium armatum* exceeds 200  $\mu$ , the di- and tetracentric species have a length between 50—100  $\mu$  and the monocentric less than 40  $\mu$ . In the flattened species of *Micrasterias* the cell combines length and breadth with a minimum of thickness. Probably as a result of this, the length is, in general, appreciable, the WESTS records up to 360  $\mu$  (*M. rotata*).

The real giants occur in the range of the more elongate, staff-shaped genera; *Closterium*, *Docidium*, and *Pleurotaenium* but also *Triploceras* and *Tetmemorus* attain, especially in the tropics, considerable dimensions. The dimensions cited are not intended to be absolute; a more extensive examination of the statements in the literature may probably give higher figures. Some examples may be given. *Closterium laterale* 535  $\mu$ , *nasutum* 638  $\mu$ , *lunula* 897  $\mu$ , and *Braunii* 988  $\mu$ . *Docidium orientale* 700  $\mu$ , *indicum* 980  $\mu$ , and *gloriosum* 1080  $\mu$ . *Pleurotaenium elatum* 900  $\mu$ , *nodulosum* 946  $\mu$ , *maximum* 1020  $\mu$ , and *eugeneum* var. *undulatum* 1094  $\mu$ . *Triploceras verticillatum* 600  $\mu$ , and *Tetmemorus giganteum* 265  $\mu$ .

The factors influencing the rate and processes of growth are rather unknown. In the elongated desmids there is a possibility of continued intercalary growth. This is clearly visible in the long *Penia* and the girdle-banded *Closteria* where the final length may reach double or treble the primary length. In the tribus *Cosmarieae* the tessellate structure of certain *Pleurotaenia* may be interpreted as a continued intercalary growth; compare the structure of the isthmal bulged zones and the cylindrical part of *P. trochiscum* with each other and with corresponding parts of *P. doliiforme* (WEST 1916, f. 227 A, B). Furthermore, the staffshaped desmids possess an advantage of rapid and continuous growth in the uniform and simple structure of the (pseudo)-stelloid and taenio-parietal chloroplast which allows a continuous growth in the length with generation of new pyrenoids.

There are several combinations of desmids, either considered as separate species or varieties of one species, where the difference is a

mere question of size, for instance *Cosmarium pyramidatum* and *pseudopyramidatum*. The former is in its dimensions double the latter and there is a further biosystematical difference in that the former possesses two pyrenoids and the latter one pyrenoid in the axile chloroplast, according to WEST. N. CARTER's detailed pictures of the chloroplasts of these species show a striking resemblance in the structure of the ridges with their fringed edges, the difference lies in the type; *pyramidatum* is tetracentric and *pseudopyramidatum* is monocentric. The difference in the shape falls within the extent of the normal variation of a species. It is natural that the larger desmid should possess a more elaborate chloroplast with more pyrenoids. Of all desmids *Cosmarium pyramidatum* has been studied most in regard to the variability of the pyrenoids. Its elongate shape and its size make it analogous to the great *Euastra* which also have a variable number of pyrenoids. The structure of the desmid nucleus and its significance for the structure of the cell have just begun to be the subject of investigation (KALLIO 1951); the difference of the species mentioned may perhaps be the results of polyploidy. A similar case is *Mesotaenium de Greyi* and its f. *major*.

### 18. The chloroplast of the desmid genera.

The statements refer to the semicell, terminology according to the description above.

*Cylindrocystis* MENEGH. Chloroplast stelloid S 2, rather short, with lacinate edges of the lamellae, one axile pyrenoid, sometimes elongated.

*Netrium* NÄGELI. Chloroplast stelloid S 2, elongate, in some species transversely divided in two parts, with lacinate or fringed edges, one elongated pyrenoid in each part.

*Spirotaenia* BRÉB. Chloroplast stelloid S 3, spirally twisted with several lamellae and one or more pyrenoids, or taenioparietal, consisting of one spirally twisted ribbon with a few scattered pyrenoids.

*Mesotaenium* NÄGELI. Chloroplast laminate S 8, common to the two semicells, axile or sometimes more or less parietal, with one or several pyrenoids. The derivation from the stelloid chloroplast is dealt with on p. 274.

*Ancylonema* BERGGR. Chloroplast agreeing with that of *Mesotaenium*, axile or parietal, insufficiently known.

*Roya* W. et G. S. WEST. Chloroplast laminate, axile, with several pyrenoids, sometimes stelloid with four lamellae. See further p. 274.

*Gonatozygon* DE BARY. Chloroplast laminate, axile, with a row of axile pyrenoids, sometimes stelloid with 3, 4, or 6 lamellae. See p. 274.

*Genticularia* DE BARY. Chloroplast 2—3 parietal, spirally twisted narrow ribbons with numerous pyrenoids.

*Penium* BRÉB. Chloroplast stelloid S 1, (in some species transversally divided in two) with one axile pyrenoid or more (in longer cells).

*Closterium* NITZSCH. Chloroplast stelloid, elongate conical, in smaller cells S 1, in thicker species S 3, S 4, or S 5, all of them with an axile row of pyrenoids, lamellae in some species anastomosing. In thicker cells the lamellae are thicker and lower with an increasing number of pyrenoids; these are situated in the peripheral layers: S 6. A hitherto unknown kind of parietal chloroplast, viz. the holo-parietal type S 7 is recorded, see p. 273.

*Clevei*-group. Chloroplast stelloid S 1 with one or more axile pyrenoids or taenio-parietal. See further p. 292.

*Staurastrum* MEYEN. The vast majority of the species have a monocentric chloroplast F 2 or F 3, larger species with accessory pyrenoids, see p. 298. Further, there are species with a dicentricoid chloroplast, e.g. *anatinum*, *sexangulare*, or even transitions to tetracentricoid, e.g. *Sebaldi* var. *altum*. In the circular basal part of species belonging to the *capitulum*-section there is a pseudo-stelloid chloroplast, e.g. *capitulum* (DEFLANDRE 1925, fig. 10).

*Stauroidesmus* TEILING. The vast majority have a monocentric chloroplast F 2 or F 3, larger species with accessory pyrenoids, or they have a dicentricoid chloroplast F 4 d, e.g. *Dickei* (GRÖNBLAD *in litt.* c. *icon.*) or, in biradiate species dicentric, e.g. *maximus* (BORGE) n. comb. (GRÖNBLAD 1945, t. 9: 178). Sector-parietal chloroplasts are recorded, e.g. *ceratophorus* (NORDST.) n. comb. and *tumidus* (LUND.) n. comb. representing the type F 11, see p. 280.

G. M. SMITH (1950, p. 330) attributes to *Arthrodesmus*, i.e. the small biradiate *Stauroidesmi*, an »axial laminate chloroplast with one or two pyrenoids», probably a slip.

*Euastridium* W. et G. S. WEST. Chloroplast monocentric, furcoid; »with a central pyrenoid and lobes radiating in each process»; this statement refers to *E. verrucosum* according to N. CARTER 1935, p. 172.

*Streptonema* WALLICH. Chloroplast furcoid, monocentric, triradiate. Because of the inflated ends of the processes the forked part of the lamellae are crescent-shaped a vertice.

*Desmidium* AGARDH. Chloroplast furcoid, 2—5-radiate, in biradiate cells dicentric, tetracentric or of the type 11, e.g. *Grevillei*, in 2—4-radiate dicentric, e.g. *Swartzii*.

*Phymatodocis* NORDSTEDT. Chloroplast furcoid, 4—5-radiate, monocentric, in certain species zygomorph, the lamellae entirely forked.

*Spondylosium* BRÉBISSEON. Chloroplast furcoid, 2—3-radiate, the smaller species monocentric F 2 or F 3, in broad and thin species with accessory pyrenoids, see p. 298.

*Cosmocladium* BRÉB. Chloroplast furcoid, monocentric or (rarely) dicentric (HEIMANS 1935, p. 109), biradiate.

*Oocardium* NÄG. Chloroplast furcoid, monocentric, biradiate.

*Onychonema* WALLICH. » » » »

*Sphaerosma* CORDA. » » » »

*Cosmarium* CORDA. 1. Angular cells. In small and thin species the chloroplast is furcoid, bi- or triradiate, monocentric, F 2 and F 3, in increasingly larger species dicentric, tetracentric, or sector-parietal F 6. 2. Rounded cells. In quasi-omniradiate and pseudo-omniradiate species the chloroplast is more



or less pseudo-stelloid, or limbo-parietal; in short sphaeroid species di-, or tetracentric. The *Clevei*-section is not considered, see p. 302.

*Xanthidium* EHRENB. The bi-, or triradiate furcoid chloroplast agrees with those of the angular *Cosmaria*: mono-, di-, and tetracentric and sector-parietal. *X. subhastiferum*, drawn by WEST as monocentric, is tetracentric in N. CARTER (1919 a, t. 18: 109—112) even with divided lobes. In *Brebissonii* N. CARTER (t. 18: 119—126) has given figures of chloroplasts varying between divided dicentric and transitions to tetracentric with varying number of pyrenoids, fig. 31. The most elaborate chloroplast is met with in *armatum* where the lobes of the sector-parietal chloroplast are irregularly divided and ridged, with numerous pyrenoids.

*Euastrum* EHRENB. Chloroplast furcoid, bi-triradiate, monocentric F 2, or dicentric F 4, or tetracentric (often of a kind characteristic for this genus) with several pyrenoids in each part, see further p. 279, 294 and 295.

*Micrasterias* AGARDH. Chloroplast furcoid discoid, di- and tetracentric. The fairly small *pinnatifida* (fig. 22) has a modified dicentric chloroplast with the double-ridged core characteristic for this genus and one accessory pyrenoid in the apical part (N. CARTER 1919 b, t. 19: 11, 12). *M. decemdentata* has a similar chloroplast (GRÖNBLAD 1921, t. 1: 1). The thick species have a dicentric chloroplast with several pyrenoids, e.g. *truncata* and *oscitans* (N. CARTER, t. 20: 25—27 and 19—22). The large *Moebii* seem to have a tetracentric chloroplast (GUTWINSKI 1902, t. 40: 58). The flattened species possess a fairly uniform laciniate discoid chloroplast with ridges and many pyrenoids.

*Docidium* BRÉB. Chloroplast stelloid, often with irregularly disposed lamellae, several axile pyrenoids.

*Pleurotaenium* NÄGELI. Chloroplast stelloid or, in most species, taenio-parietal. The narrow species, e.g. *rectum* and *minutum* have a stelloid chloroplast with several (6—12) pyrenoids (GRÖNBLAD 1824, 1). The latter species shows transitory forms to parietal chloroplast. The thicker species examined have taenio-parietal chloroplast, either consisting of longitudinal ribbons, sometimes, perhaps invariably, stretching from apex to apex, or shorter, often irregularly shaped tessellate pieces, e.g. *coronatum* (WEST, Monogr. I, t. 28: 4) and *ovatum* var. *laeve* (BERNARD 1908, t. 5: 105).

*Tetmemorus* RALFS. Chloroplast pseudo-stelloid with one elongated or several axile pyrenoids. The radial plates have their edges lacinate or thickened, extended and sometimes »more or less parietal» according to N. CARTER on *Brebissonii* and *granulatus* (1920 b, p. 315). In this case it is of the limbo-parietal type. See further p. 282—283.

*Triploceras* BAILEY. Chloroplast pseudo-stelloid, elongated, with several axile pyrenoids. Probably the apical part is radiate according to the 2, 3, or 4 hollow processes.

*Ichthyocercus* W. et G. S. WEST. Chloroplast pseudo-stelloid(?). There seems not to be any statement on the chloroplast in the literature. BOURBELLÉY has found it »axial du meme type que *Tetmemorus*», kindly communicated to me *in litt.*

*Triplastrum* IYENGAR et RAMANATHAN. Chloroplast furcoid, elongated, tri-radiate with 1—2 pyrenoids.

- Hyalotheca* EHRENB. Chloroplast pseudo-stelloid, short, one pyrenoid.  
*Bambusina* KÜTZ. Chloroplast pseudo-stelloid, one pyrenoid.  
*Groenbladia* TEIL. n. gen. Chloroplast axile, laminate, two or more axile pyrenoids. Diagnosis on p. 275—276.

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## Hepaticae collected in South and West Africa 1951.

New and little known species.

By SIGFRID ARNELL.

*Riccia (Ricciella) undulata* S. ARNELL nov. spec.

Type: ARNELL 2252, Africa occidentalis, Sierra Leone, Freetown, stream-side above Cabalar Point.

Monoica, dilute glauco-viridis. Frons usque ad 12 mm longa et 7 mm lata, apice breviter biloba, profunde sulcata, marginibus attenuatis et undulatis, antice plana-convexa, reticulata, cavernis haud prominentibus, parvis.

Squamae nullae vel rudimentariae. Costa crassa, postice convexa, lateribus in alas exstantes abeuntibus, margine ipso acuto, undulato. Sporae 50—70  $\mu$ , facie convexa reticulatim lamellata foveolis vix 8—12  $\mu$  diam. instructa, non papillatae, marginibus planis angustissime radiatim lamellatis.

Hab. Africa occidentalis, Sierra Leone, coll. S. ARNELL.

