TRIQUETROUS FORMS IN THE GENUS MICRASTERIAS

by

J. HEIMANS
(Amsterdam).

In the winter and early spring of 1916 Mrs. Anna Weber-van Bosse at her hospitable residence near Eerbeek initiated me in the study of Freshwater Algae.

For several years after that date in numerous trips all over this country I collected and studied some thousands of samples from all kinds of freshwater ponds and lakes, canals and streams. The Desmids soon drew my special attention, when an unexpectedly rich and varied Desmid flora was found in certain fens and ponds in the diluvial and moor districts of our country.

Still more surprising was the presence of a considerable number of those Desmid species which in the publications of W. and G. S. West, whose Monograph at that time was the only handbook for the study of Desmids, are held to be confined to the Western rocky districts of the British Isles in the drainage area of precarboniferous rocks.

One of the most beautiful and most characteristic species of this "Caledonian type" of Desmid vegetation, *Staurastrum Ophiura* Lund. had been found by Mrs Weber herself some years before in a sample from the province of North Brabant.

Not until several years afterwards did we learn from the publications of R. Grönblad, A. Donat, H. Homfeld and others that this "Atlantic Element of the Desmid flora" is spread over the N.W. parts of Europe from Finland to Portugal.

Besides *Staurastrum Ophiura* a considerable number of species belonging to this Western element was found in the Netherlands, although most of them are of rare occurrence, e. g. *Staurastrum brasiliense* var. *Lundellii, St. arctiscon, St. elongatum, St. cerastes, St. Clevei, Docidium undulatum, Micrasterias furcata.*

Another element of the Desmid flora, as unexpected in our Low Countries as the former, is the one considered by West and others to live by preference in upland districts or even in mountain areas.

To this "mountain element" these authors reckoned the group of species: *Cosmarium Ralfsii, Euastrum insigne, Micrasterias oscitans, Micr. Jenneri,* etc. that here as well as elsewhere so constantly keep together that they inevitably suggest an "association" in the phytosociological sense, more evident than many well established phanerogam communities. Indeed the distinction of plantcommunities of freshwater Algae (at least of Desmids) is quite as justified as in phanerogamic land vegetation.

Even some supposed arctic-alpine Desmid species have been found in this country e. g. *Euastrum montanum*; yet, from the circumstances of the station the conclusion is justified that the most characteristic of them are not really indigenous, but recently imported by migratory birds (e. g. *Cosmarium holmiense* var. *integrum* found by Mr J. F. Obbes in temporary freshwater pools on the North Sea dune-coast).

A considerable number of our Dutch species do not extend their range to the British Isles, which fact notably impeded identifications at the time when the Monograph of W. and G. S. West was our only resource. A most striking example of this, *Cosmarium striolatum* Arch. (*C. Cohnii* Rac., *C. tessellatum* Nordst.) has decidedly its centre of distribution eastward and might be considered a continental element.

A much greater coincidence is to be stated between our Desmid flora and that described by Prof. H. Homfeld, Dr A. Donat and others from N.W. Germany. But, although the area of these authors' researches borders on and is conformable with ours, there are differences which certainly cannot be wholly referred to insufficient exploration and identification or to mere chance. Up to now, for instance, I failed to find here such conspicuous species as *Micrasterias americana, Pleurotaenium tridentulum.* On the other hand, we can boast of *Cosmarium didymoprotupsum, obtusatum, protuberans, monomazum* var. *polymazum, Staurastrum asperatum, irregulare, Johnsonii, dimazum, echinatum, Onychonema laeve,* etc. Some of those might be supposed to have a narrow eu-atlantic distribution not surpassing our eastern frontier. At least for *Cosmarium monomazum* and *Staurastrum asperatum* this supposition is justified.

In any locality where a luxuriant growth of some Desmid species is found, the apparition of abnormal, monstrous or at least aberrant forms may be expected.

It is difficult to discriminate between abnormalities and extreme normal variation.

The range of variation in form and size is strikingly dissimilar in the different species of Desmids. Some of them, including forms with extremely complex outline (e. g. *Staurastrum arctiscon* with thirty long crenulated processes) so constantly stick to their accurate type, that not any noteworthy difference can be discovered between the specimens from different places or years. Other species, however, show such a free and wide variability of form and size in every direction, that any discrimination from allied species is made vague and arbitrary. (See *Fig. 6*).

