ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. XXVIII — Nr 2
1959

On the Morphology and Biology of *Centronella Reicheltii* Voigt

by

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The monotypic genus *Centronella* Voigt covering the species *C. Reicheltii* Voigt (1902), synonym *C. Rostafińskii* Wołoszyńska (1922), has been of special interest to many algologists.

Usually only single specimens of this diatom were found in the plankton of numerous lakes and, more rarely, rivers of Central Europe. *Centronella* was described, among others, by Voigt (1902), Wołoszyńska (1911, 1913, 1922), Bennin (1923), Schröder (1923), Utermöhl (1923), Krieger (1927) and Germain (1936). The small number of specimens has been the cause of difficulties in establishing the correct systematic rank and the ecological requirements of these organisms.

The more frequent occurrence and, on rare occasions, the mass development of *Centronella* were observed only in some lakes in Germany (Voigt 1902, Utermöhl 1925, Krieger 1927).

In the case of *Centronella* it has been impossible so far to establish any relationship of its occurrence with the season, the temperature, and the trophic conditions prevailing in a water reservoir. On the ground of earlier reports it seems that the species is eurythermic (Utermöhl 1925) and eurotopic (Utermöhl 1925, Krieger 1927, Zabielina 1951), but it has been reported most frequently from lakes providing medium nutritive conditions (Krieger 1927).

Experiments in which microscope slides were suspended in the second littoral zone of a lake near Olsztyn, Poland (Wysocka 1952, 1958) supplied about 150 specimens of the species. The examination of this material revealed the considerable variability of morphological traits and some hitherto unknown details of the life cycle of *Centronella*. A new light was thrown on the mechanism of the development of *Centronella* colonies and on the role of often disregarded biocoenotic factors that regulate the sporadic occurrence of *C. Reicheltii* in the plankton.

MORPHOLOGY

C. Reicheltii differs from all the other diatoms by a three-armed structure of its cells which form delicately shaped stars. The three arms lie in one plane (Schröder 1923), have a geniculate bend at the base, widen somewhat asymmetrically above the bend, and taper to a tiny head at the end.

The three angles formed by the arms and the angle formed by the geniculate bend at the base of every arm are very important morphological traits of this species.

Voigt (1902) in his description of *Centronella* states that „Arme regelmässig Winkel von 120° bilden". Similarly Wołoszyńska (1922), Schröder (1923), and Huber-Pestalozzi (1942) report that the three angles equal about 120 degrees.

Hustedt (1930) does not define the angles between the arms of the specimens he examined but mentions that the symmetry of the arms was almost complete. He writes that „...lediglich durch die etwas verschiedenen basalen Anschwellungen und durch die Knickung der Arme gestört wird". Further on in the same work he remarks that „Arme in Schalenansicht an der Basis geknickt". In his later report (Hustedt 1932) he adds that „...an der Basis etwas geknickt". Huber-Pestalozzi (1942) states that the arms are „...an der Basis schwache Knickung".

All reports seem to indicate that the base of the arms in *Centronella* is characterized by a small geniculate bend causing a slight disturbance of symmetry.

The regularity and the complete symmetry of the structure of the cell described by Wołoszyńska from the Firlejowskie lake (Wołoszyńska 1922, Figs. 1 A and B, also reproduced by Schröder 1923, Fig. 8, Krieger 1927, Plate V, fig. 10, and Hryniewiecki 1951, Plate II, figs. 4 A and B) was exceptional. The angles between the arms of this cell equalled 120 degrees, the arms, though widening at the base, had no geniculate bend, while the outline of the central part of the cell was very nearly circular.

Hustedt (1930, 1932) considered the species identified by Wołoszyńska as merely a synonym of the species originally established by Voigt. However, he disregarded the characteristic morphological traits of the arm-base structure and of the central part of this cell.

The majority of the *Centronella* cells from the lakes in the Olsztyn region differed from all earlier descriptions. Among the most evident of these differences is the irregular arrangement of the arms and the resulting lack of symmetry.