Monoicous, bright blue-green, old parts becoming white with a brown tinge, once or twice dichotomously branched, up to 12 mm long and 7 mm broad, although the breadth varies in the same plant: the margin is undulate. Apex emarginate or obtuse, often with pellucid margin, consisting of one layer of almost chlorophyll-less cells. Surface with small areolae supplied with a central pore, hardly visible by means of a hand-lens. Short furrow at the apex. Cross-section shows a thicker central part and broad thin wings, the breadth being about 6 times the height. Ventral scales absent or rudimentary. Dorsal epidermis with one layer of thin-walled cells with cupola-formed outer surface, often destroyed. Air-chambers small, only 2—4 cells high and narrow. Antheridial osteoles often numerous, colourless, rather long. Archegonial neck sometimes purple. Sporangia in the mid-line, often numerous and slightly protruding on the dorsal surface. Spores bright

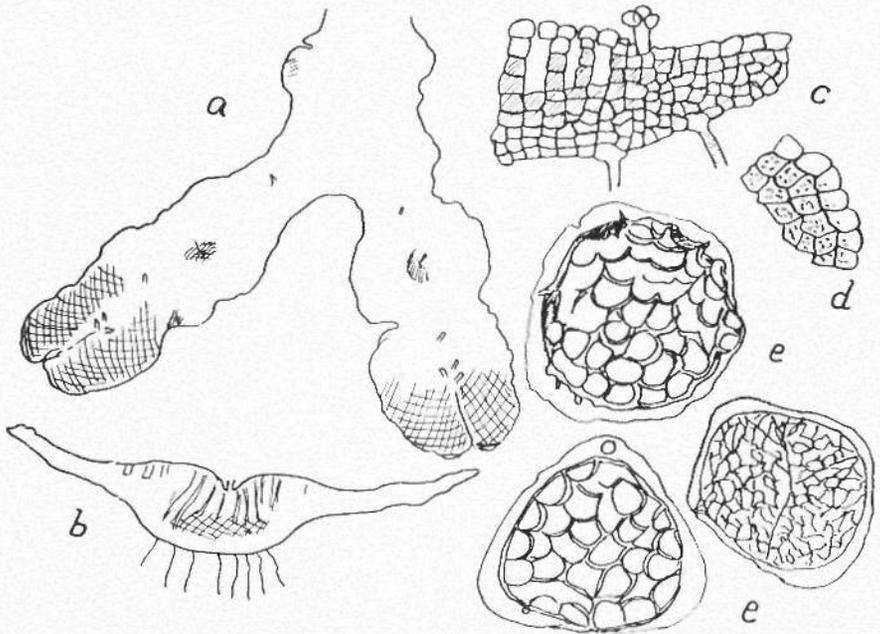


Fig. 1. *Riccia (Ricciella) undulata* S. ARN. a Thallus from dorsal side. b Cross-section of thallus. c Cross-section of thallus. d Marginal cells near the apex. e Spores from both sides.

brown, 50—70  $\mu$ , with a margin up to 8  $\mu$  in breadth, outer face with reticulum forming arcs and areolae (diam. 8—12  $\mu$ ), no papillae. Rhizoids colourless, smooth and tuberculate.

Type-specimen in Riksmuseum, Stockholm.

*Riccia (Ricciella) montaguensis* S. ARNELL nov. spec.

Type: ARNELL Nos. 714, 741, 747, Cape Province, Montagu, Bath Kloof, near the caves. Montagu, Cogmans Kloof No. 784.

Type specimens in The Bolus Herbarium, Cape Town and Riksmuseum, Stockholm.

Dioica?, magna, dilute viridis—flavo-rubescens. Frons ad 12 mm longa, 4—5 mm lata, 1—2 furcata, furcis 4—5 mm latis, apice breviter biloba, profunde sulcata, antice concava, marginibus decurvis, cavernis bullatim prominentibus rugulosa, poris e 5—6 cellulis concentricis formatis, costa crassa, postice convexa, lateribus rotundatis abrupte in alas exstantes abeuntibus. Sporae c. 80  $\mu$  diam., nigrae, 4—5 foveolis, 20—40  $\mu$  diam., instructae.

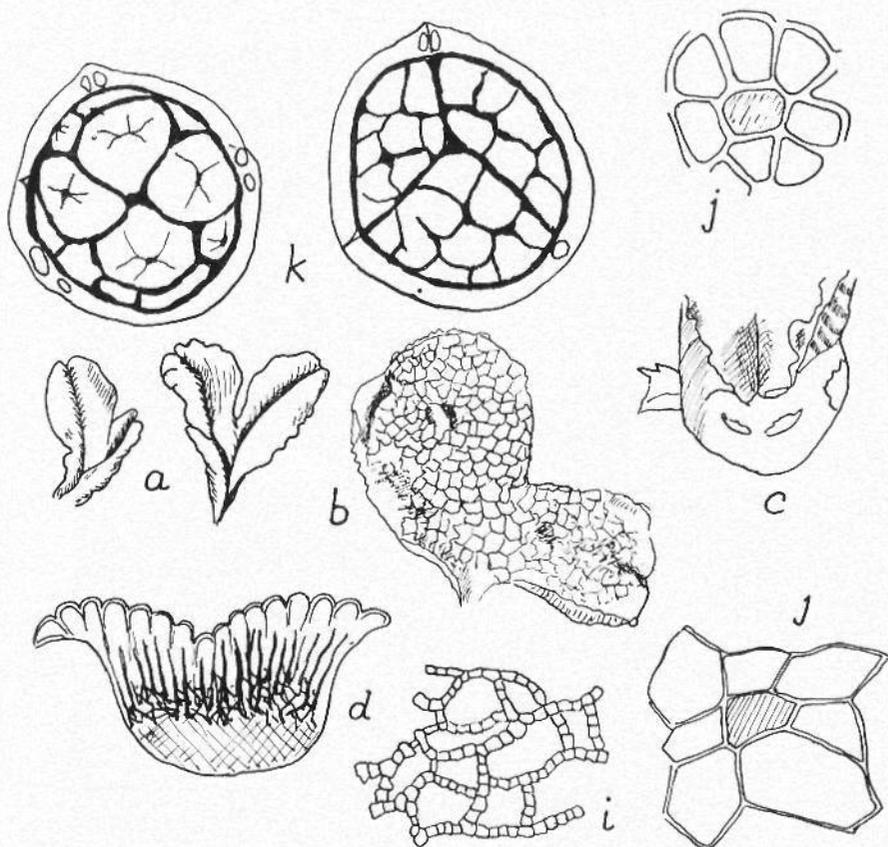


Fig. 2. *Riccia (Ricciella) montaguensis* S. ARN. a Thallus. b Young plant with reticular surface pattern. c Apex of a thallus with scales. d Cross-section of thallus. e Assimilation tissue. f Pores. g Spore from both sides. h Thallus. i Assimilation tissue. j Pores. k Spore from both sides.

Dioicous?, thallus single or once or twice dichotomously branched, often crowded in carpet-like groups. Thallus up to 12 mm long and 4–5 mm broad, bright green with lighter, often yellowish white wings, when old often bright yellowish brown. The surface on young thalli marked with polygonal areas, when old bullate and raised by the protruding air-chambers. Very similar in habitus to *R. bullosa*. The cells of the surface-epithelium are quadrate-polygonal, 30–40  $\mu$ , in the middle of the end-segments with a breadth about twice the height, the dorsal surface with a deep sharp furrow, the ventral surface in the middle part convex, then steeply ascending side-surfaces, in the upper

part becoming concave below the rather broad wings. Air-chambers large, in a single layer, but communicating with the labyrinthine channels in the lower parts of the respiratory tissue, built of one-cell thick broad balks. Ventral scales colourless, few, usually one pair at the apex and a larger pair behind them. In the peripheral part of the wings only large air-chambers. Both smooth and tuberculate rhizoids, the latter more abundant. Archegonia and antheridia not observed. Sporangia near the mid-line, sometimes causing a cupola-formed prominence on the dorsal surface, usually not observable from the surface. Spores dark, about 80  $\mu$  in diameter, with a 5—6  $\mu$  broad wing, which is often perforated at the three corners. On the convex outer-side 4—5 large foveolae 20—40  $\mu$  in diameter, and a few smaller areolae near the periphery. The larger areolae, as a rule, have a papilla in the centre, from which fine ridges run out giving it a triradiate to stellate form. Triradiate marking very distinct, of three ridges meeting at the spore apex and extending to the spore margin. The inner sides are delimited by thick ridges and have a reticular drawing with relative large areolae.

*R. montaguensis*, when dry, has the same buff or straw colour as *R. bullosa*, and somewhat resembles small specimens of the latter plant.

*Riccia (Ricciella) spongosa* S. ARNELL nov. spec.

Type: ARNELL No. 1393, Cape Province, George, Wilderness, forest-path  $\frac{1}{2}$  mile east of the hotel. Type specimen in The Bolus Herbarium, Cape Town.

Monoica?, major, viridis, sicca flavo-virens. Frons ad 8 mm longa, 2 mm lata, apice obtusa, non sulcata, antice convexa et porosa, marginibus rotundatis, cavernis magnis. Sporae permanentes adhaerentes in tetrade, nigro-brunneae, reticulatim lamellatae, foveolis 4  $\mu$  diam. instructae, non papillatae.

Monoicous? Thallus up to 8 mm long and 2 mm broad, linear, once or twice dichotomously branched or in long-branched rosettes, the young parts green, the older parts bright yellow-green. Dorsal tissue, except in the immediate neighbourhood of the growing point, very loose and spongy. Air-pores rapidly enlarging, the dorsal surface becoming pitted with large holes. Ventral scales not seen. Rhizoids mostly tuberculate. Spores dark brown, permanently adhering in tetrads, which are about 90  $\mu$  in diameter. Convex face with low ridges, forming complete or incomplete areolae, about 4  $\mu$  in diameter. No spines.



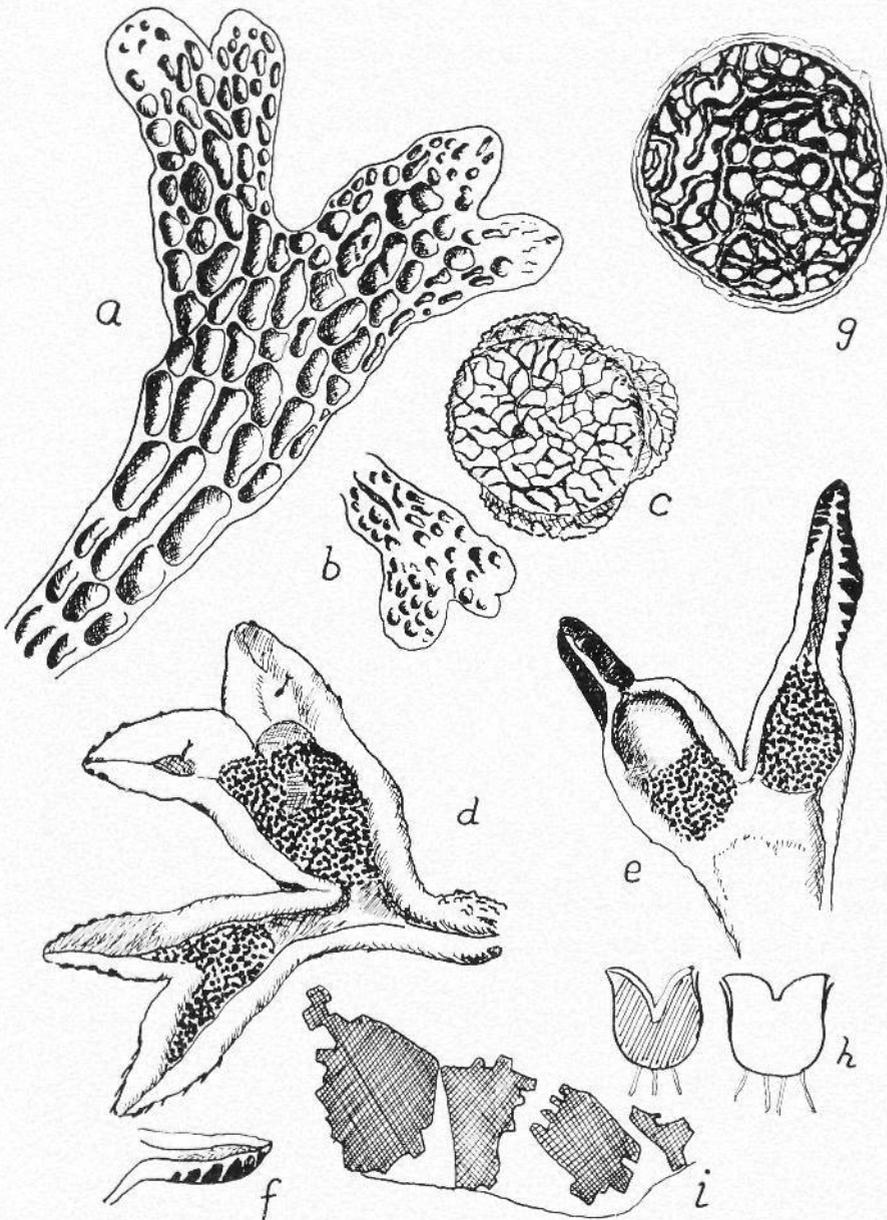


Fig. 3. *Riccia (Ricciella) spongosa* S. ARN. a Thallus. b Small thallus. c Tetrad of spores. — *Riccia capensis* STEPH. d Thallus. e Dry thallus. f Side view of thallus. g Spore. h Cross-sections of thallus. i Scales.

Differs from *R. Curtisii* in being larger and having linear branches and quite a different pattern on the spores.

*Riccia capensis* STEPH. [BRUNNTHALER, 1913, i, 14, ap. SIM, Trans. Royal Soc. S. Afr. XV (1926) p. 13.]

Cape Province, Peninsula: Wynberg, cultivated ground (Park Hotel) Nos. 162, 186, 189, 302. Wynberg, roadside No. 150. Lions Head above Fresnaye Nos. 26, 36, 49, 50, 59.

Montagu: Cogmans Kloof Nos. 802, 792.

The type specimen of BRUNNTHALER in Vienna contains only sand and no *Riccia* can be found in it. The drawings of STEPHANI show a *Riccia* of the same appearance as the one in my collection and I therefore use the name of STEPHANI for this plant. As the type for my plant I will use Nos. 59 and 162.

Monoicous, of about the same size as *R. sorocarpa* L. Usually in rosettes, 10—18 mm in diameter, bright glaucous green in the young portions, the margins soon changing to yellow-brown, in the older parts yellow-brown, sharp, when dry convex in the proximal parts of the thalli and therefore appearing swollen, in the apical parts the margins when the thallus is dry bend towards one another, so when seen from above the dark scales cover the apex. The fresh green segments are about 2 mm long and 1—1½ mm broad, the thallus 2—3 times dichotomously branched with acute angle, the segments acutely lingulate and with a deep sharp furrow. Ventral scales in one line, dark blackish-red, quadrangularly serrate, reaching the margin of the thallus. In cross-section the breadth is equal to or somewhat less than the height, the dorsal surface with narrow deep furrow, the ventral surface strongly convex in the basal part, in the upper part concave to the sharp margin. Epidermal cells in one layer, rectangular-quadrate, with nearly plane or faint convex free surface, thin-walled. The archegonial neck almost black, the sporangium causing a pillow-like prominence on the dorsal surface, which at this place soon becomes dark red in the centre and orange-brown in the periphery, frequently two sporogonias in line one behind the other. The dorsal wall is soon destroyed and the interval between the lateral wings of the thallus filled by black spore-masses. Spores 50—60  $\mu$ , red-brown, marginal wing 2—3  $\mu$ , often broader at the corners and at that place with rounded emarginations. Coarse ridges on the convex side, forming a complete reticulum, the ridges often with a brighter mid-line or two bright lines and a dark

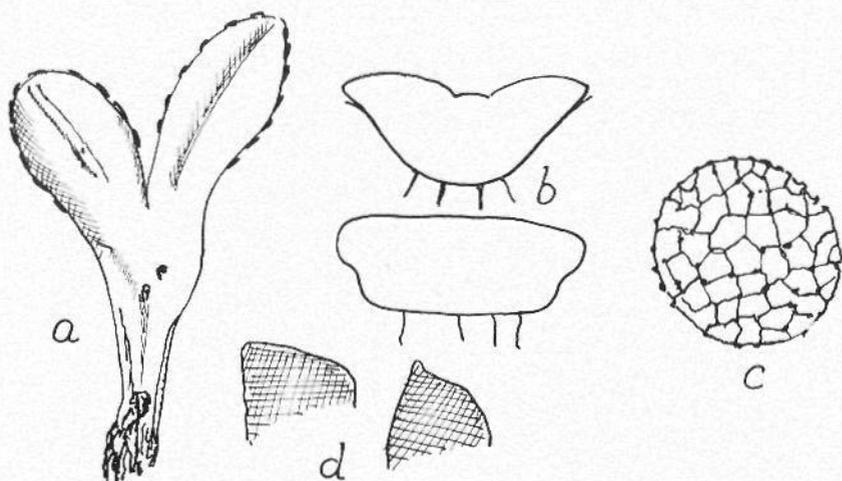


Fig. 4. *Riccia rhodesiae* S. ARN. a Thallus from dorsal side. b Cross-sections. c Spore. d Scales.

mid-line, with a very short, truncate papilla at each of the nodes of the areolae, on the convex side. The areolae small, usually 3—4  $\mu$  in diameter. The inner side of the spores with similar, but lower ridges. Antheridial osteoles blackish red.