Abnormal forms in Desmid species have been studied by several authors such as Jacobsen (1875), Ducellier (1915), Laporte (1931).

Ducellier and Laporte divide the anomalous forms of Desmids into "division-anomalies" and "form-anomalies". A division-anomaly is the result of a cell-division accomplished without formation of a separating cell-membrane. In form-anomalies Laporte again distinguishes "hypertrophies" and "atrophies", with respectively a more elaborate or a simplified outline as compared with the normal cell-form.

In the majority of placoderm Desmid genera (*Cosmarium, Euastrum,* *Micrasterias, Staurastrum,* a. o.) cell-division proceeds in one and the same way. Soon after the nucleus has undergone mitotic division the septum is formed, attached to the specialised short cylindrical strip of membrane which forms the conjunction between the semicells at the isthmus. Than the two adult semicells slowly move apart, while the girdle-ring with the septum protrudes and bulges out to a pair of semiglobular bodies, attached to each other at the apices. The gradual growth and definite evolution of these formless corpuscula to the final outline of the new semicells, identical to that of the adult ones, in such a complicated type as *Micrasterias,* is quite as marvellous and incomprehensible a phenomenon as is the predeterminate development of an animal egg-cell into the embryo or that of the primordium at the stem apex of a plant into a flower.

In the formation of a division-anomaly the whole process is performed without the intercalation of a separating membrane. The result is a binuclear tripartite monstrum, the middle part of which consists of a more or less regular contraction of two semicells. Everyone who has worked in Desmids has occasionally come across such remarkable figures. Krieger (1933 pg. 57) gives a selection of drawings as well from literature as original. Our *Figs. 1—3* are some more instances of unexceptional type.

A much more interesting specimen of such division-anomaly is that of *Micrasterias truncata* reproduced in *Fig. 5.* Here the younger semicells are quite normal and fullgrown but for an open communication at the mutual apex, recalling concrescent siamese twins ("acropagus" of animal teratology). Noticeable is the slight but obvious twisting along the main axis which is normal in cell division of most Desmids, but here seems to be somewhat exaggerated.

Atrophic form-anomalies result from a normal cell-division by stagnation in the growth of the young semicells, in the course of which the cellwall attains the adult chemical and physical condition before the definite form, characteristic of the species, is reached. Such atrophies are not very rare in most of the Desmid-genera with a complex outline, such as *Micrasterias, Euastrum, Xanthidium, Arthrodesmus* and the spinous species of *Staurastrum.*

Several authors have expressed the supposition that a low temperature of the water would be responsible for the production of atrophic forms. More probably not only cold, but in general unfavourable conditions of life can be the cause of this kind of anomalies.

The *Micrasterias truncata*-forms of our *Figs. 7* and *8,* quite similar to the formae *immaturae, reductae, inevolutae* or *mixtae* figured by Jacobsen, Dick, Homfeld, Laporte, Krieger among others, were collected the 21st of May 1918 in water that was not at all very cold. Moreover, it is a fact that in collections kept and cultivated for several months or a couple of years in small glass bottles, often the few Desmid species that keep alive and multiply to the end, at last degenerate into mere cripples and immature forms.

Very much rarer are the anomalous forms called by Laporte "hypertrophic form-anomalies". Here abnormal additions make the outline more complicated than is usual for the species. Fine examples have been published by Ducellier and by Dick of *Euastrum* species with reduplication of the polar lobe. These hypertrophic forms decidedly make the impression of real teratologic malformations.

Without hesitation everyone will call forms like the *Staurastrum Manfeldtii* of our *Fig. 4* with a supernumerary arm attached awry a monstrous form. If the fourth arm were quite equal to the others and attached at equal angles, there would be no reason to call such quadriradiate semicells monstrous, not when a species is concerned, which as a rule is triradiate, not even if the other semicells had remained in a normal triangular condition.

That a triradiate *Staurastrum* sometimes becomes quadriradiate is such a common fact that it needs no separate mentioning in the diagnoses. Yet I am sure that it does not occur equally often in every species. In some species it is so common that one hardly can tell which of the two forms is the normal one and which is the deviation.

Biradiate varieties of normally triradiate Staurastra are also known, as well as the exact reverse: triradiate forms of normally biradiate species. The least rare instance in our country of these Staurastra with only two processes at each semicell is *Staurastrum tetracerum* Ralfs, of which a fa. *trigona* is occasionally found.