The angles between arms are strictly associated with the angle at which every arm bends and with the outline of the central part of a cell. In the specimens collected in the Olsztyn lakes the geniculate bend at the base of arms and the shape of the central part varied considerably. Some cells had arms with only a small bend at the base and these corresponded to the descriptions of Voigt and Hustedt (Plate I, fig. 1) Other cells had arms with a distinct (Plate, fig. 2) or even very distinct

(Plate I, fig. 3) bend. In the first group the central part was shaped ± triangularly, and in the other two groups irregularly ± cordately.

The angles between two arms were measured with an accuracy of 0.5—4 degrees at the point of intersection of the lines running along the centre of the arms from the top to the base. With some approximation these angles can be considered as three axial planes summing up to 360 degrees. Measurements of angles between arms of 100 *C. Reicheltii* cells from the Kortowskie lake are assembled in Table 1.

Table 1

Angles between arms and the type of bend at base of arms in *C. Reicheltii* from the Kortowskie lake

Group of cells		Angle formed between arms Degrees			Number of specimens Per cent	Type of bend at base of arms
I	a	120	120	120	17	slight
	b	120	125	115	21	
	c	125	125	110	8	
II	d	130	120	110	25	distnict
	e	130	125	105	7	
	f	130	115	115	11	
	g	130	130	100	3	
	h	135	115	110	2	
III	i	140	110	110	2	strong
	j	140	115	105	1	
	k	145	115	100	3	

The cells were divided into three groups according to the angle formed by the geniculate bend at the base of the arms: 1) arms bending slightly, 2) arms bending distinctly, and 3) arms strongly bent. Every group consists of cells with different