Hab. Sandy soil, also on cultivated ground.

Distrib. Cape Province. Common in the surroundings of Cape Town. Also noted from Montagu and Genadendal.

Looks like *R. limbata* (the black scales), but much smaller and with quite a different decoration of the spores.

*Riccia rhodesiae* S. ARNELL nov. spec.

S. Rhodesia, Victoria Falls, on soil near the Trolley Junction, Nos. 1271, 1291.

Type specimens in The Bolus Herbarium, Cape Town, and Riksmuseum, Stockholm.

Dioica?, olivaceo-viridis. Frons 5—8 mm longa, 3—4 mm lata, 2—3 furcata, acuteque sulcata. Squamae majores, triangulares, purpureae, marginem haud excedentes. Sporae 80—100  $\mu$  diam., rufo-brunneae, reticulatim lamellatae, foveolis 6—8  $\mu$  diam. instructae.

Thallus dark olive-green, 5—8 mm long, 2—3 times dichotomously branched, with sharp but shallow furrow. Lobes narrow ovate, with

rounded apex. Breadth about  $2\frac{1}{2}$  times the depth. The surface often pitted in the mid-line. The dorsal surface with a sharp furrow in the apical part, the side parts convex. In the proximal parts of the thallus the furrow is not so distinct or is absent, the dorsal surface then faintly convex and the margin obtuse. The ventral surface in the basal part convex, the upper parts straight and forming a sharp margin. The ventral scales large, triangular-lanceolate, dark purple, hardly protruding over the margin of the thallus. Epithelial cells in one layer, with thin walls and cupola-formed outer-surface. Spores 80—100  $\mu$ , bright brown-dark brown, regularly reticulated, papillae in the corners of the areolae, areolae 6—8  $\mu$ . Antheridial neck colourless.

*Fossombronina capensis* S. ARNELL nov. spec.

Type ARNELL No. 1876, Bracken Hill Forest, Knysna, Cape Province. Other collections: Knysna; Parkes Station 1470, 1474, 1477; Guona Forest Reserve Nos. 1756, 1757, 1783, 1799.

Dioica, major, ad 12 mm longa, 2 mm lata. Sectio transversa cum facie dorsali plano-concava, facie ventrali convexa. Perianthia campanulata, margine undulato et dentato. Sporae ad 40  $\mu$  diam., furcatim lamellatae, lamellis laxe dispositis. Elateres lamellati, spiralibus incompletis et rudimentariis. Antheridia bracteis tecta.

Dioicous. Rather large, up to 12 mm long and 2 mm wide, with strong aromatic smell. Stem on cross-section somewhat higher than broad, dorsally plane-concave, ventrally convex, the ventral part coloured dark purple. Cells in the stem 24—30  $\mu$ , thin-walled. Leaves entire, somewhat emarginate, slightly undulate, marginal cells  $35 \times 35$ — $36 \times 40$   $\mu$ , cells in the middle of the leaf about  $50 \times 50$   $\mu$ . Pseudoperianth campanulate, with undulate and bluntly dentated margin. Sporogonium-wall with irregularly formed cells, yellow half-ring threads and pointformed thickenings in groups. Spores of the same appearance as in *F. pusilla*, with distant ridges forming incomplete areolae, yellow, incomplete marginal wing between the 12—16 marginal spinae. Elaters rudimentary, mostly consisting of a thin leaf  $10$ — $15 \times 70$   $\mu$ , with incomplete spiral thickenings. Archegonia on the dorsal side of the stem, numerous, nude. Antheridia on the dorsal side, covered by large bracts.

The curious elaters seem to be very characteristic for this species. The large male bracts also distinguish it from the European *F. pusilla*, the pattern of the spores being very similar to that species.

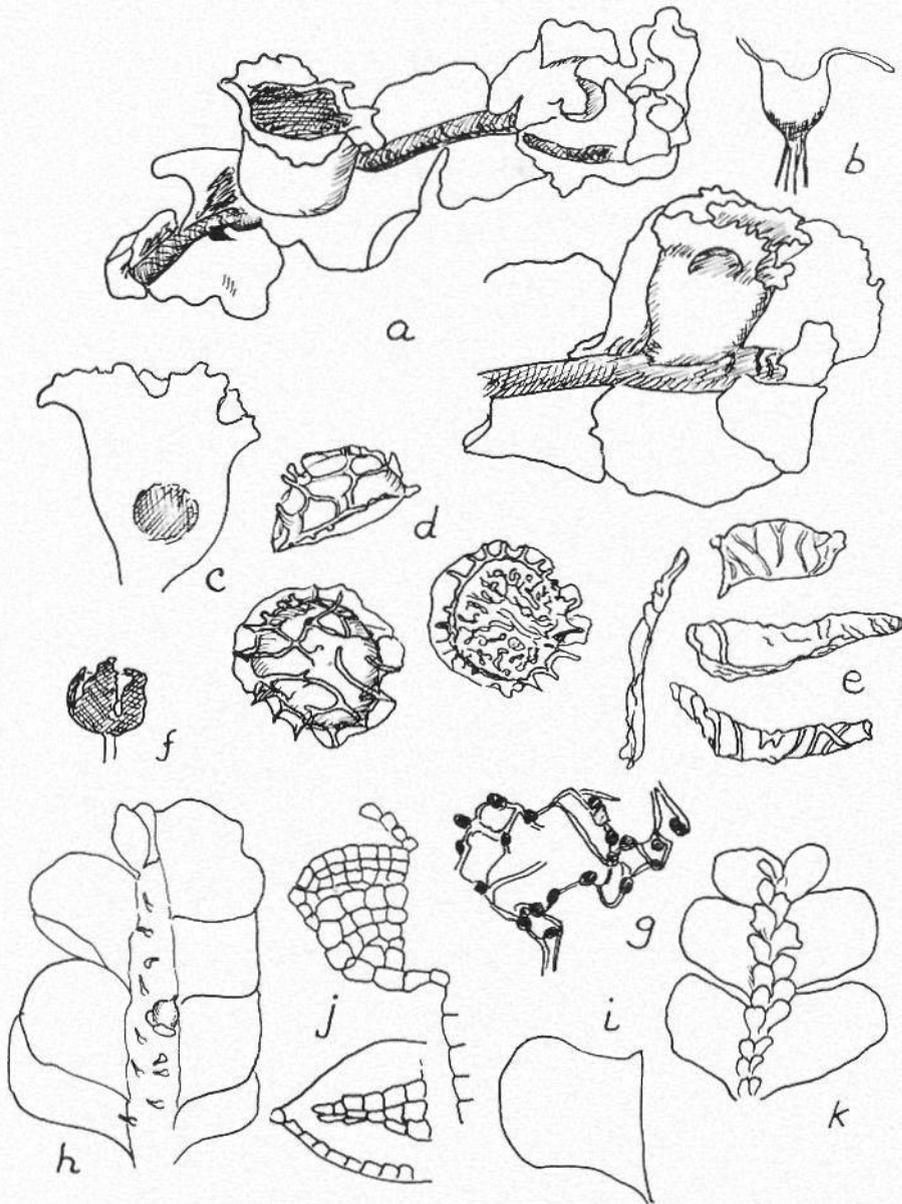


Fig. 5. *Fossombronia capensis* S. ARN. *a* Plants with pseudoperianths. *b* Cross-section of the stem. *c* Pseudoperianth. *d* Spores. *e* Elaters. *f* Capsule. *g* Capsule-wall. *h* Female plant with archegonia. *i* Leaf. *j* Male bracts. *k* Male plant.

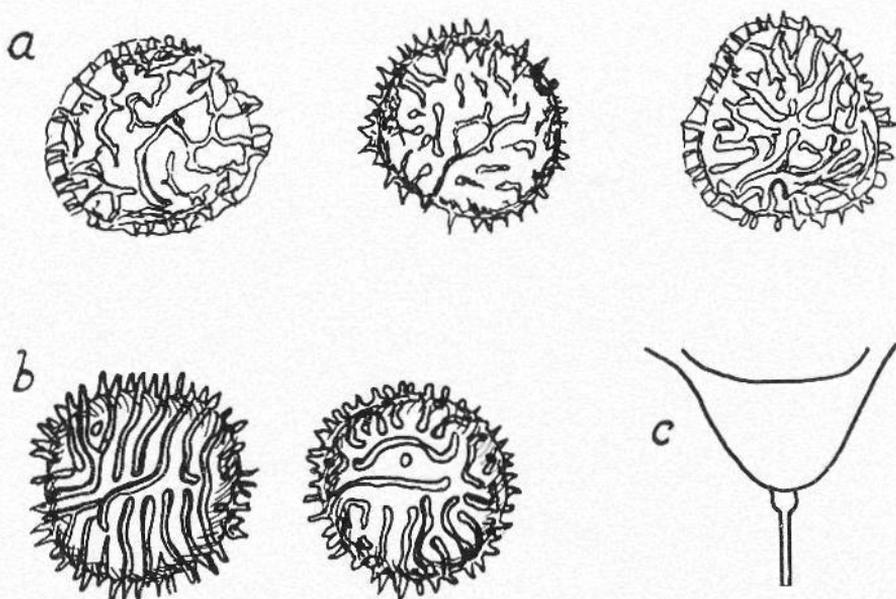


Fig. 6. *a* *Fossombronia montaguensis* S. ARN. Three spores. *b* Two spores of *P. densilamellata* S. ARN. *c* *F. occidento-africana* S. ARN. Cross-section of stem and rhizoid.

*Fossombronia montaguensis* S. ARNELL nov. spec.

Cape Province, Montagu, Bath Kloof, 724, 731, 739, 774, 785.

Dioica, dilute viridis, ad 8 mm longa, 2 mm lata. Folia haud lobata, integerrima vel obtuse dentata. Cellulae marginales  $30 \times 40$ – $50 \mu$ , basales ad  $40 \times 100 \mu$ . Pseudoperianthium campanulatum, margine integerrimo vel crispato. Sporae  $30$ – $32 \mu$ , obtuse et irregulariter lamellatae. Elateres  $4 \mu$  lati et ad  $140 \mu$  longi.

Dioicous, pale green, about 8 mm long and 2 mm broad. Stem on cross-section with plane dorsal surface, strongly convex ventral surface, height equal to breadth. Rhizoids purple. Leaves slightly lobate, entire or with a few obtuse short teeth. Marginal cells  $30 \times 40$ – $50 \mu$ , in the middle of the leaf  $50 \times 50$ – $60 \mu$ , basal cells  $40 \times 100 \mu$ . Pseudoperianth campanulate or, when the sporogonium is mature, as a wide cup with entire and somewhat crispate margin, sometimes open on the basal side and then not completely surrounding the sporogonium. Spores  $30$ – $32 \mu$ , on the convex side with irregularly branched ridges with obtuse or sharp spines, often connected with one another by thin lamellae, on the inner side with low short ridges and low plump spines. Elaters up to  $140 \mu$  long and  $4 \mu$  wide, with 2 spirals.

*Fossombronia densilamellata* S. ARNELL nov. spec.

*F. tumida* SIM, Trans. of Royal Soc. S. Afr. XV p. 35 1926. Cape Province; Lions Head near Kloof Nek 257, 265, 295. Montagu, Cogmans Kloof 762.

Dioica, major, viridis, ad 15 mm longa, 4 mm lata. Folia crispata, concava-plana,  $\pm$  dentata. Perianthia campanulata, ore dentato et crispato. Sporae 40  $\mu$ , dense lamellatae, spinae ad 50. Antheridia bracteis lecta.

Dioicous, rather large, green. Plant up to 15 mm long, with leaves 4 mm wide. Cross-section of the stem shows in the posterior portions a breadth about 3 times the height, in the middle and peripheral end a breadth equal to the height or somewhat larger. Leaves in the apical part slightly crispate, in the other part of the plant plane-slightly concave, somewhat lobate and with a few  $\pm$  obtuse and short teeth. Cells in the margin  $20 \times 40$ — $30 \times 50$   $\mu$ , in the middle of the leaf about  $30 \times 40$   $\mu$ , at the base  $40 \times 70$   $\mu$ . Cuticula smooth. Old leaves soon decolorized, often with entire margin, concave or almost plane. Archegonia on the dorsal side of the stem, nude as young and unfertilized. Perianth widely campanulate, the margin slightly crispate and obtusely dentate. Spores 40  $\mu$ , red-brown, with numerous sharp lamellae, mostly running parallel to one another, about 50 spines in the periphery. Male plants with antheridia on the dorsal side of the stem, covered by concave bracts.

MITTEN describes *F. tumida* as having spores »obscurae papillosae»; therefore it can not be this plant in which the spores have lamellae, and I think SIM is wrong in identifying it with *F. tumida* MITT.

*Fossombronia occidonto-africana* S. ARN. nov. spec.

Sierra Leone, Freetown, Mont Oriel, 2409, 2413, 2418, 2431, 2448, 2449, 2468, 2476, 2497.

Dioica, ad 10 mm longa, 1,5 mm lata, viridis, terricola. Sectio transversalis caulis triangularis, radicellis purpureis basibus bullosis instructis. Perianthium campanulatum, margine crispatum et lobatum. Sporae 34—40  $\mu$ , brunneae, lamellis interruptis vermicularibus. Antheridia flava, 100  $\mu$  diam., bracteis masculis longis.