If this type of variation occurs in a *Staurastrum* without processes, but e. g. with spines at the angles, this biradiate modification decidedly belongs to the type of another genus such as *Arthrodesmus* or *Xanthidium.* On the contrary a triradiate form of one of these genera, when the connection is not known, would undoubtedly be described as a Staurastrum.

It is even more remarkable that in such a complicatedly built and so typically biradiate a genus as *Micrasterias* (of which the cellform is substantially that of a disk) both the above mentioned different manners of triradiate deviation occur. One is obviously a hypertrophic form-anomaly, with an irregular and really abnormal third radius, the other a quite regular triquetrous form, where the biradiate longest axis has become a purely triradiate axis of symmetry. The latter form is not in the least a teratological but a regular pleiomeric deviation. Both kinds of aberration have been described and represented in West's Monograph (Pl. XLV, fig. 4 and Pl. LV, figs. 2 & 3), but a detailed description of instances which I found in Holland may be given here.

The *Figs. 10—14* of *Micrasterias truncata* Breb. show a series of triquetrous anomalies of the first kind.

First we note that in all observed cases of this type only one semicell shows the anomaly, as is usually the case with other hypertrophic anomalies. From this it is to be concluded that the deviation is only an accidental one, which is not transmitted to the new semicells in cell-division.

Gistl (1914) has cultivated and observed under the microscope during cell-division a *Micrasterias rotata* with reduplication of one polar-lobe; two normal young semicells were formed which did not show any anomaly. I did not succeed in imitating this, but the fact that in *Fig. 9* and in *Fig. 12* the normal semicell just bends out a little at the sinus and surpasses the line of the isthmus at the cost of the abnormal semicell, perhaps shows that the normal semicell is the younger of the two.

The least deviating of the figured specimens are those of *Fig. 10* and *Fig. 11.* These have only the lateral lobes doubled at one side. The toplobe has remained normal.

In the specimen of *Fig. 12* at one side only the lateral lobes are split, at the other side the polar lobe also. This drawing, like all the others of this type, clearly shows that the doubled lobes have also been retarded in the development of their outlines; so these semicells may be called at the same time hypertrophic and atrophic, however contradictory this may sound. Indeed, they are hypertrophic in their symmetrical construction, atrophic in the evolution of the outline. Probably the latter fact is the consequence of the former, in so far as the lateral splitting of a young sidelobe might prevent the final growth of the edge into the typically elaborated outline. Perhaps we had better put it thus: the cause which gives rise to the monstrosity, disturbs the development of the young semicell in such a manner, that it is split transversily instead of further subdividing the outline.

Of what nature this cause may be, we hardly can guess. An indication might be found in the fact, that I once met with a considerable number of these deviations together in one sample, which was taken home alive on a long bicycle-trip and was not fixed with formaline until the next day. One feels inclined to suppose that in this sample numerous cells happened to be in cell-division, and that the continuous shaking on the road may have caused the anomaly. My intention to place such a sample, rich in quickly dividing *Micrasterias,* on a shaking-apparatus could not be carried out. However, artificial shaking cannot be the only possible cause for this kind of monstrosities, for they were found as well in samples, which had been fixed at the finding-place immediately after they had been fished up from the water, though never in so great a number together again.