PLATE I

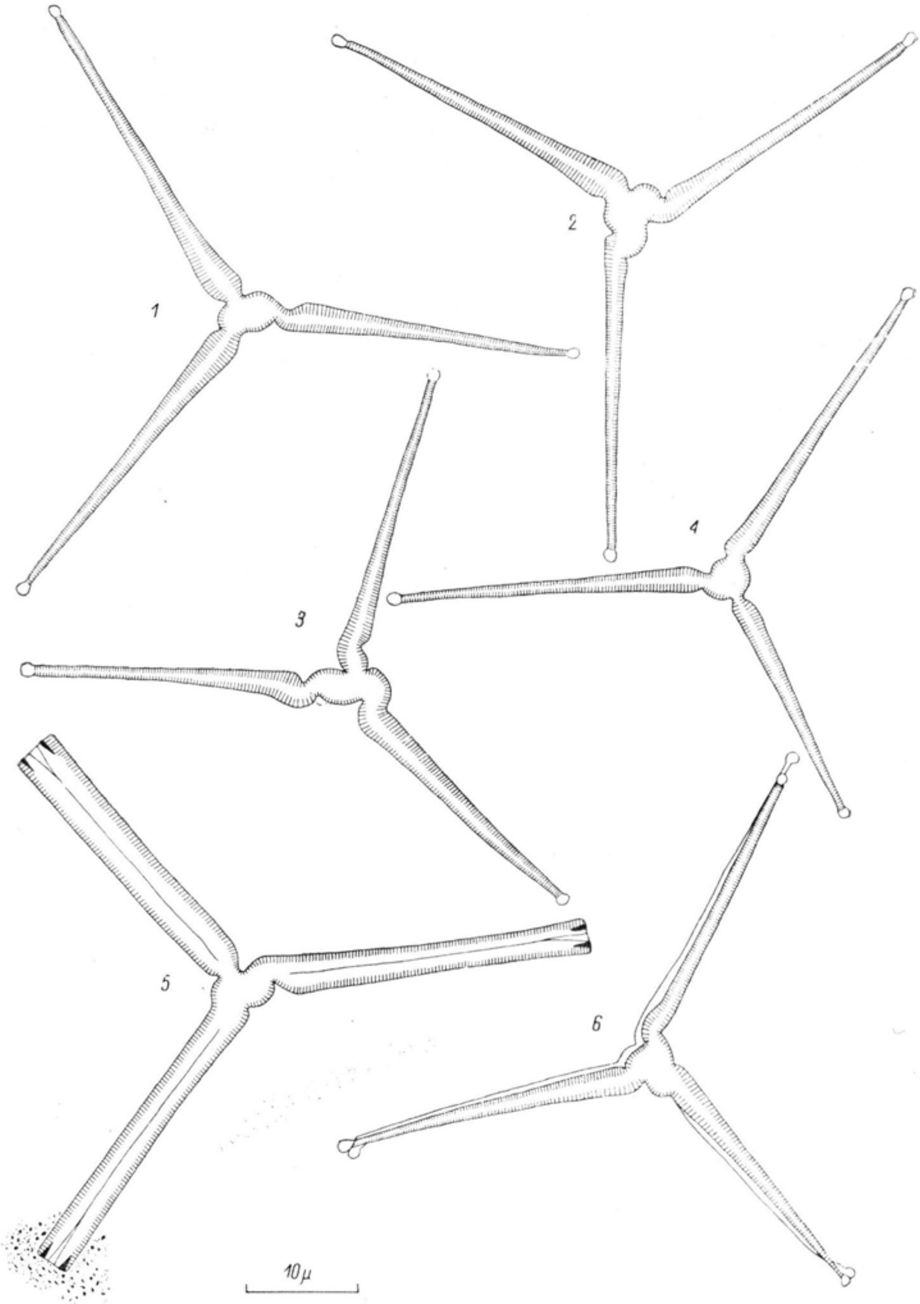

Fig. 1-4. *Centronella Reicheltii* Voigt from lakes in the Olsztyn region. Morphology.

1—Cell with arms slightly bending at base, left arm a little longer than the others; 2—Cell with arms bending distinctly at base, low arm a little longer than the others; 3—Cell with arms strongly bending at base, left arm a little longer than the others; 4—Cell with one (low) arm much shorter than the other two.

Fig. 5-6 *Centronella Reicheltii* from lakes of the Olsztyn region.

5—Dividing cell girdle view; 6—Two cells after division, valve view.

angles between the arms as marked in Table 1 by letters a — k. In the first group the most obtuse angle between two arms equaled 125 degrees; in the second group this angle was 130 or 135 degrees; and in the third group the most obtuse angle was 140 degrees. The other two angles were always complementary to 360 degrees.

The second group (d — h) was the most frequent in the Kortowskie lake. It amounted to 48 per cent of all cells. The first group (a—c) consisted of 46 per cent and the third (i — k) of 6 per cent of cells.

In the Sukiel lake the distribution of cells according to their shape was similar, though the number of specimens examined was smaller. In this lake one cell had arms arranged in a manner not observed in the Kortowskie lake. The angles between the arms of this cell were 135, 120, and 105 degrees. The cell can be classified in the second group.

The angles between the arms of *Centronella* cells in the drawings of various authors were measured so as to compare them with the present results. The specimens from Holstein lakes were mostly of the type here defined as group I b (120, 125, 115 degrees) and exceptionally of the type in group I a. Only the *C. Reicheltii* cell found by Wołoszyńska (1911, Plate VII, fig. 9) in a lake at Ostrowiec was not like the cells in group I. The angles between its arms were 135, 120, and 105 degrees, and it should be classified in group II similarly as the cell from the Sukiel lake.

The outline and the size of the central part of cells are important traits noted only by Wołoszyńska (1922). So far as can be judged from drawings the specimens from German lakes are characterized by the ovally-triangular shape of the central part. The only exception to this are the specimens with very slightly bending arms drawn by Hustedt (1932, Fig. 724 d). These cells fit well to the Latin description of the central part of the *C. Rostafińskii* cell: „...area centralis orbicularis vel orbiculari-triangularis...".

Mention has already been made that the specimens of group I from lakes in the Olsztyn region had the central part ± triangular. The outline of the central part of specimens of groups II and III was ± cordate. The breadth of the central part was 3—5 μ. According to Wołoszyńska (1922) the breadth of the central part of the *C. Rostafińskii* cell was 3 μ.

The Centronella specimens collected in the lakes of the Olsztyn region displayed also some variability in the length of arms.

According to earlier reports the length of arms ranges from 22 to 40 μ. Krieger, after measuring many specimens of *Centronella* from a lake near Brandenburg, states that the average length of arms is 32—35 μ. and adds that „...wie überhaupt die Variabilität der Art sehr gering ist", though further in the same report he mentions that „Zuweilen ist ein Arm erheblich kürzer als die beiden anderen".