Dioicous, about 10 mm long and  $1\frac{1}{2}$  mm wide, dark green, on moist soil, especially on stream-banks. Cross-section of the stem triangular, about 200  $\mu$  high and 250—300  $\mu$  wide, with plane dorsal surface, almost straight lateral sides and a narrow convex ventral mid

portion with purple rhizoids with a strongly bulbous base. Leaves lingulate-rotundate, often rather strongly crispate, with slightly lobate-entire margin. Marginal cells  $20 \times 20$ — $34 \mu$ , basal cells up to  $40 \times 70 \mu$ , cuticula with 1—2 long striae per cell, sometimes small trigones. Pseudoperianth campanulate, with rather long narrow basal part, margin recurvate, slightly crispate, lobated, not dentated. Spores brown, 30—40  $\mu$ , with the same pattern as *F. Stephani* (lamellis interruptis vermicularibus). Elaters up to 150  $\mu$  long and 8  $\mu$  wide, mostly composed of 3 spirals, sometimes only 2 spirals or 2 spirals at the ends and 3 in the mid part. Capsule-wall shows broad and close semicircular thickenings. Male plants with antheridia on the dorsal side near the apex, covered by rather long narrow bracts with deeply bidentate apex. Antheridia about 100  $\mu$  in diameter, pale yellow, globose. Differs from *F. Husnoti* in having purple rhizoids and 3 spirals in the elaters, from *F. Stephani* in having smaller spores and 3-spired elaters.

*Cephaloziella tabularis* S. ARNELL nov. spec.

Type: ARNELL 844, 857, 859, 1223, 1227, Cape Province, Table Mountain, near the upper Cable Way Station.

Cape Province, Peninsula, above Bakoven 865. The Flats, between Claremont and Cement Works, near St. John's Tower.

Paroica, gracilis, fusco-brunnea. Caulis ad 15 mm longa, 60  $\mu$  diam. Folia concava, brunnea-purpurea, ad  $1/2$  bifida, lobi breves, acuti, sinus obtusus. Cellulae marginales 12  $\mu$ , basales ad 20  $\mu$ . Amphigastria lanceolata vel bifida. Bracteae feminae crenulatae—dentatae, 1—2 jugae. Perianthia triplicata, purpurea, ore decolorato, crenulato. Androecia subfloralia vel intercalaria, bracteis 4—8 jugis, quam folia caulina majoribus.

Paroicous, prostrate on soil, or mixed with other bryophytes. Stem up to 15 mm long and 60  $\mu$  in diameter, dark brown, cortical cells rectangular-quadrate,  $12 \times 16$ — $16 \times 28 \mu$ , in regular longitudinal rows. Leaves distant, mostly dark brown, at the apex purple or hyaline, convex, bifid to  $1/2$ , sinus obtuse. Cells in the margin of the lobes about 12  $\mu$ , at the base of the lobes  $10$ — $12 \times 18$ — $20 \mu$ , in the middle of the male bracts up to  $16 \times 30 \mu$ . Amphigastria lanceolate-bifid. Female inflorescences apical on long branches, crenulate-dentate, in 1—2 pairs, connate with the bracteole at the base. Often innovations below the sterile perianths. Perianth purple with hyaline mouth, mouth crenulate, apical cells with very thick walls, about  $10 \times 40 \mu$ . Spores not seen.



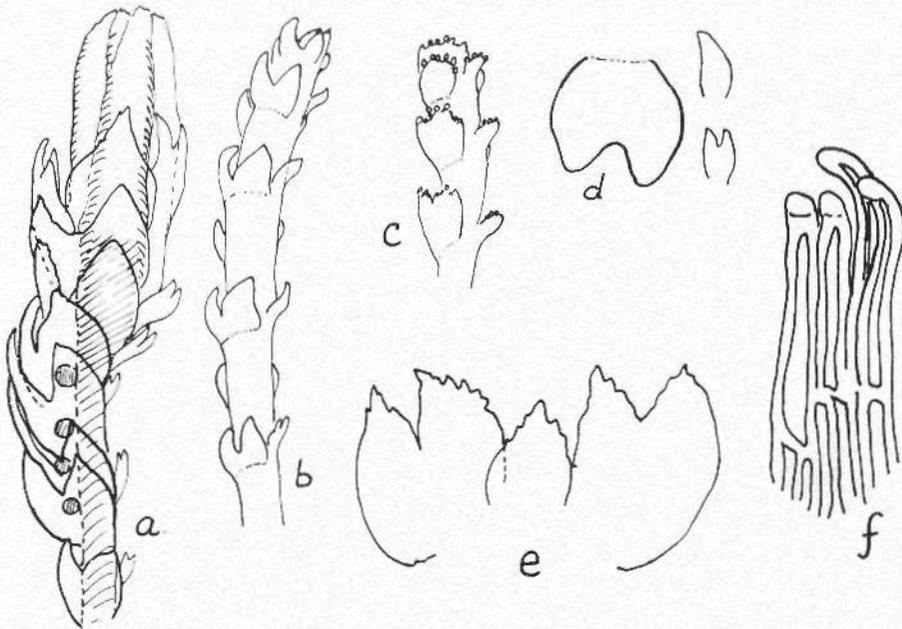


Fig. 7. *Cephaloziella tabularis* S. ARN. a Plant with perianth. b Sterile plant. c Plant with gemmae. d Leaf and amphigastria. e Female bracts and bracteole. f Cells from the margin of the perianth.

Male bracts in 4—8 pairs below the female bracts, larger than the leaves, otherwise of the same appearance, sometimes also intercalary androecia.

Grows in moist places on the Plat Kliff as a dark carpet of black threads on soil or usually mixed with other bryophytes. The dark colour, the very small and distant leaves give it a characteristic appearance. Gemmae on the margin of deformed leaves.

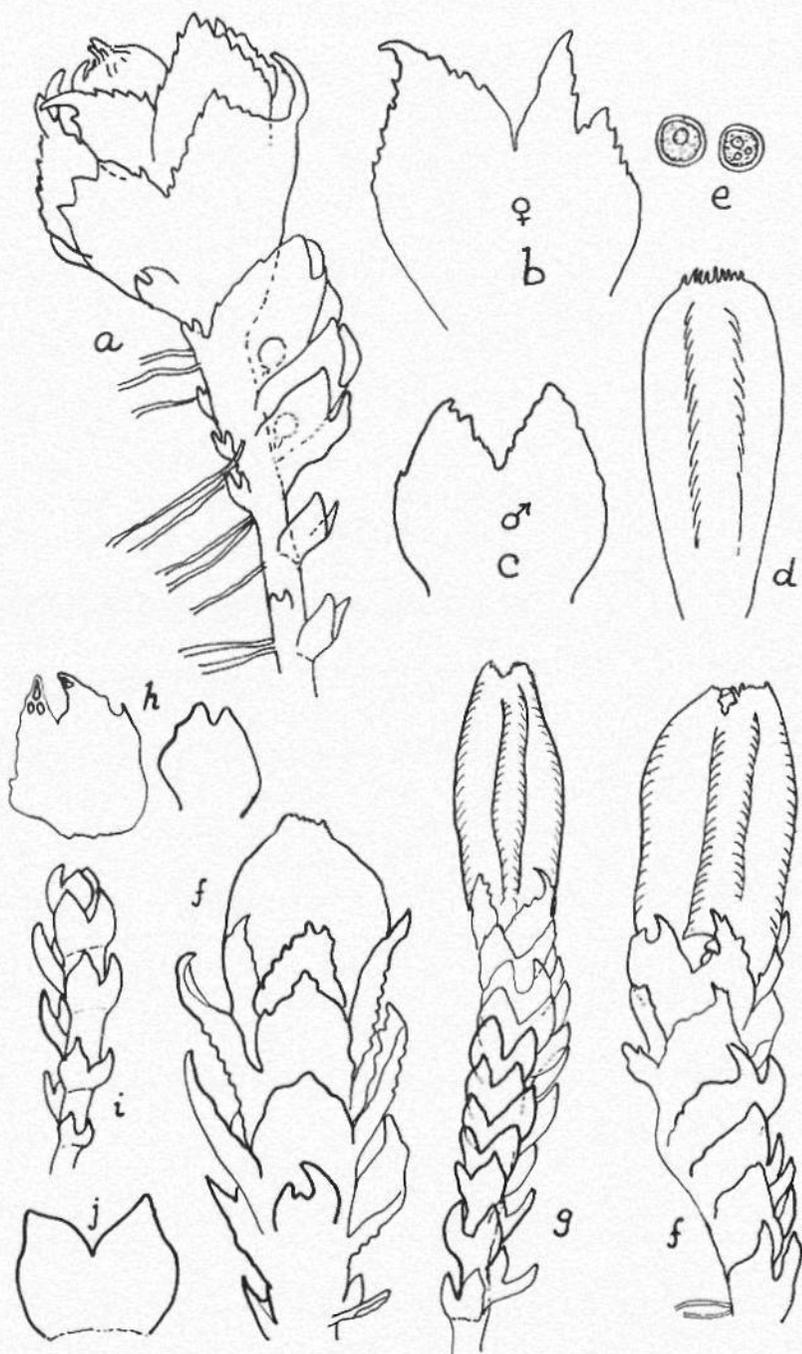
*Cephaloziella Kiaerii* (AUST.) S. ARN. nov. comb.

*Jungermania Kiaerii* AUSTIN, Torrey Bot. Club 1875 p. 18.

*Cephalozia Kiaerii* STEPH., Spec. Hep. III p. 329.

Cape Province, Peninsula, Constantia Nek No. 319. Between Constantia Nek and Kirstenbosch Nos. 128, 129, 131, 134, 135. Kirstenbosch No. 1218.

Monoicous, pale green—dark brown, creeping on soil and among other mosses, prostrate or erect when growing in dense carpets. Stem



up to 2 cm long and 60—70  $\mu$  in diameter, thicker towards the top, with few rhizoids, especially on the lower part, sparsely and irregularly branched, cortical cells 10—14 $\times$ 24—40  $\mu$ , cuticula striated. Leaves  $\frac{1}{3}$ — $\frac{1}{2}$  bilobed, insertion transverse-oblique (30—60°), lobes triangular up to 6 cells broad, somewhat conduplicate—plane and squarrose, margin entire or seldom with an occasional tooth. Marginal cells 10—20  $\mu$ , internal cells (12—)20—30  $\mu$ , walls of medium thickness, cuticula smooth or fine papillose. Amphigastria on sterile branches absent or small near the peripheral end, on fertile shoots larger, of varying form, bifid or entire. Female bracts in 1—2 pairs, large, bilobed, dentate, the lobes pointed with a mostly hyaline apical cell. Perianth triplicate, cylindrical-ovoid, with constricted mouth, ciliate by long cells. Spores red-brown, 8—10  $\mu$ , elaters 5 $\times$ 100  $\mu$ , red-brown. Male bracts in 3—10 pairs below the female bracts, with an antheridium 54 $\times$ 60—60 $\times$ 70  $\mu$  in the axil, larger and more convex than of the leaves, sometimes apical andraecia. Gonidia round-ellipsoid, on the top of shoots.

The oblique insertion of the leaves is remarkable, in *Cephaloziella* the leaves otherwise have a transverse insertion.

*Cephaloziella lycopodioides* (SIM) S. ARN. nov. comb.

*Cephalozia lycopodioides* SIM, Trans. Royal Soc. S. Afr. XV (1926) p. 85.

Cape Province, Montagu, Bath Kloof, 765.

Dioicous or autoicous. On soil, dark purple. Stem 3—4 mm long, 60—120  $\mu$  (in male bracts) wide, cortical cells 8—10 $\times$ 20—34  $\mu$ , cuticula smooth. Leaves imbricate, to  $\frac{1}{2}$  bilobed, lobes triangular, subacute, entire, distal portion and margin purple, apex often decolorized, sinus acute. Marginal cells 9—10  $\mu$ , internal cells up to 14  $\mu$ , in the base up to 10 $\times$ 20  $\mu$ , cuticula smooth. Walls of medium thickness, no trigones. Oil-bodies 2—8 per cell, 2 $\times$ 2—2 $\times$ 4  $\mu$ . No amphigastria except in the inflorescences. Rhizoids brownish, long and abundant. Female inflorescence short and thick. Bracts in 2 pairs, the inner bract connate, with broad, shortly pointed lobes and marginal cells 10—16  $\mu$ , inner cells of the same magnitude, walls very thick, margin decolorized, base red.

Fig. 8. *Cephaloziella Kiaerii* (AUST.) S. ARN. *a* Plant with paroecious inflorescence. *b* Female bract. *c* Male bract. *d* Perianth. *e* Spores. *f* Plant from ventral side and in side view. *g* Unusually long inflorescence. *h* Female bract and bracteole. *i* Sterile plant. *j* Leaf.

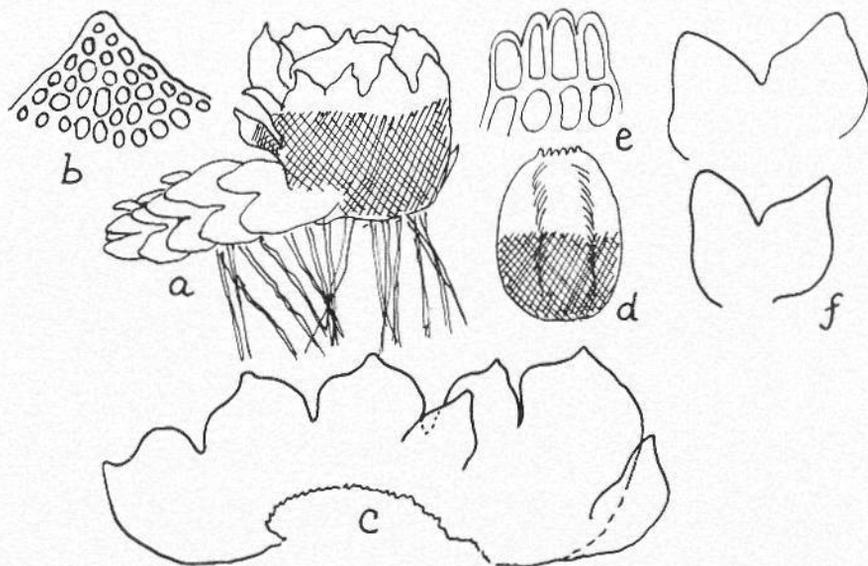


Fig. 9. *Cephaloziella lycopodioides* (SIM) S. ARN. a Plant with perianth. b Cells from margin of a female bract. c Female bracts (internal row). d Perianth. e Cells from the margin of the perianth. f Leaves.