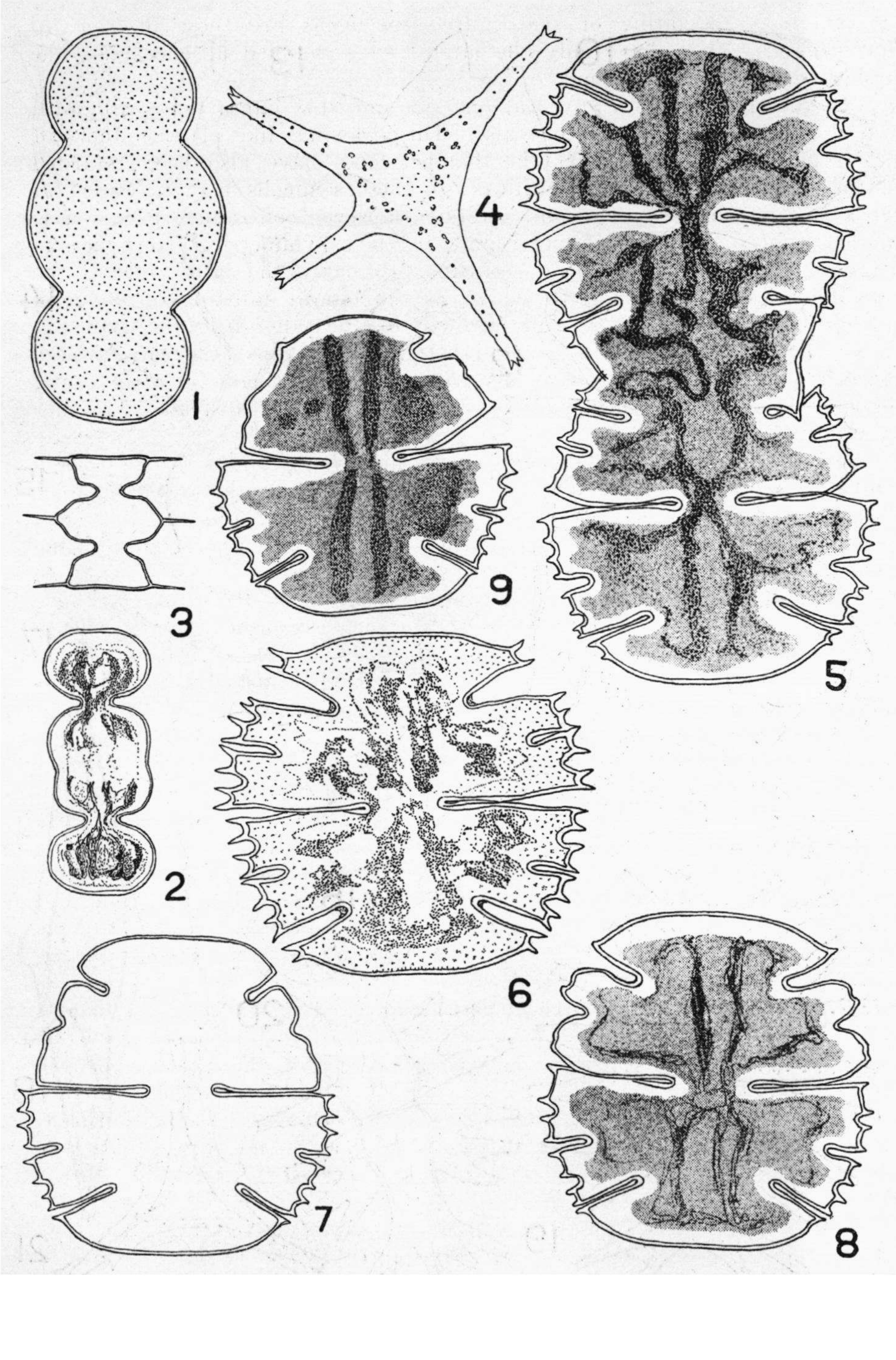
Fig. 13 too, which is seen *e latere,* with the normal side turned up to us, shows strongly reduced outlines of the doubled other edge. The pleiomery, however, has gone further in this figure and in *Fig. 14.* The specimen of *Fig. 14* indeed has nearly reached regular triradiate symmetry; here at least we cannot at once point out one edge as a normal one and two others as the result of splitting. Yet this specimen clearly belongs to the irregular semi-triradiate type. The purely regular and constant triradiate form is something quite different.