In contradiction to Krieger's observations among the specimens from the lakes in the Olsztyn region the same length of all three arms was an exception. This is shown in Table 2.

In the Kortowskie lake cells with one arm longer than the other two predominates. On the other hand, in the Sukiel lake cells with one arm shorter were more common. The difference in the length of arms ranged from 1 to 7 μ. but the most frequent difference was 1—2.5 μ. Similarly the breadth of the arms directly above the bend was not — 2 μ. as reported by other workers. The breadth of arms in the specimens of the Olsztyn region was 2.1 — 2.2 — 2.3 — 2.5 — 2.6; the most frequent breadth was 2.1, 2.3, and 2.6 μ.

Table 2

Lengths of arms in *C. Reicheltii* *

According to earlier reports **	Kortowskie lake	Sukiel lake
22—**32**—**35**—40 u	26.5—**28**—**29**—**29.5**—30—31—32,5 μ	23.5—26—27—**28**—**29.5**—**30.5**—32.5 μ
Note: some cells from a lake near Brandenburg had one arm much shorter (Krieger 1927)	Note: 68% of cells had one arm longer by 1—**1.5**—2—2.5 μ. 26% of cells had one arm shorter by **1**—1.5—3 μ. 6% of cells had 3 arms of equal lengths	Note: Cells with one arm shorter by 1—**2.5**—7 μ wer more numerous. Cells with one arm longer by 1—**2.5**—3.5 μ were less numerous. No cells had arms of equal lengths.

* Most frequent values are underlined.
** Voigt 1902; Wołoszyńska 1911, 1922; Bennin 1923, Krieger 1927; Hustedt 1930, 1932.

No relationship was established between the variable length of arms, the angle between the arms, and the angle formed by the bend. Cells with a distinct or strong bend of the arm have, on the whole, broader arms directly above the bend.

The average length of arms of *Centronella* cells from the lakes in the Olsztyn region was shorter than the length of arms in specimens from German lakes. According to Krieger the very small size of *C. Reicheltii* cells (about 22 μ) found in a lake near Brandenburg was the result of the unfavourable conditions prevailing in that lake. However, in the Sukiel lake very small as well as very large specimens of *Contronella* were found (cf. Table 2).

Two morphological traits of *C. Reicheltii,* distinguished by Wołoszyńska (1922) for *C. Rostafinskii,* must still be mentioned. They are: 1) the distance between the tips of arms and 2) the outline of the cells as seen from the side. Wołoszyńska writes that „Apices radiorum 60 μ remoti", and then that „Frustula a latere visa valde complanata, linearia, apicibus solum paulo dilatata".

The distance between the tips of arms is a function of the length of arms, the former being directly proportional to the latter. In cells with short arms from the lakes near Olsztyn the distance between arm tips was usually less than 60 μ, and varied over a wide range: 45 — 46 — 52 — 53 — 54 — 60 μ.

In the general morphometry of *C. Reicheltii* cells the distance between arm tips has proved useful for estimating the symmetry or the asymmetry of cells. The straight lines connecting the tips form a triangle circumscribed on the cell. When all three sides of such a triangle are of different length the cell is asymmetric, e.g. the cell from the lake at Ostrowiec drawn by Wołoszyńska (1922) and the cells from the lakes in the Olsztyn region shown in Plate I, fig. 1, 2 and 4 in this report.

When two or three sides of a circumscribed triangle are equal the heights of the triangle must be traced out. Then if two angles between the arms of the cell are equal one height of an isosceles triangle runs along the axis of one of the cell arms thus marking out one plane of symmetry. The heights of an isosceles triangle circumscribed on a cell in which the angles between the arms are not equal disclose the lack of symmetry of such a cell. This last instance is illustrated by the cell in Fig. 1 B of this report and the cells in Hustedt's drawings (1930, page 133 Fig. 121; 1932, Fig. 724).