Perianth short, obovate, mouth constricted, crenulate by protruding, short, thick-walled cells, distal  $\frac{1}{2}$  frequently decolorized, then a purple band and the basal portion green. Male inflorescences apical, with 5—6 densely imbricated pairs of bracts. Bracts somewhat larger than the leaves but of the same form, antheridia 1—2 in the axils, globose, 40  $\mu$  in diameter, stalk short, with one cell row.

*Cephaloziella anthelioides* S. ARNELL nov. spec.

Type: ARNELL no. 766, Cape Prov. Montagu, Bath Kloof.

Peninsula, Constantia Slopes No. 392.

Type specimens in Bolus Herbarium, Cape Town and Riksmuseum, Stockholm.

Autoica, dense intricata, viridis-brunnescens. Caulis ad 2 cm longa, 100  $\mu$  diam., viridis. Folia ad  $\frac{2}{3}$  bifida, transverse inserta, conduplicata, lobis triangularibus, acutis. Cellulae marginales 14—20  $\mu$ , cuticula papillosa. Amphigastria magna, triangularia vel bifida. Folia floralia bilobata, dentata, dentibus recurvatis.

Perianthia ovata, ore crenulato. Androecia in ramis sub inflorescentia feminea, bracteis conduplicatis, dentatis, minoribus.

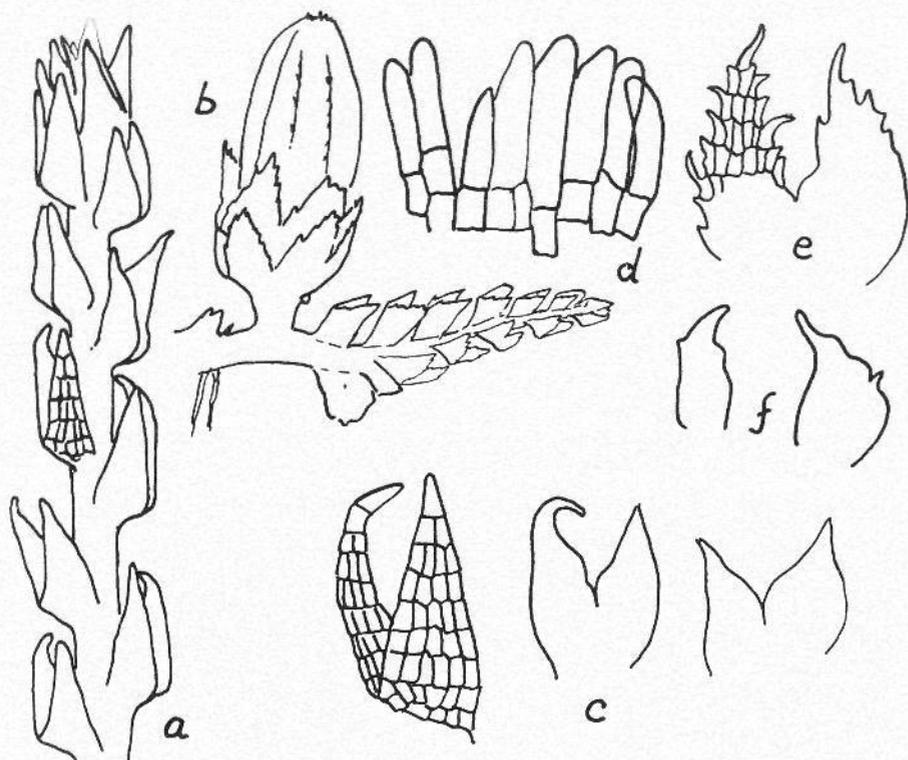


Fig. 10. *Cephaloziella anthelioides* S. ARN. a Sterile plant. b Plant with perianth and male branch. c Three leaves. d Cells from the mouth of the perianth. e Female bract. f Female bracteoles.

Autoicous, in dense intricate carpets on soil. Stem up to 20 mm long and 100  $\mu$  in diameter, green, cortical cells 14—20  $\times$  20—40  $\mu$ . Cuticula slightly striated. Leaves approximate, up to  $\frac{2}{3}$  bifide, lobes triangular-lanceolate, conduplicate up to 8 cells wide sometimes a short tooth basally, apex of ventral lobe often clow-like recurved, apex acute, sinus acute. Marginal cells 14—20  $\mu$ . Cuticula papillose, especially at the margin and on the base. Amphigastria large, triangular or bifid. Female bracts in 2 pairs, bilobed, dentate, with long acute, often recurved teeth. Perianth ovoid, mouth crenulate by long cells. Spores 10  $\mu$ , pale brown, fine papillose. Elaters 5  $\times$  80—160  $\mu$ . Male inflorescences on separate branches below the female inflorescence, triangular, the bracts decreasing in size towards the apex, bilobed, conduplicate and dentate.

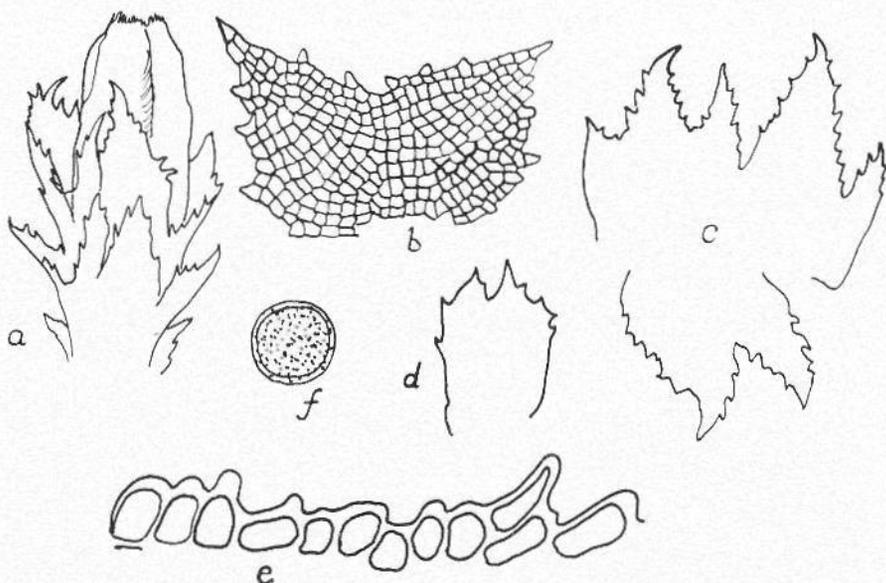


Fig. 11. *Cephaloziella tenuissima* (L. & L.) S. ARN. *a* Plant with perianth. *b* Leaf. *c* Internal female bracts and bracteole. *d* Bracteole. *e* Margin of mouth of perianth. *f* Spore.

*Cephaloziella tenuissima* (L. & L.) S. ARN. nov. comb.

*Jungermania tenuissima* LEHM. & LINDENB., Syn. Hep. p. 143. 1844.

*Cephalozia tenuissima* STEPHANI, Spec. Hep. III p. 514.

Cape Province, Peninsula, Lions Head: between Kloof Nek and Round House Nos. 201, 214, 217, 232, 249, above Clifton No. 509. Wynberg Park 143. Above Bakoven 942.

Montagu; Bath Kloof 779, 794. Cogmans Kloof 808.

Autoicous. Growing on soil, usually in thin, intricate carpets, pale green-dark purple. Stem up to 10 mm long and 70–90  $\mu$  in diameter, yellow-brown, sparsely branched. Cortical cells 10  $\times$  20–24 (–36)  $\mu$ , irregularly rectangular, walls of medium thickness. Cross-section shows cortical cells with thickened walls, internal cells of the same diameter (16–18  $\mu$ ) but with thin walls. Leaves approximate-distant, on sterile branches more distant,  $\frac{1}{2}$ – $\frac{2}{3}$  bifide, obtusely conduplicate, on the dorsal side frequently with papillose or spinose protruding cells, base diverges 60–90° from the stem, lobes parallel to—diverging 20° from the stem, triangular and acute, dentate, frequently decolorized at the apex. Sinus on flattened leaves about 150°, often with deflexed margin.

Marginal cells 10—12  $\mu$ , internal cells up to 16  $\mu$ . Cell walls of medium thickness. Oil-bodies 1—7 (—9 in bracts) per cell,  $2 \times 2$ — $2 \times 8$   $\mu$ , colourless, marginal cells without oil-bodies. Cuticula slightly papillose-smooth. Rhizoids abundant, colourless. Amphigastria rather large, entire—bifid. Female bracts larger than the leaves, 2—3 pairs, conduplicate and strongly dentated at the margin, connate to  $\frac{1}{2}$ . Perianth obovate, rather broad and short, mouth dentate by 30—40  $\mu$  long cells, when young purple, when older usually decolorized at the margin. Spores 10  $\mu$ , red-brown. Elaters  $8 \times 130$ —150  $\mu$ .

*Cephaloziella leonensis* S. ARNELL nov. spec.

Type: ARNELL No. 2, Cape Province, Lions Head above Fresnaye and Round House Nos. 2, 6, 15, 16, 27, 43, 196, 197, 201, 218, 251, 272, 279, 481.

Hottentotts Holland, Steenbrass River, at the outlet No. 703.

Type specimen in Bolus Herbarium, Cape Town and Riksmuseum, Stockholm.

Dioica?, tenuis, viridis, terricola. Caulis ad 6 mm longa, 60  $\mu$  diam. Folia squarrose patula, ad  $\frac{3}{4}$  bifida, carinata, lobi inaequales, triangulares, dentati. Cellulae marginales 10—12  $\mu$ . Amphigastria minima. Folia floralia caulinis majora. Perianthia longa at tenuia, triplicata, ore ciliato. Sporae 6—8  $\mu$ , leves.

Dioicous?, small and gracile, green, on soil. Stem up to 6 mm long and 60  $\mu$  in diameter, cortical cells  $12$ — $18 \times 30$ — $40$   $\mu$ . Leaves rather distant, up to  $\frac{2}{3}$ — $\frac{3}{4}$  bilobed, base diverging  $90$ — $45^\circ$  from the stem, lobes triangular, the dorsal lobe frequently longer, sparsely dentate by protruding cells, marginal cells 10—12  $\mu$ , internal cells  $12$ — $18 \times 20$   $\mu$ , in the mid line of the lobes, especially in the dorsal lobe, often long cells,  $10 \times 30$ — $34$   $\mu$ . Sinus acute, up to  $90^\circ$ . Cuticula smooth or with few fine papillae. Amphigastria small, mostly subulate. Female bracts 2—3 pairs, free, of the same form as the leaves but larger. Perianth long and narrow, 3-plicate, mouth crenated by protruding cells, 20—60  $\mu$  long, green or decolorized. Spores 6—8  $\mu$ , light brown, with chloroplasts in the centre, cuticula smooth. Elaters 4—8  $\mu$  broad, yellow brown. Capsule wall light brown, with semicircular thickenings, cells  $10$ — $12 \times 30$   $\mu$ . Gemmae 1-celled, round, from the margin, apex and dorsal side of deformed leaves and amphigastria.

It looks like a gracile and small *Cephaloziella tenuissima*, but the very different form of the perianth and bracts distinguish the two species at

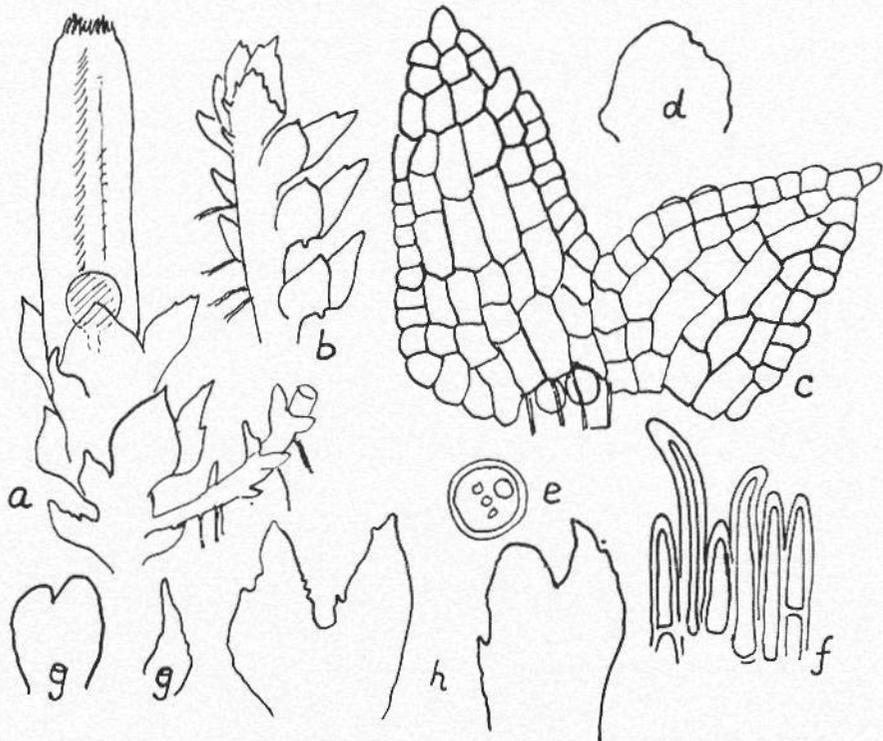


Fig. 12. *Cephaloziella leonensis* S. ARN. *a* Plant with perianth, *b* Sterile plant, *c* Leaf, *d* and *g* Bracteoles, *e* Spore, *f* Cells from mouth of perianth, *h* Female bracts.

once. They frequently grow mixed together. The type specimen of SIM (9787, Kloof of Constantia Nek) in National Herbarium, Pretoria, contains both this species and another, identical with what I have described as *C. capensis*. To judge from his drawings, I think SIM had the latter in view when he described his species.

*Cephaloziella capensis* (SIM) S. ARNELL nov. comb.

*Cephalozia capensis* SIM, Trans. Royal Soc. S. Afr. XV, p. 87, 1926. Cape Province, Peninsula; Constantia Nek, No. 467, Orange Kloof Forest Department No. 2198.