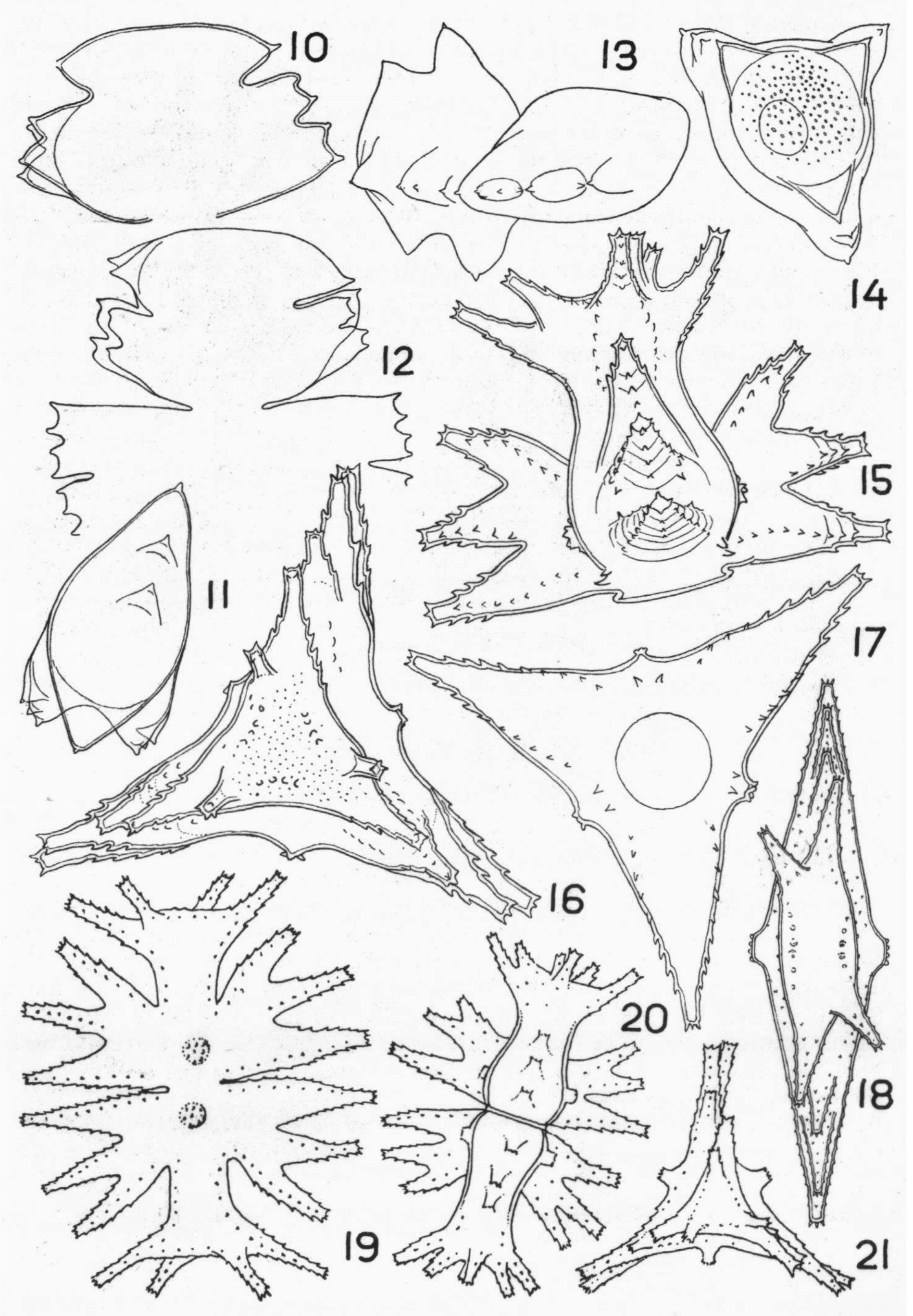
For the first time in June 1916 I happened to come across a magnificent example of this second type in the Van Esscheven, a pool near Oisterwijk, North Brabant, which belongs to a reserve of the Society for the Preservation of Natural Sites. This beautiful Desmid (see *Figs. 15—17*) could be recognised as a triquetrous form of *Micrasterias mahabuleshwarensis* Hobson var. *Wallichii* West, because the frontal side agrees with the

Figs. 1—3. Division-anomalies: Fig. 1. *Cosmarium connatum* Breb.; Fig. 2. *Cosmarium contractum* Kirchn.; Fig. 3. *Arthrodesmus incus* Hass.

Fig. 4. *Staurastrum Manfeldtii* Delp. Hypertrophic form-anomaly.

Figs. 5—9. *Micrasterias truncata* Breb.: Fig. 5. Division-anomaly; Fig. 6. Extreme normal variation of the two semicells; the lower as in the var. *semiradiata* Cleve, the upper semicell tends to the var. *bahusiensis* Wittr.; Figs. 7—9. Atrophic form-anomalies.