Similarly, the lack of structural symmetry is revealed by the heights of equilateral triangles circumscribed on cells with unequal angles between arms (e.g. the cells illustrated by Voigt 1902, Plate II, fig. 10, Krieger 1927, Plate V, fig. 1, Hustedt 1923, Fig. 724 c). On the other hand all the heights of the equilateral triangle circumscribed on the arm ends of the C. Rostafińskii cell (Wołoszyńska 1922) run conformably with the axes of the three arms and at the same time trace out the three planes of symmetry of the cell. The centre of this cell lies exactly at the point of intersection of the three heights of the circumscribed triangle.

The other trait distinguished as significant by Wołoszyńska is the outline of a cell in the side view. The arms of *C. Reicheltii* cells in a side view taper at the ends and in this they differ according to Wołoszyńska from *C. Rostafińskii* cells, but this trait must still be checked on a larger number of specimens. Actually, the ends of arms of *C. Reicheltii* cells from the lakes near Olsztyn seem to widen distinctly at the time of cell division (Plate I, fig. 5).

BIOLOGY

Most authors are of the opinion that *C. Reicheltii* is a pelagic species. It is also considered as a plankton or possibly even an euplankton species. On the other hand Schröder (1923) reports that in one of the Silesian lakes he frequently found *Centronella* specimens in samples taken from the bottom of the lake at a depth of approximately 10 metres, whereas in a sample taken from a depth of about 0.5 metre *Centronella* was not discovered. Wawrzyniak (1923) found *Centronella* cells in the littoral plankton of one of the lakes in the Kujawy region, on the under surface of a Nuphar luteum leaf, and on the bottom of the lake.

The fact that he found no *Centronella* specimens in the pelagic zone of the lake lead him to believe that the species was tycholimnetic.

In the Kortowskie lake many specimens of *Centronella* were collected on the surface of slides suspended for five days (July 23—28, 1956) at a depth of 10—40 centimetres, whereas in the surface plankton very few specimens were found.

In the Sukiel lake *Centronella* was found only on slides suspended (July 20—25, 1956) at a depth of 10—40 centimetres. In plankton samples collected simultaneously there was not one specimen of *Centronella*.

On the slides from both lakes there were individuals in the course of division (Plate I, fig. 5) or directly after division (Plate I, fig. 6). However, single cells, presumably before division, were more numerous.

The reports of Schröder and Wawrzyniak, as well as the observations on dividing cells or on cells after division made in the course of this investigation seem to indicate that *Centronella* passes in its life cycle through a sessile stage and that it requires a stable substratum at the time of vegetative reproduction. Thus the pelagic zone is not the only zone where *Centronella* lives.

Mention must be here made of the other constituents of the periphyton developing on the slides suspended in water. In the Kortowskie lake all diatoms temporally fixed on a stable substratum, and with them *Centronella*, were very common, whereas *Chlorophyceae* were few. In the Sukiel lake, on the other hand, diatoms including *Centronella* were less common and *Chlorophyceae* predominated. Among the green algae the most common was the glandulifera form of *Pediastrum boryanum* var. *longicorna* identified by Wołoszyńska (1924, Plate II A) in the hydropsammon of the Wigierskie lake. A drawing of this hitherto rare form collected in the Kortowskie lake is reproduced in an earlier report (Wysocka 1958, Plate I, fig. 7).

The mutually antagonistic relations of diatoms and green algae were already observed by Smaragdowa (1937). Her experiments and the present observations seem to indicate that biocoenatic factors are among the factors responsible for the rare occurrence of *C. Reicheltii* in natural water reservoirs.

In some descriptions of *Centronella* one trait has often been disregarded. This trait is the ability of *Centronella* to form colonies and to secrete a gelatinous substance from the tips of arms.

Voigt (1902) found a colony of 15 cells „....alle mit einem Arme zusammenhängend". The connections between cells were in that case facilitated by a viscous substance. Wołoszyńska (1911), quoting Voigt, states that *Centronella* cells „connect to form chains composed of several individuals". Similarly Schröder (1923), also on the ground of Voigt's description, writes that „Mehrere dreistrahlige Sterne mit je einem Arme durch Gallertpolster zu Ketten von kleinen Kolonien verbunden zusammen".

More recent descriptions in keys state briefly that „Zellen einzeln lebend", and also on the ground of Krieger's (1927) results that „...in Kulturen auch Bänder bilden".