Dioicous?, on soil, green. Stem 2—3 cm long, 60—90  $\mu$  in diameter, prostrate—sub-erect, with few branches, cortical cells 12—14  $\times$  20 (—40)  $\mu$ , mostly nearly quadrate, cuticula striated. Leaves approximate—distant on sterile shoots, regularly arranged, transversally inserted,



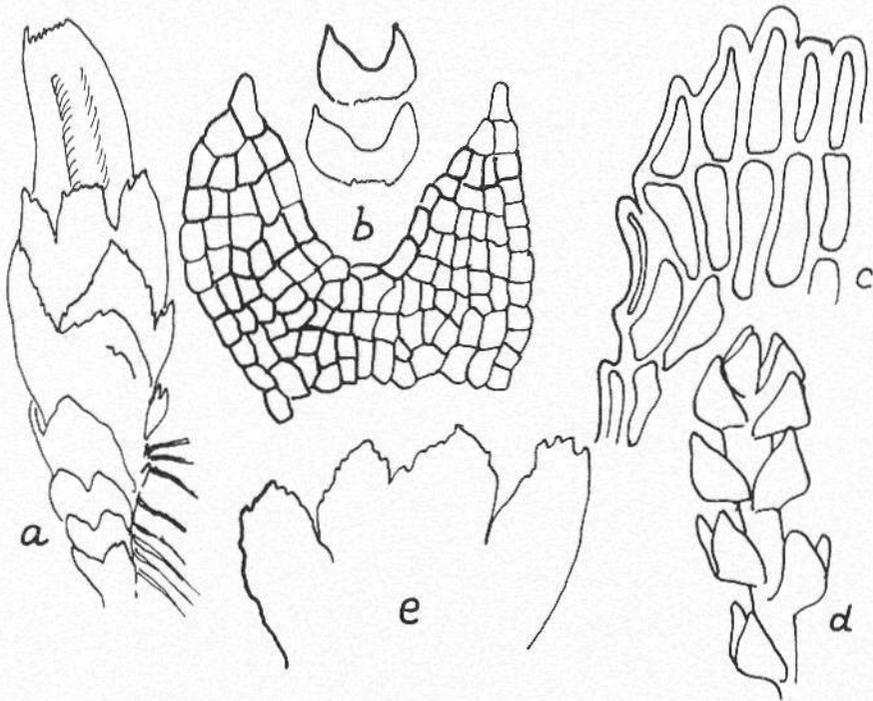


Fig. 13. *Cephaloziella capensis* (SIM) S. ARNELL nov. comb. *a* Plant with perianth. *b* Leaves. *c* Margin of a female bract. *d* Sterile plant. *e* Female bract.

sinus lunate, bifid to  $\frac{2}{3}$ — $\frac{3}{4}$ , lobes lanceolate, subacute, entire, 6—7 cells wide at the base, conduplicate. Cuticula with few small papillae, cell walls thin, no trigones. Oil-bodies not seen. Amphigastria small, subulate, present only near the apex. Female bracts in 2—3 pairs, the inner pair connate with each other and the bracteole, margin decolorized, crenated by protruding, thick-walled long cells and dentate. The second pair has also a similar margin. Perianth triplicate, with low plicae also on the sides, obovate, decolorized in the distal  $\frac{1}{3}$ , mouth crenated by protruding long cells. Spores 10—14  $\mu$ , brown, fine papillose. Elaters  $6 \times 100 \mu$ .

*Cephaloziella marionensis* S. ARNELL nov. spec.

Type: Bolus Herbarium No. 23884, South Atlantic, Marion Island, legit Commander COPENHAGEN Feb. 1948.

Dioica, gracilis. Caulis ad 2 cm longa, 60—80  $\mu$  diam., pluriramosus, cuticula papillosa. Folia bilobata ad  $\frac{1}{3}$ , lobi lanceolati, acuti. Cellulae

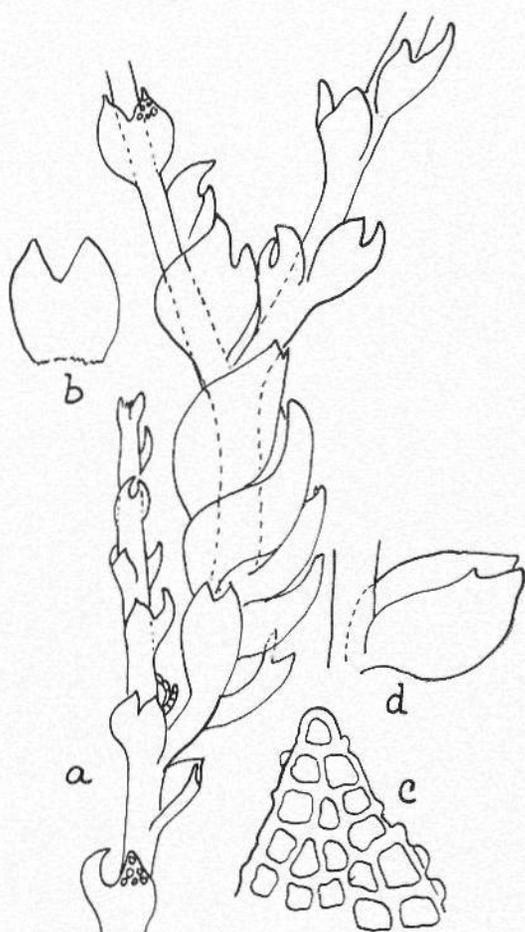


Fig. 14. *Cephaloziella marionensis* S. ARN. a Plant with androecium. b Leaf. c Lobe. d Male bract.

marginales 10–16  $\mu$ , basales 20  $\times$  20  $\mu$ , validae. Amphigastria desunt. Androecia intercalaria, bracteis concavis, ad  $\frac{1}{8}$  bilobis.

Dioicous, mixed with *Jamesoniella colorata*. Stem to 2 cm, 60–80  $\mu$  in diameter, repeatedly branched. Cortical cells 10–12  $\times$  16–20  $\mu$ , thick-walled, cuticula with rather large papillae. Leaves distant, bilobed to  $\frac{1}{3}$ , ovate, lobes lanceolate, acute, 4–5 cells broad at the base, sinus acute. Marginal cells 10–16  $\mu$ , internal cells up to 20  $\times$  20  $\mu$ , walls thick, cuticula papillose. Amphigastria absent. Female inflorescence not seen. Male inflorescences intercalary, frequently several on the same branch. Male bracts large, in 4–10 pairs, margin entire — occasionally dentated, 3 times as large as the leaves, very concave, internal and basal cells up to 20  $\times$  22  $\mu$ .

#### Key to the South African species of *Cephaloziella*.

- a. Paroicous.
  - b. Thread-like, dark brown, with small, short, concave leaves hardly broader than the stem, amphigastria present, mostly barren. *C. tabularis* S. ARN.
  - bb. Of varying length, green-brown, leaves larger, often obliquely inserted, amphigastria fugitive. *C. Kiaerii* (AUST.)
- aa. Autoicous or dioicous.
  - b. Perianth on short lateral branches. *C. lycopodioides* (SIM)
  - c. Leaves densely imbricate, slightly concave.

- cc. Leaves with long triangular lobes, conduplicate, female bracts serrate with often recurved teeth. *C. anthelioides* S. ARN.
- bb. Perianth apical on long branches.
- c. Leaves dentate and conduplicate, perianth short, female bracts connate basally, amphigastria present. Perianth often purple with decolorized margin. *C. tenuissima* (L. & L.) S. A.
- cc. Leaves entire or only with an occasional tooth.
- d. Leaves conduplicate, lobes unequal, the dorsal longer and usually with long cells in the centre, female bracts free, perianth long and narrow, green or decolorized, very small plant. *C. leonensis* S. ARN.
- dd. Lobes of about equal size, amphigastria absent or fugitive.
- e. Leaves bilobed to  $\frac{2}{3}$ — $\frac{3}{4}$ , sinus obtuse, female bracts crenated. *C. capensis* (SIM)
- ee. Leaves not so deeply bilobed, female bracts dentate, sinus acute.
- f. Male bracts smaller than the leaves, conduplicate. Prostrate, numerous rhizoids the entire length. *C. radicans* (SIM)
- ff. Rhizoids only basally. Male bracts larger than the leaves. *C. natalensis* (SIM)  
(*C. marionensis* with rough papillose cuticula. Dioicous. Male bracts bilobed to  $\frac{1}{8}$ .)

### Summary.

The author describes the following new species from West Africa, Sierra Leone: *Riccia* (*Ricciella*) *undulata* S. ARN., *Fossombronia occi-dento-africana* S. ARN. and from South Africa: *Riccia spongosa* S. ARN., *Riccia montaguensis* S. ARN., *Riccia rhodesiae* S. ARN., *Fossombronia capensis* S. ARN., *Fossombronia montaguensis* S. ARN., *Fossombronia densilamellata* S. ARN., *Cephaloziella tabularis* S. ARN., *Cephaloziella anthelioides* S. ARN., *Cephaloziella leonensis* S. ARN., *Cephaloziella marionensis* S. ARN. He also gives more complete descriptions of *Cephaloziella tenuissima* (L. & L.) S. ARN., *Cephaloziella lycopodioides* (SIM) S. ARN., *Cephaloziella Kiaerii* (AUST.) S. ARN., *Riccia capensis* STEPHANI.

## Några sädeskornsavtryck från Sydsveriges stenålder.

AV H. HJELMQVIST.

(With a summary in English.)

Alltsedan den danske forskaren SARAUW i slutet av 1800-talet började använda metoden att med hjälp av tillfälligtvis bildade avtryck av sädeskorn i keramik från förhistorisk tid fastställa vilka sädeslag som voro i odling under tiden ifråga, har särskilt i Danmark med denna metod en mängd bidrag lämnats till kulturväxternas historia (i senare tid särskilt av JESSEN och HELBÆK). De uppgifter som föreligga från Sydsverige på detta område (SARAUW 1899, KJELLMARK 1905, LIDÉN 1940), äro emellertid mycket sporadiska och delvis allmänt hållna. För att i någon mån fylla den lucka som alltså finnes i kännedomen om Sydsveriges äldsta kulturväxter har jag företagit en granskning av ett stort antal lerkärl och lerskärvor (de senare kanske c:a 20.000 i antal) i Lunds universitets historiska museum från den yngre stenåldern, vår äldsta jordbrukstid, och ehuru hittills blott ett ringa antal kornavtryck påträffats, lämnas i det följande en redogörelse för dessa första fynd. För välvilligt bistånd tackar jag museets tjänstemän, särskilt docent C.-A. ALTHIN och amanuens MATS PETERSSON.

Från tidig döstid, enligt en utbredd uppfattning den första tid, då jordbruk förekom i vårt land, föreligger ett fynd från en boplats vid Oxie (nr 28377 Bb) med ett tydligt kornavtryck. Avtrycket visar ventralsidan av ett sädeskorn, med den karakteristiska fåran (fig. 1 a, 2 a). Längden är 5,7 mm, bredden 2,8 mm. Till storlek och form överensstämmer avtrycket alltså väl med skallöst korn, och kommer nära danska typer från stenåldern. Strax intill kornavtrycket finnas avtryck av två borst och troligen en del av ett tredje (fig. 1 b), vilka bilda en grupp liksom de borstlika skärmfjällen i ett kornax och därför säkerligen höra till samma art.

I en annan krukskärva från samma fynd (27857:147) finnas två avtryck, vilka av storlek och form att döma säkerligen äro av sädeskorn,

ehuru de tyvärr ej äro gjorda av ventralsidan. Det ena har en längd av 6,8 mm, bredden är 3,2 mm (kornets bredd möjligen något mindre, då avtrycket synes vara något snett). Storlek och form, bl.a. den starkt krökta rygglinjen, överensstämmer med emmer, *Triticum dicoccum*. Något märke av grodden är dock ej synligt. Det andra avtrycket är ofullständigt och visar blott nedre delen, c:a hälften av ett korn. Bredden är 3,0 mm. Även detta liknar mest emmer i storlek och form. Om båda får alltså sägas, att de sannolikt äro avtryck av emmerkorn.

En annan skärva från samma fynd (28377 B) har ett avtryck, som ej är bildat av ett sädeskorn men som dock i detta sammanhang är av intresse. Avtrycket är c:a 2,0 mm brett och minst 6 mm långt (hela längden är ej med) och försett med längsstrimmor. Säkerligen är det bildat av ett gräsfrö; ett märke vid basen kan motsvara grodden. Något annat gräs än råglösta, *Bromus secalinus*, kan ej gärna komma i fråga.

Av ungefär samma ålder som kornavtrycken från Oxie, d.v.s. från tidig döstid, är ett avtryck i en trattbägare från St. Herrestad: Fredriksberg. Detta är omtalat i den arkeologiska litteraturen som ett vetekorn (I.ex. hos MOBERG 1951). Avtrycket, som är bildat på bägarens insida, visar en något snedställd ventralsida av ett korn. Längden är 5,7 mm och bredden 3,0, och form och storlek visa därmed, att det är skallöst korn, medan vete har en mera brett rundad form.

Från något senare döstid föreligger ett kornavtryck (fig. 2 b) i en lerskärva från Maglarp: Albäcksborg (nr 28443: 3). Också här är det fråga om en ventralsida, och form och storlek äro nästan exakt desamma som i föregående fall: längden är 5,7, bredden 2,9 mm. Också detta avtryck är alltså bildat av skallöst korn.

Bland de avtryck, som härstamma från gånggrifttid, är ett av de äldre omtalat och avbildat i litteraturen av RYDBECK (1938), som betecknar det som ett vetekornsavtryck. Det finnes i en trattbägare från Södervidinge (nr 20155), som enligt RYDBECK härstammar från gånggrifttidens första tredjedel, och det var det äldsta avtryck av detta slag, som vid denna tid var honom bekant från Lunds historiska museum. Avtrycket är bildat av ett korn, som varit alldeles inneslutet i bägarens vägg, och vid dess sönderfallande har det delats på två skärvor; på den ena är ventralytan avgjuten, på den andra större delen av kornet. Vid jämförelse mellan de båda avtrycken framgår, att ventralytan snarast är vinkelrät mot kornets största genomskärning, d.v.s. att kornets bredd är mindre än dess höjd eller tjocklek. Bredden beräknades till 2,6 mm, höjden till 3,1 och längden till c:a 5,4. Detta förhållande, att

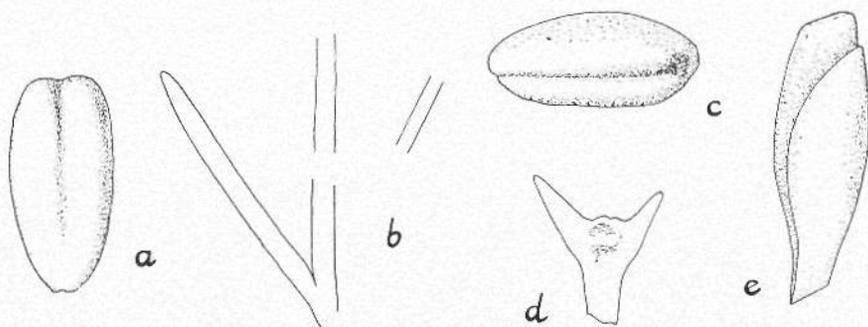


Fig. 1. *a* avtryck av skallöst korn från Oxie, tidig döstitid; *b* borstavtryck av samma; *c* avtryck av enkorn från Södervidinge, tidig gånggrifttid; *d* avtryck av småaxbas av emmer från Nosaby, gånggrifttid; *e* småaxavtryck av emmer från Barsebäck, Gillhög, gånggrifttid. Alla teckningar utom *d* gjorda efter plastilinaavgjutningar. — Impressions in pottery from Neolithic time of (a—b) naked barley, grain and bristles, (c) small belt, (d—e) emmer, spikelet base (spikelet fork) and spikelet. All drawings, except *d*, made after plastilina casts. —  $\times 5$ .

tjockleken är markerat större än bredden, visar att det är fråga om en korn, *Triticum monococcum*, varmed även i övrigt dimensionerna överensstämmer; en likhet är också den asymmetri, som ventralytan visar och som väl åtminstone till en del är ursprunglig. I samma bågare finnes även ett annat avtryck, djupt insänkt; bredden är c:a 2,7, tjockleken c:a 3,6 mm, medan längden är ofullständig. Förhållandet tjocklek : bredd liksom den här mycket starkt asymmetrisk och sneda ventralytan visa, att det även här är fråga om enkorn.