1
2
3
4
5
6
7
8
9


10
13
14
12
15
11
17
16
20
18
19
21

drawings in West's Monograph of this species, in which book also the existence of triquetrous forms in *Micrasterias* is mentioned under *M. pinnatifida* and *M. Murrayi.* Had this not been so, I undoubtedly would have tried to identify this form as a *Staurastrum.* The contrast with the semi-triquetrous forms, as described above in *Micrasterias truncata* is evident. In the first place the triradiate symmetry is absolutely complete and quite regular, as is best shown in the figures *e vertice* and *e basi,* but in the second place both semicells are perfectly alike in this respect. Evidently here the aberration is passed on to the new semicells at cell-division as a constant specific or varietal character. Its constancy is also clearly proved by the fact that this beautiful triquetrous form is regularly to be found in the above-mentioned pool and the pools in connection with it. Since 1916 it was always present though never in abundance in the gatherings, which I took there for more than ten years, once or twice a year; in this way I have observed some dozens of specimens, but I could never detect any irregularity in the triradiate symmetry.

The normal biradiate compressed type of the species was never found in that locality. Yet we must assume that the trigonal form has originated from the compressed one, as the latter undoubtedly is the normal type of this rare and peculiar Desmid species.

Probably we must think that this transition from the biradiate to the triradiate state took place via an accidental semitriquetrous abnormality such as *Fig. 14* of *Micrasterias truncata.* We may conceive this transition in the following way.

If the normal biradiate symmetry has been destroyed by an unknown cause in such a manner that an irregular semitriquetrous form arises, then, as soon as that cause is stopped again, the normal form will be restored at the first following cell-division. The "organizing forces" for the building of new semicells fall back into the bipolar equilibrium from which they were only temporarily removed.

On the contrary, if by a similar cause the transformation to a regular triquetrous cellform has been achieved, a new and quite as stable tripolar equilibrium of those forces is reached, which in future produces the triquetrous cellform as its normal effect. A support for this reasoning may be found in the remarks in West's Monograph on the variability of the same species which, in the British Isles, has been found only in some Scottish lochs: "In some cases the specimens were subject to great variation, and this was especially the case in Loch Bhaic, Pertshire. The variation was principally in the duplication of the lateral processes. In some individuals the upper process of the superior lateral lobules was duplicated (vide Pl. LV, fig. 2) and in others the lower process was similarly doubled.

Figs. 10—14. *Micrasterias truncata* Breb.: Semitriquetrous form-anomalies.
Figs. 15—21. *Micrasterias mahabuleswarensis* Hobs. var. *Wallichii* West:
Figs. 15—17, fa. *triquetra,* empty semicell resp. seen *e fronte, e vertice* and *e basi,* orig.;
Fig. 18. The normal form seen *e vertice,* after W. & G. S. West;
Fig. 19. The normal form seen *e fronte,* after H. Homfeld;
Fig. 20, 21. fa. *triquetra, e fronte, e vertice,* after H. Homfeld.

A few individuals showed a duplication of the large processes of the polar lobe (vide Pl. LV, fig. 3). This curious abnormal state, with six processes on the polar lobe, was first mentioned by Lundell (Desm. Suec. 1871, p. 15)."

The variations described here, as appears from the plates, are sidewise reduplications of lateral and polar lobes of exactly the same kind as I called above "beginning semitriquetrous deviations". That this remarkable *Micrasterias* species should show a special predisposition for such doubling of the side-edge, may perhaps be caused by the fact that in its normal form it already breaks the pure triaxial bipolar symmetry of this Desmid genus with a pair of accessory processes disposed asymmetrically at the apex of the polar lobe, the one projecting obliquely to the left-front side, the other backward to the right side. So far as this detail of the cellform is concerned, this Desmid species is asymmetric with regard to each of its three planes of symmetry (See *Figs. 18* and *19*).

Summarising, we must sharply distinguish between the pure trigonal variety and the "semitriquetrous" deviations in *Micrasterias*, that is to say between an absolutely regular, irreversible leap from one grade of symmetry into another, and an only partial, irregular, temporary deviation.

All these observations and discussions involuntarily suggest a comparison with the peloric forms of flowers e. g. in toadflax (*Linaria vulgaris*). There, exactly as here, we must sharply distinguish between a completely peloric race, with purely 5-radiate flowers, and the accidental and temporary appearance of irregular reduplications in stray specimens of the normal race. The peloric race exclusively produces absolutely regular 5-radiate flowers with five equal spurs and is quite constant by propagation from seed as well as from root buds. It is very rare, but yet has been found repeatedly in various countries since its discovery at Uppsala in Linnaeus' time.