In Krieger's experiments in laboratory conditions *Centronella* cells divided after one week. After about six weeks characteristic wing-shaped colonies (Krieger 1927, Plate V, fig. 9) of about 70 cells developed, of which „....Endzellen stark konwex waren" (Plate V, fig. 8).

It is noteworthy that the first two links of this colony formed in laboratory conditions (Krieger 1927, Fig. 9) closely resemble the two cells collected from a natural environment shown in Plate I, fig. 6 of this report.

THE MECHANISM OF GROWTH OF COLONIES

The reports of other writers and the observations assembled in the course of this work indicate that *C. Reicheltii* is a species of considerable individual variability. The variable traits are as follows: the angle between arms, the angle formed by the bend at the base of arms, the breadth of arms above the bend, the outline and the breadth of the central part of a cell, the average size of cells, the length of arms in one individual, and the distance between the tips of arms.

If the cell sub. *C. Rostafińskii* Woł. with straight arms and of absolute symmetry is considered to be the original mother-cell of the species *C. Reicheltii,* then, through successive divisions, cells of different degrees of symmetry are obtained owing to the varying arrangement of arms and the varying angle of the geniculate bend at the base of arms. The cells shown in Hustedt's drawings (1932, Figs. 724 c and d) represent instances of small asymmetry. So far the final links in this sequence are represented by *C. Reicheltii* cells with very asymmetric arms from the Kortowskie lake (Table 1, j and k).

Owing to the different lengths of the arms of the particular *C. Reicheltii* cells from the lakes of the Olsztyn region the symmetry of the cells was maintained at the most with regard to one axis only, even when all the three angles between the arms were equal (Table 1, a). There was also only one axis of symmetry in cells with two equal angles adjacent to the arm that was longer or shorter than the other two (Table 1, b, d, e, h, j, and k).

The gradual change of the angles between arms, the deformation of the base of arms and of the central part of cells, and the increasing breadth of the central part of cells and of the arms above the geniculate bend are undoubtedly the result of the specific nature of vegetative reproduction of cells. According to Krieger the successive divisions of *Centronella* cells do not underlie one another directly, but are mutually helically twisted. Consequently if every arm of a mother-cell was superimposed on the corresponding arms of the daughter-cells they would resemble an unfolded fan.

It seems that the predominance in the Olsztyn lakes of *C. Reicheltii* cells of medium and very small sizes is primarily caused by phenomena common in the vegetative reproduction of diatoms. According to Krieger unfavourable environmental conditions have only a secondary influence on the dwarfishness of *Centronella*. This opinion is supported by the fact that small (lengths of the three arms: 26.0, 26.0, 28.0 μ) as well as large (lengths of the thrre arms: 33.0, 29.5, 29.5μ) cells were found in the Sukiel lake.

The mechanism underlying the development of colonies is, furthermore, associated with the plane in which the cells lie when resting on a stable substratum.

On the slides there were dividing cells with some gelatinous substance distinctly visible (Plate I, fig. 5) near one of the arms. This lead to the supposition that such cells were attached to the stable substratum by the tip of the arm with the gelatinous substance. Thus the plane of these cells could not lie in the plane of the slides forming the substratum, but had to diverge from it at some angle.

The *Centronella* colony found by Voigt at the sessile stage in which all the cells were connected by one arm only may support this supposition. Similarly the colony obtained by Krieger in laboratory conditions could not develop as it did if it had not been connected with some substratum and if the planes of all cells had not been in strict relation to the plane of the substratum.

The different lengths of the arms of an individual are probably caused by the different environmental conditions in a colony at the sessile stage, i.e. when one arm is fixed and the other two are free, or when two arms are fixed and the third diverts away from the substratum. The different lengths of arms are, moreover, an indirect proof of the sessile nature of colonies.

From what has been said above it follows that the individual variability of *C. Reicheltii* cells from the lake of the Olsztyn region (average length of arms is 28—30 μ) is probably associated with the vegetative reproduction of cells at the sedentary stage of their life.