Till fyndet från Södervidinge höra också många lerskärvor, och vid genomgång av dessa ha också några kornavtryck anträffats. Ett större väggparti av en bågare visade sålunda på utsidan ett vackert avtryck av enkorn (fig. 1 c). Att det var enkorn visades i detta fall främst genom den bågformigt rundade konturen av ventralsidan, utmärkande för detta sädesslag, samt vidare genom de olikstora partierna på ömse sidor om fåran. Längden var 5,7 mm, avtryckets bredd 2,5; då ventralytan tydligen har varit något snedställd, har kornets bredd varit något mindre, kanske c:a 2,2 mm. Tjockleken var ofullständig. En mindre skärva visade ett avtryck av en ventralsida, 5,6 mm långt men med bredd och tjocklek ofullständiga. På grund av den bågformiga konturen och den tydligen asymmetriskt löpande fåran måste detta också vara bildat av enkorn. Detsamma gäller om ett annat avtryck i en liten skärva (längd 5,9, bredd troligen 2,2 mm); det måste också represen-

tera enkorn, då de av ventralfåran skilda partierna äro olikstora och olika höga.

Det är alltså fem olika avtryck av enkorn, som äro konstaterade i fyndmaterialet från Södervidinge, medan avtryck av någon annan art ej där anträffats.

Från Barsebäck: Gillhög föreligger ett stort antal lerskärvor, de flesta från gånggrifftid. I allmänhet sakna dessa fynd helt kornavtryck, men i en fyndgrupp (från gånggrifftid) anträffades flera avtryck. Två av dessa voro ofullständiga; att de bildats av sädeskorn var dock tydligt, då ventralfåran väl framträdde på båda och ett märke efter grodden var tydligt synligt på det ena av dem. Bredden var i båda fallen c:a 3 mm; längd och tjocklek voro ofullständiga. Med hänsyn till avtryckens form och de mått som kunde beräknas kunde man antaga, att de voro bildade såväl av emmer som av skallöst korn; då emellertid emmer har en markerat smalare kornbas, medan den här var brett rundad, och då vidare kornens tjocklek, om den också ej var exakt mätbar, dock föreföll att vara mindre än bredden, måste det vara fråga om skallöst korn. Ett tredje avtryck visade en del av ett småax (fig. 1 e). Två fjäll framträdde här; det ena, yttre var  $6\frac{1}{2}$  mm långt, vasst kölät, det andra sköt något upp över detta. Till utseendet överensstämde avtrycket med emmer eller enkorn, vilka båda ha skarpt kölade skärmfjäll; då det ej fanns märke av någon tand på skärmfjället som hos enkorn, måste det vara fråga om emmer. Ett avtryck av ett korn i en fjärde skärva härrörde också från emmer: längden var 7 mm, tjockleken c:a 3 mm, bredden ofullständig, ventralsidan var plattad, dorsalsidan välvd. — Utom denna fyndgrupp, där alltså fyra kornavtryck kunde fastställas, funnos i andra grupper enstaka avtryck, troligen härrörande från sädeskorn. I en skärva av en »konhalsskål» (nr 9) fanns sålunda ett avtryck, som var 7,4 mm långt och c:a 3,4 mm brett, medan tjockleken var ofullständig, dock troligen något större än bredden, och ryggsidan var rundat välvd. Helt säkert var detta avtryck bildat av ett emmerkorn (ryggsidan). Ett avtryck i en annan skål (nr 11) var troligen också, med hänsyn till den jämnt rundade formen, bildat av ryggsidan av ett sädeskorn. Bredden var c:a 3 mm, längd och tjocklek ofullständiga. Formen erinrade mest om skallöst korn; sannolikt var avtrycket bildat av detta sädesslag.

Även av råglosta, *Bromus secalinus*, fanns det ett par avtryck i Gillhög-materialet. I en skål fanns det alltså avtryck av två bildningar bredvid varandra, som till utseendet överensstämde med ett småaxfragment av *Bromus secalinus*, ett skärmfjäll och en blomma därovan-

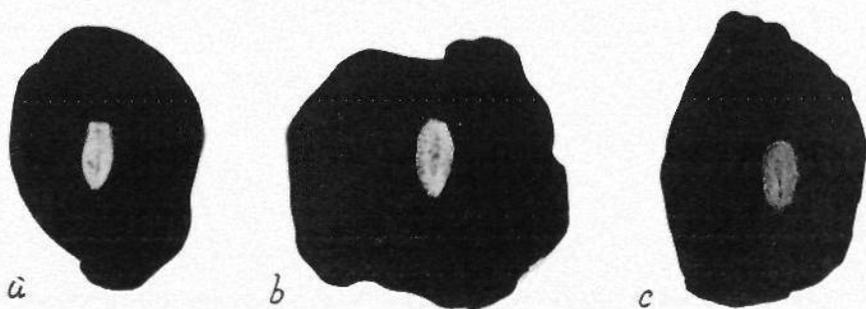


Fig. 2. Avtryck av skallöst korn från olika stenåldersfynd i Skåne. Plastilinaavgjutningar. *a* från Oxie, äldre döstid; *b* från Maglarp, Albäcksborg, något senare döstid; *c* från Svedala, Hylltarp, yngre gånggrifftid. — Naked barley from Neolithic time. Plastilina casts of impressions in pottery from three places in Scania. — C:a  $\times 1\frac{1}{2}$ .

Foto Å. PERSSON.

för. I en skärva av ett annat kärl fanns avtryck av ett korn, c:a 5 mm långt och 1,6 mm brett, med en svag längsstrimma på ryggsidan. Dimensionerna äro desamma som hos smärre frukter av *Bromus secalinus*.

I ett annat fynd från gånggrifftid, från Nosaby (nr 28171), förekom ett avtryck, som var bildat av ett sädeslag, om också ej av ett korn. Det visade basalpartiet av ett småax med de nedre, grövre delarna av de båda skärmfjällen (fig. 1 *d*). Liknande avtryck äro ofta funna bl.a. i Danmark (»smaaaksforke»). De äro bildade av enkorn eller emmer; till utseendet överensstämma de ganska mycket hos dessa båda arter, men vissa kvantitativa olikheter finnas, som närmare påvisas av JESSEN (1939). Det här föreliggande avtrycket överensstämmer i måtten med emmer, om det också har relativt små dimensioner i jämförelse med recent emmer.

Slutligen finnes från yngre gånggrifftid ett sädeskornavtryck i ett lerkärl från Svedala: Hylltarp (nr 25573 g). Längden är 5,3 mm, bredden 2,7 mm, och genom storlek såväl som form visas därmed, att det är bildat av skallöst korn (fig. 2 *c*).

I material från gånggrifftid fanns även ett avtryck, som visserligen ej bildats av ett sädeskorn men som ändå är av intresse, då det härrör från en växt, som möjligen varit odlad eller i varje fall stått i samband med kulturen. I en skärva från Trolle-Ljungby: Hammaren iaktogs nämligen ett avtryck, som måste vara bildat av en äpplekärna. Ytan var mycket slät och jämn, längden 6,7 mm, bredden c:a 2,4 (ej alldeles fullständig), tjockleken c:a 4,0 eller möjligen något mer (ej fullständig);



bredden var stor nära basen och avsmalnade starkt mot den smala spetsen liksom hos äpple, varmed dimensionerna även visa överensstämmelse.

Från Lackalänga (gånggrifftid) fanns ett avtryck, som uppenbarligen var bildat av *Bromus secalinus*; längden var 5,7, bredden 2,0 mm, avsmalnande särskilt mot ena hållet; den ena sidan var rak och den andra krökt, varför avtrycket tydligen visade kornet något från sidan.

De sädeslag, som därmed blivit konstaterade från Skånes neolitium, äro följande.

1. Skallöst korn, en form av *Hordeum polystichum*, som erinrar om var. *coeleste* utan att dock helt överensstämma därmed. Härav ha sex avtryck påvisats, från tidig döstid till yngre gånggrifftid, medan ett sjunde avtryck, från gånggrifftid, sannolikt också hör hit. De äldsta avtrycken (från Oxie och St. Herrestad: Fredriksberg) tillhöra den allra tidigaste jordbrukskulturens tid.

Skallöst korn är tidigare påvisat från Danmarks yngre stenålder av SARAUW, vilken (se HATT 1937) från denna tid anger 26 fynd med 40 avtryck därav, medan han av skalkorn endast anträffade 14 avtryck i 7 fynd. JESSEN (1939) har i Bundsö på Als (gånggrifftid) även funnit skallöst korn, däremot ej skalkorn. Enligt BRÖNDSTED (1938, s. 141) gå ett par fynd av skallöst korn (Birkeröd Mose och Bornholm: Vallensgaard) tillbaka till den allra äldsta jordbrukstiden i Danmark. Från Sydsverige synes ej någon exakt uppgift föreligga om skallöst korn från förhistorisk tid, men JESSEN (1939) förmodar, att de rikliga fynden av *Hordeum vulgare* från pålbyggnaderna vid Alvastra (gånggrifftid) tillhöra den skallösa typen. Detsamma gäller säkert om åtminstone något av de av SARAUW (1899) i korthet omnämnda kornfynden från södra Sverige, utan närmare fyndortsuppgift, att döma av en uppgift hos JESSEN och HELBÆK (1944, s. 43).

Som visas av BRÖNDSTEDS (1938) och JESSENS (1939) framställningar, har skallöst korn i Danmark varit den äldsta kornsorten, medan skalkorn först något senare kommit i odling. Också för Storbritannien påvisa JESSEN och HELBÆK (1944), att fynd av skallöst korn överväga under äldre perioder, medan senare skalkorn blir dominerande. I Sverige ha förhållandena förmodligen varit likartade. Det skallösa kornet har emellertid länge hållit sig kvar i mindre utsträckning; en form därav, himmelskorn, förekom i odling i Sverige, ehuru sällsynt, ännu i senare hälften av 1800-talet.

2. *Emmer*, *Triticum dicoccum*. Av detta sädeslag ha tre avtryck anträffats från gånggrifftid, medan ett fjärde från samma period troligen hör hit. Från tidig döstid (Oxie) föreligga två avtryck, som också efter all sannolikhet äro bildade av emmer.

Av emmer äro talrika fynd gjorda från Danmarks neolithicum. Enligt HATT (a.a.) har sålunda SARAUW från denna period anträffat 288 avtryck i 40 fynd, ett antal som senare utökats av andra forskare. Också från Sydsverige finnas ett par uppgifter om emmer. Från stenålderbopplatsen i Järavallen vid Limhamn omtalar således KJELLMARK (1905, s. 101) ett kornavtryck, som enligt SARAUWS bestämning härrör från en veteart, snarast kanhända *Triticum dicoccum*, och från stenåldersboplatserna i Jonstorpsområdet uppgiver LIDÉN (1940) fynd av två korn och ett kornavtryck, varav ett av de förra är bestämt till emmer, medan beträffande de båda andra fynden det uppgives, att de tillhöra vete, förmodligen åtminstone i det ena fallet *Triticum compactum*. Utan tvivel har emmern varit ett viktigt sädeslag i Skandinavien under stenåldern; sedan mycket länge är den helt försvunnen därifrån.

3. *Enkorn*, *Triticum monococcum*. Av enkorn ha fem avtryck anträffats, alla från samma fyndplats (Södervidinge) och från äldre gånggrifftid.

Enkorn är relativt sparsamt representerat i SARAUWS fynd från Danmarks stenålder. Avtryck av detta sädeslag uppgivas endast (HATT, a.a.) från två fynd, båda på Jylland; avtryckens antal var sammanlagt 21. Från Bundsö på Als föreligga emellertid enligt JESSEN (1939) ytterligare talrika fynd av *Triticum monococcum*, och även från Bornholm är ett avtryck känt (BRÖNDSTED 1938, s. 140), härstammande från den allra äldsta jordbrukstiden. Från Sydsverige synes det ej föreligga någon tidigare uppgift om *Tr. monococcum*, och fyndet från Södervidinge är därför av ett visst intresse. Då kornavtrycken anträffats i olika bågare och inga spår av andra sädeslag blivit funna, har enkorn här säkerligen odlats som en självständig odling och inte t.ex. i blandning med emmer, som man kanske skulle kunnat vänta sig.

Liksom emmer har enkorn för mycket länge sedan helt kommit ur bruk i Nordeuropa; till nutiden ha dessa sädeslag blott hållit sig kvar — på europeiskt område — i några trakter med ålderdomlig åkerbrukskultur i Mellan- och Sydeuropa.

Utom av de odlade sädeslagen ha avtryck även påträffats av råglosta, *Bromus secalinus*, som förmodligen förekommit som ogräs. Härav föreligger ett avtryck från döstid, medan tre avtryck från gång-

grifftid med större eller mindre säkerhet förts hit. Fruktar av denna art ha tidigare påträffats i åtskilliga förhistoriska fynd från olika områden, bl.a. föreligga uppgifter från Ungern (DEININGER 1890), Schweiz, Österrike och Tyskland (NEUWEILER 1935, 1946), England (JESSEN och HELBÆK 1944), de äldsta fynden äro från stenåldern. Även från södra Sverige föreligga några fynd, nämligen från Jonstorsområdet gropperamiska kultur i senare stenålder (LIDÉN 1940). *Bromus secalinus* förekommer ju numera som ogräs i höstsäd av råg och vete och är en tämligen utpräglad vinterannuell, som vid sådd om våren ofta ej kommer till blomning under första året. Man frågar sig då, om något av de under neolitisk tid odlade sädeslagen odlats som höstsäd, närmast korn eller emmer, tillsammans med vilka råglostan ofta anträffas i fynden. Detta är väl högst osannolikt; troligare är väl då, att primitiva jordberedningsmetoder möjliggjort för *Br. secalinus* att hålla sig kvar från det ena året till det andra, som ett 2-årigt ogräs. Man har också tänkt sig möjligheten, att arten varit odlad som sädeslag i förhistorisk tid (jfr LIDÉN, a.a.).