According to Hugo de Vries it has arisen every time anew by a mutation out of the normal type; i. e. a polytopic mutational origin.

On the other hand, it is not by any means so rare to find a normal plant of *Linaria vulgaris* bearing a single peloric flower. Still such a stray peloric flower is hardly ever purely 5-radiate, but as a rule shows only a tendency in that sense by having two or three spurs or only a bifurcated one. This anomaly is not hereditary, neither through the seeds of normal or abnormal flowers, nor through the buds.

Of course the comparison of the two different kinds of peloric Toadflax with the two types of trigonal Micrasterias must not be drawn too far. In peloria a zygomorphous flower has become actinomorphous; the transition of biradiate to triradiate symmetry would not be called pelorism in phanerogam morphology, but rather pleiomery. Moreover it is a matter of fact that the constitution of a flower must not be compared unconditionally with that of a unicellular alga, though here, in the case of *Micrasterias*, the development of the young semicells strikingly reminds us of the evolution of a flower out of its primordium. Undoubtedly in both cases a similar interaction of organizing forces must be supposed to act.

A quite comparable case is probably that of the peculiar Diatom *Centronella Reicheltii* M. Voigt, which is triradiate, just like a *Staurastrum*, but in each of its three processes shows the type of a naviculoid pennate Diatom.

Still another point of agreement of our trigonal *Micrasterias* with the peloric *Linaria* is found in the supposed origin by a polytopically occurring mutation, as we shall see from what follows.

The purely triquetrous *Micrasterias mahabuleshwarensis* was regularly to be found, though in a small number, in the Van Esscheven and confluent pools of the Nature Reserve at Oisterwijk, but to my astonishment the normal compressed form, from which it must have taken its origin, could never be found there. In those years I specially searched the district all over to find it, or rather to discover a locality where the compressed and triquetrous forms would occur together, that is where the point of origin of that triquetrous mutation might have been.

I actually succeeded in finding the normal compressed form in the neighbourhood, in the Rietven. After that bog has temporarily been drained, I have never seen the species again there. Only the normal compressed form occurred without any indication of a tendency towards the trigonal state. The Rietven is situated at a few miles to the S.W. of the above mentioned finding-places, but is separated from them by the rivulet, the "Achterste Stroom". This situation as little argues for the triquetrous form to have sprung there.

At last I did find what I was searching for: the compressed and triquetrous forms living together. This locality was the Allemansven, which is at a somewhat greater distance to the South, but separated from the pools in the Nature Reserve by a patch of higher sandy soil which forms a barrier, so that it has its flow-off to the other side, to the Rosep brook. Thus it seemed as if the origin could not be found in this direction either.

However, by searching in old maps and by inquiring at the townhall at Oisterwijk, I found that the conditions formerly had been quite the reverse. The Allemansven actually at one time had communication to the North with the pools of the Nature Reserve. The last connections left were closed about 1905. Meanwhile also the Rosep brook that used to overflow towards the Allemansven has been partly normalized, so that no more water from this little rivulet could come into that bog, but only the reverse is possible.

Consequently not much doubt remains as to the direction in which we must look for the origin of the triquetrous form of the Van Esscheven.

Perhaps we might trace it even farther to the south and suppose that the species originally may have come down together with several other rare and interesting Desmids, along the Rosep brook out of the bog and swamp district of the "Moergestelsche Broek" from which the Rosep springs and which formerly possessed a rich Desmid flora.

Unfortunately, some years ago this whole bog district was brought into cultivation and the Rosep has been further normalized. Moreover, in 1927 the Allemansven was drained for the fishing, by which catastrophe the Desmid flora has been destroyed for the greater part, whilst by the above mentioned cultivations and normalizations of the Rosep and its sources, repair will not well be possible.

By these events the only known two stations in the Netherlands of the normal *Micrasterias mahabuleshwarensis* have gone lost and the fa. *trigona* alone has remained as an indigenous species. Just as in the above mentioned reasoning we compared the origin of this triquetrous form with that of a new phanerogam species by mutation, so we can see here an analogous case in miniature of the isolation of a mutation into a well defined species by extinction of the connecting intermediate forms.

It is quite conceivable that the triquetrous form might be favoured in the struggle for existence above the compressed type, as its three formidable edges of denticulate processes will leave less space for the attack of enemies or parasites than is the case in the ordinary type.