In the case of the large, absolutely symmetrical *C. Rostafińskii* cell with arms 35 μ long the supposition might be made that it originated directly from an auxospore. If this was true the slight asymmetry and the relatively small variability of the cells from the lakes in Holstein and Brandenburg would perhaps indicate the close relation, through vegetative divisions, of these cells with cells formed by sexual reproduction. Then, the cells from the Kortowskie lake having at least two arms strongly bent would originate from individuals with a long series of divisions in their background and far removed from the perfectly symmetrical mother-cell. However, sexual reproduction has never been observed to prove this supposition.

CONCLUSIONS

1. *Centronella Reicheltii* Voigt, generally considered as a typical plankton species, has in its life cycle a sedentary stage on a stable substratum.

On a stable substratum, in the course of a series of vegetative divisions, *Centro-*

nella forms characteristic wing-shaped colonies. The colonies, after becoming detached, can float for some time in water before disintegrating into isolated cells.

2. The rate of reproduction of *Centronella* on a stable substratum has a direct influence on the frequency of occurrence of these cells in the plankton. The rate of reproduction depends not only on ecological conditions but also on other organisms simultaneously associated to a larger or smaller degree with the substratum. The time that division lasts after the deposition on the substratum is at present difficult to estimate. On the slides suspended in water for five days single cells, probably before division, predominated. Dividing cells or double cells immediately after the first division were relatively few.

3. Cells of *C. Reicheltii* Voigt manifest much individual variability of the following traits: the angle between the arms, the angle at which the arms bend at the base, the breadth of arms above the bend, and the breadth and shape of the central part of cells. This morphological variability is caused by the specific mechanism of the development of colonies at the sessile stage in which the daughter-cells are helically twisted with regard one another.

The lengths of arms of an individual frequently differ. This may be due to the environmental conditions when a cell is attached by one or two arms at the sedentary stage of its life.

4. The differences in the size of cells are in fact greater than is generally reported in the literature. The average cells from the lakes in the Olsztyn region were distinctly smaller than the cells from German lakes. Consequently, also the distance between the arm tips was correspondingly shorter.

The greater range of variability in the size of cells seems to be associated with the decrease of the size caused by the vegetative reproduction of cells. Unfavourable environmental conditions have probably only a secondary influence on this process.

5. The diagnosis generally accepted at present should be supplemented by the following points:

a) The angles between the arms lying in one plane are very variable. Consequently the structure of cells can either be perfectly symmetrical with regard to three axes, or lack symmetry in various degrees, e.g. with only one axis of symmetry or complete asymmetry.

b) In the great majority of cells the arms bend at the base. The angle of the bend may differ. Sometimes the bend is only slight, in other cases clearly marked or even very strong. The outline of the central part of cells depends on the geniculate bend of the arms and may be ovally-triangular or cordate. There are some cells, however, with straight arms and a round central part (e.g. *Centronella Rostafińskii* Woł.).

c) The breadth of the central part of cells varies from 3 to 5 μ and the breadth of the arms above the bend from 2.0 to 2.6 μ.

d) The particular arms of a cell are frequently of different lengths; one arm may be longer or shorter than the other two, and the difference in length may range from at least 1 to 7 μ.

e) The distances between the tips of arms are not always the same and may range from 45 to 60 μ.

f) The ability to secrete a gelatinous substance from the ends of arms and to form colonies in natural conditions is a trait often omitted, in spite of its significance for the description of this species.

Because of the inaccuracy of the descriptions of the species the description of the monotypic genus *Centronella* Voigt must be completed and modified.

SUMMARY

Centronella Reicheltii Voigt, known so far as a typical plankton species occurring sporadically, has now proved to be more frequent on stable substrata. Experiments in which slides were suspended in the littorall zone of two lakes in the region of Olsztyn have supplied more specimens than catches of plankton. Moreover, a sessile stage at the time of the vegetative reproduction of this diatom and the significance of a stable substratum in the development of colonies have been demonstrated.

C. Reicheltii cells manifest much individual variability. The variable traits are as follows: 1) the angle between the arms, 2) the angle formed by the bend at the base of arms, 3) the breadth of arms above the bend, and 4) the shape and breadth of the central part of cells.

The differences between the present observations on the morphology of cells and their earlier descriptions seem to be due to the specific mechanism underlying the growth of colonies of these diatoms at the sedentary stage of their life.

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(Presented on July 4th, 1958.)

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