Av äpple, *Malus communis*, har slutligen ett avtryck påträffats, från gånggrifftid. Från Danmark är ett sådant avtryck känt redan från döstid (BRÖNDSTED 1938, s. 147), och fynd av äpple föreligga också från de schweiziska påbyggnaderna (HEER 1866) och från boplatserna vid Alvastra (WULFF 1910). På den senare fyndplatsen har det konstaterats, att det förekommer dels större, dels mindre frukter, varför man antagit, att den ena typen härstammat från odlade träd (jfr HOLMBOE 1921, DAHL 1945). Då tiden är ungefär densamma som för det skånska fyndet, är det ju ej otänkbart, att även detta kan härröra från ett odlat träd, om det också är mest troligt, att det härstammar från en insamlad vildfrukt.

De kornavtryck, som i det föregående omtalats från Sydsveriges stenålder, äro ju relativt få i jämförelse med de talrika fynd, som gjorts i Danmark under motsvarande tid, där också ett större antal sädeslag blivit fastställt, nämligen utom emmer, enkorn och skallöst korn, de äldsta, även skalkorn och två sorters vete (BRÖNSTED a.a.). I främsta rummet beror ju detta på att det från Danmark undersökta materialet är många gånger större än det svenska, och delvis kunna också tillfälligheter spela in, när det gäller fynd av denna art. Man får dock kanske också det intrycket, att fynden av kornavtryck äro mera sällsynta i Sydsverige, på grund av en mindre utvecklad sädesodling under förhistorisk tid. Fortsatta undersökningar få lämna ytterligare bidrag till belysningen av denna fråga.

**Summary. Some cereal impressions from Neolithic time in South Sweden.**

The author has made an investigation of impressions of cereal grains in South Swedish pottery from Neolithic time, present in the Historical Museum in Lund. Such impressions were stated for three kinds of cereals, viz. naked barley, emmer, and small spelt. Impressions of naked barley were found even in pottery from the early Dolmen Period, generally regarded as the first agricultural time in South Sweden. Impressions of emmer were probably also present in pottery from this time, though quite sure impressions could be stated only from the following period, to which also the finds of small spelt belong. Small spelt is apparently not formerly reported from prehistoric time in Sweden.

In addition some impressions of chess, *Bromus secalinus*, and one such of apple, *Malus communis*, were found. The possibility of the cultivation of the apple tree in this time is briefly discussed.

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## Litteratur.

FRANZ RUTTNER: Grundriss der Limnologie (Hydrobiologie des Süßwassers), 2. Auflage. — Walter de Gruyter & Co, 1952. Ganzleinen DM 16,80.

RUTTNERs bok är av största värde för studiet av limnisk ekologi, en forskning, som ligger väl till för våra biologer. Limnologi är en forskningsgren, som kommit i gång relativt sent i vårt land trots dess 96.000 sjöar. Det förefaller, som om sjöarna äro en allt för vanlig beståndsdel i vår landskapshild för att väcka forskarens intresse. Liknande förhållande kan noteras från Norge, under det att finnarna och särskilt danskarna ligga före oss.

För den limnologiskt intresserade är RUTTNERs bok oundgänglig såsom katekes. Även andra biologer, speciellt botaniska ekologer ha mycket att hämta där; den limnobotaniska ekologien är förenklad och lättare förståelig, tack vare den omständigheten, att fuktighetsfaktorn, som så starkt präglar den terrestra växtekologien, här är eliminerad. Likaså saknar temperaturfaktorn de ytterligheter, både temporalt och termometriskt, som gälla för *terra firma*.

RUTTNER klagör först biotopen i partiet »Das Wasser als Lebensraum», som bildar bokens första häft och omfattar avsnitten »Die physikalische Umweltsbedingungen» om 49 sidor och »Die gelösten Stoffe und ihr Umsatz» om 48 sidor. I det förra ges en ingående översikt av vattnets interna fysik samt sjöns termik och dynamik. I det senare avsnittet behandlas koloxidens och syrets kretslopp, vilka här kunna följas på ett särdeles ingående sätt, samt sjövattnets mineraliska och även organiska beståndsdelar. Ett litet kapitel om minimilagen avslutar.

På denna ekologiska grund bygges partiet »Die Lebensgemeinschaften», där avsnittet »Das Plankton» intar huvudparten, 57 sidor. Efter en kort historik behandlas svävproblemet och planktonets sammansättning samt dess utbredning, speciellt i vertikal led, varvid neuston i denna upplaga fått utvidgad behandling. De temporala växlingarna i planktonsammansättningen har fortfarande en väl knapp behandling. Planktonavsnittet avslutas med en översikt av det så viktiga produktionsproblemet.

De övriga biocenoserna: litoral, »Aufwuchs» samt zoneringsen behandlas rätt kortfattat, under det att sedimenten ägnas 24 sidor. I fråga om dessa diskuteras huvudsakligen de kemiska förändringarna vid sönderdelningen av de organiska sedimenten. Nyheter äro kapitlen om redox-potentialen, skiktningen och utbytet mellan sediment och limnion.

Åt myrarna ägnas ett kort kapitel, som av naturliga skäl har föga att ge åt initierad svensk publik. Därefter kommer ett kapitel om det rinnande vattnets biocenoser, där helt naturligt den zoologiska sidan dominerar. Ett litet

terminologiskt lexikon och en förteckning på den viktigaste litteraturen avslutar boken.

Denna upplaga är i många delar, text och illustrationer, utvidgad och utökad med de viktigaste nya rön, som framkommit sedan första upplagan 1940. Sidantalet har formellt ökats med 65 sidor, tack vare en något minskad textyta är den reella ökningen cirka 45 sidor.

EINAR TELLING.

A. F. HILL: *Economic Botany. A Textbook of Useful Plants and Plant Products*. Second ed. McGraw-Hill Book Co. New York-Toronto-London 1952. 560 s. 56 Sh.

Den nya upplagan av A. F. HILLS »*Economic Botany*» är en fullt modern handbok i kännedomen om gagnväxterna. Författaren är amerikan, research fellow i ekonomisk botanik vid Harvard-universitetet, men om också huvudvikten lägges vid de växter, som äro av intresse ur amerikansk synpunkt, så behandlas också alla övriga, som äro av någon betydelse i världshandeln. För varje växt lämnas en framställning av dess viktigaste egenskaper, dess förekomst, eventuella odling och dess användning; givetvis varierar framställningens utförlighet mycket alltefter växtens betydelse. Bokens innehåll är delat på fyra större avdelningar. Den första av dessa behandlar »*Industrial plants and plant products*», ett mycket omfattande avsnitt, som behandlar fiberväxter, skogsträd och skogsprodukter, färgväxter, gummi- och oljeväxter, socker- och stärkelseväxter m.m. I den andra delen, »*Drug plants and drugs*», behandlas medicinalväxter och deras användning, varvid även så moderna produkter som de av olika *Streptomyces*-arter erhållna antibiotica, chloromycetin, neomycin o.s.v., äro medtagna. I samma avdelning behandlas även tobaksväxterna, en kanske något diskutabel anordning. Det tredje avsnittet ger en framställning av näringsväxterna, sädesslag, grönsaker och fruktväxter; den mest utförliga skildringen får här vete, majs och ris. Det fjärde avsnittet slutligen handlar om kryddor och njutningsväxter.

A. F. HILLS bok är lättläst och rikt illustrerad, huvudsakligen med fotografier. Många av dessa visa växter, som man kanske inte är så van att se avbildade i handböckerna; i regel äro illustrationerna goda, om också en del av dem kanske kunde ha varit något tydligare. Papper och tryck äro utmärkta.

I viss mån bildar »*Economic Botany*» en motsvarighet till det svenska arbetet »*Gagnväxter*» av JÖNSSON-SIMMONS. Den kan emellertid vara ett lämpligt komplement till denna genom de något olika aspekter den anlägger och genom att den är förd fram till fullt moderna förhållanden och bl.a. också tager hänsyn till den utveckling, som föranletts av det andra världskriget.

H. HJELMQVIST.

## Notiser.

**Docentförordnanden.** Fil. dr BENGT KIHLMAN har förordnats till docent i cytogenetik och fil. dr MATS WÆRN till docent i limnthalassologi vid Uppsala universitet.

**Vetenskapsakademiens Linnémedalj.** Vid sammanträde den 5 juni 1952 beslöt K. Vetenskapsakademien att utdela sin större Linnémedalj i silver till professor F. FIRBAS, Göttingen, och till statsgeologen dr. phil. J. IVERSEN, Köpenhamn, för deras även för svensk vetenskap betydelsefulla undersökningar rörande den kvarlära vegetationshistoriska utvecklingen.

**Forskningsanslag.** K. Vetenskapsakademien har ur Enanderska fonden utdelat 1.000 kr. till assistent K. H. MATTISSON för fortsatt undersökning av släktet *Dactyloctenium* i Fennoskandien och 1.600 kr. till fil. dr G. HAGLUND för fortsatta studier av släktet *Taraxacum* i Norden.

Statens naturvetenskapliga forskningsråd har, förutom anslag till fullföljande av tidigare påbörjade och av rådet understödda undersökningar, även utdelat följande anslag till botanisk forskning: Till professor H. BURSTRÖM 7.000 kr. för undersökningar över auxinhomologers inverkan på cellsträckningen och cellsträckningens mekanism, till fil. dr G. ERDTMAN 29.800 kr. för palynologiska forskning, till professor F. FAGERLIND 5.500 kr. för kompletterande insamlingar i Buitenzorgs botaniska trädgård av morfologiskt, embryologiskt och cytologiskt material i samband med en resa till Sydamerika, till docent M. FRIES 1.500 kr. för pollenanalytiska arbeten och 2.000 kr. för vegetationshistoriska undersökningar i det centrala Västergötland, till professor R. FLORIN och docent G. HARLING 7.000 kr. för forskning vid Bergianska stiftelsen, till agr. dr G. JULÉN 1.550 kr. för undersökning av röntgenbehandlad *Poa pratensis*, till fil. lic. C. L. KIELLANDER 8.290 kr. för embryologiska undersökningar inom släktet *Poa*, sekt. *Stenopoa* och *Tichopoa*, till fil. lic. N. LINNEMARK 12.000 kr. för vegetations- och markstudier inom östra Skånes ås- och skogsområden, till fil. lic. F. LUNDBERG 500 kr. för limnologiska undersökningar i Dalarna, till laborator A. NYGREN 7.200 kr. för undersökningar inom släktena *Calamagrostis* och *Poa*, till fru ELSA NYHOLM 4.740 kr. för utarbetande av en illustrerad skandinavisk bladmos flora, till fil. dr H. PERSSON 4.000 kr. för bryologiska undersökningar på Madeira, till professor C. SKOTTSBERG 3.430 kr. för framställning av vegetationskartor och klimatkurvor samt utförande av jordanalyser och för arbetshjälp vid kromosombestämmingar, till professor M. G. STÅLFELT 17.300 kr. för undersökning av de ekologiska faktorernas inverkan på protoplasmans viskositet och därmed sammanhängande fysiologiska processer, till docent H. VIRGIN 5.000 kr. för undersökningar över protoplasmans spektrala känslighet med avseende på viskositetsförändringar och 2.900 kr. för ljusretningsundersökningar vid Carnegie Institution, Palo Alto, Californien, till docent S. ÖSTERLIND 6.060 kr. för undersökningar rörande planktiska grönalgers oorganiska kolkällor.

Jordbrukets forskningsråd har utdelat bl.a. följande anslag: Till assistent T. DENWARD 600 kr. för fortsatt undersökning av rödklöverns fertilitetsförhållanden, till assistent S. ELLERSTRÖM 3.600 kr. för fortsatta undersökningar av reaktionen gentemot varierande miljöbetingelser hos olika kromosomtalsraser av timotej, till fil. dr I. GRANHALL och förste assistent E. J. OLDÉN 5.100 kr. för teoretiska undersökningar av befruktungs- och polyploidiförhållanden hos vissa äppelformer, speciellt *Malus Sieboldii* och korsningsprodukter av denna, till fil. mag. A. HAGBERG och assistent S. ELLERSTRÖM 5.000 kr. för undersökning av effekten av vicinism och inblandning hos artificiella polyploida marknadssorter, till professor N. HELLSTRÖM, laborator E. ÅBERG och docent E. ÅKERBERG 10.500 kr. för vissa försök i samband med en undersökning av köldhärdigheten hos raps och rybs, till laborator E. ÅBERG 2.900 kr. för kombinerade växtföljds- och ogräsbekämpningsförsök i kampen mot flyghavre och 10.000 kr. för fortsatta undersökningar över sambandet mellan mognadsförloppet hos vissa kulturväxter och skördetröskningen.

Fonden för skoglig forskning har beviljat bl.a. följande anslag: Till professor Å. GUSTAFSSON 26.100 kr. för ett års försök att med hjälp av radioaktiva isotoper klarlägga näringsupptagandet hos genetiskt skilda plantmaterial av olika skogsträd, till fil. mag. J.-H. TEGNÉR 10.200 kr. för undersökning av skogsmarkernas bakterier och deras betydelse för nedbrytning av skogsförna, till professor H. BURSTRÖM 10.000 kr. för fortsatt undersökning över sulfittavlutens verkan som gödsel- och jordförbättringsmedel.

Från Helge Ax:son Johnsons stiftelse ha följande anslag utdelats till botanisk forskning: Till fil. lic. O. ANDERSSON 1.000 kr. för avslutande undersökningar av den svenska ädellövskogens storsvampar, till amanuens N.-O. BOSEMARK 2.000 kr. för fortsatta undersökningar över accessoriska kromosomer hos *Festuca pratensis*, till docent N. HYLANDER 2.000 kr. för fortsatt arbete med verket »Nordisk kärväxtflora», till fil. kand. A. LUNDQUIST 1.500 kr. för undersökning av tetraploidens inverkan på självsterilitet och inavelseffekt hos råg, till fil. kand. BERTA SANTESSON 1.060 kr. för fortsatta undersökningar över polyploidi inom släktet *Prunus*.

Prefekten för Göteborgs Botaniska trädgård B. LINDQUIST har erhållit ett statsanslag å 2.500 kr. för en resa till Japan för studier av typvariationen hos de japanska skogsträden, särskilt av släktena *Larix*, *Picea* och *Betula*.