Without doubt it would have been considered as a separate new species, if it had been found alone, and if the connected species-type were not known from other countries, and indeed as a new species of *Staurastrum*!

The trigonal symmetry as yet proves to be kept unchanged, as a constant species-character, in vegetative propagation only. But in this and many other Desmid species cell-division is the only mode of multiplication or at least the absolute rule. Zygospore-formation is unknown in *Micrasterias mahabuleshwarensis* as it is in several of the rarer species of this genus. It is more significant that in the most common species, *M. truncata*, spread all over the world, conjugation has only once been stated (by Homfeld). In this respect our form may be compared with apogamous phanerogam species such as occur in the genera *Alchemilla, Hieracium* or *Taraxacum*.

Later on I got the var. *triquetra* from yet another locality in the Oisterwijk-district, i. e. from the Belversven and again only the trigonal form. It is very well possible that these specimens may originate from the same source as those discussed above, since the Belversven also is in the basin of the Rosep brook and at times may have received water from that rivulet.

The same cannot possibly be the case with the specimens, once more only triquetrous ones, found in a pool near Weert, at such a distance from the other localities, in the neighbouring province of Limburg, that we must assume a second independent origin, i. e. by polytopic mutation. This finding-place again has since been destroyed by cultivation.

The polytopic origin was fully proved when we learned from Prof. H. Homfeld's book (1929) that this author has found exactly the same triquetrous form together with typical *Micrasteras mahabuleshwarensis* near Celle (to the N.W. of Hannover). The accompanying *Figs. 20* and *21* have been taken from Homfeld's drawings. But also this locality has been lost, so that at present, as far as is known, this interesting Desmid-type exists nowhere in the world except in the Oisterwijk-Reserve.

My thanks for inking my pencil drawings are due to Mr J. F. Obbes of Voorschoten, the artistic and accurate illustrator of the late Prof. Max Weber's and Mrs A. Weber-van Bosse's publications of recent years.

Literature.

J. DICK, Beiträge zur Kenntnis der Desmidiaceen-Flora von Südbayern — Kryptogamen-Forschungen, Bayer. Botan. Ges. IV, 1919.

A. DONAT, Zur Kenntnis der Desmidiaceen des Nordwestdeutschen Flachlandes — Pflanzenforschung 5, 1926.

——, Ueber die geographische Verbreitung der Süsswasseralgen in Europa — Fedde's Repertorium, Beih. Bd. 46, 1926.

F. DUCELLIER, Contribution à l'étude du polymorphisme et des monstruosités chez les Desmidiacées — Bull. Soc. Bot. de Genève, 1915.

R. GISTL, Beiträge zur Kenntnis der Desmidiaceenflora der bayerischen Hochmoore — Diss. München, 1914.

R. GRÖNBLAD, Finnländische Desmidiaceen aus Keuru — Act. Soc. Faun. Flor. Fenn., 1920.

J. HEIMANS, De Desmidiaceeënflora van de Oisterwijksche vennen — Nederl. Kruidk. Archief (1924), 1925.

——, Sociologie van Zoeterwaterwieren, in het bijzonder Desmidiaceeën — Natuurwetensch. Tijdschr. 41, 1932.

—— in H. C. REDEKE, Synopsis van het Nederlandsche Zoet- en Brakwaterplankton — Publ. Hydrobiol. Club 2, 1935.

——, Desmidiaceeën van Winterswijk — Ned. Kruidk. Archief 50, 1940.

H. HOMFELD, Beitrag zur Kenntnis der Desmidiaceen Nordwestdeutschlands — Pflanzenforschung 12, 1929.

J. P. JACOBSEN, Aperçu systématique et critique sur les Desmidiacées du Danemark — Bot. Tidsskrift (1874), 1875.

W. KRIEGER, Die Desmidiaceen — Rabenhorst's Kryptogamen-Flora, XIII. Band, Abt. 1, II, 1933 (—1939).

L. J. LAPORTE, Recherches sur la Biologie et la Systématique des Desmidiées — Thèse, Paris, 1931.

J. F. OBBES, Rapport over het voorkomen van eenige zoetwateralgen. Meyendelonderzoek — De Levende Natuur 35, 1930.

W. & G. S. WEST, A Monograph of the British Desmidiaceae I—IV, 1904—1912; V. by Nellie Carter, 1923.