ACTA BOTANICA NEERLANDICA, Vol. 3 (3), 1954

A TAXONOMIC SPECTRUM OF THE SECTION EU-CALLITRICHE IN THE NETHERLANDS

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(*received June 18th 1954*)

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INTRODUCTION

Several years ago I received the request from Dr W. H. WACHTER to work up the family of the Callitrichaceae for the Flora Neerlandica.

It soon proved that doing so for this family of somewhat shady reputation in botanical circles could not be based on herbarium and literature studies only.

As for the literature: it is not very extensive and comprises only foreign works; investigations about the Dutch Callitriches are entirely missing.

Of the foreign works we mention the monographs of KÜTZING, LEBEL, and HEGELMAIER, based on morphological studies, the articles of JÖRGENSEN and SOKOLOVSKAJA, who started cytological research, furthermore the studies of modifications by GLÜCK, and the work of SAMUELSSON, in which, among other things, some geographical and ecological data are discussed.

On account of the confusion in the nomenclature—cause of which is a.o. the synonymy of LINNAEUS—it is impossible, in certain cases, to determine for which species a certain investigation was made.

In the herbaria as well we find this confusion reflected, whilst moreover an insufficient knowledge of the polymorphy has given rise to many incorrect determinations.

For illustrative purposes one single example. Many people call every Callitriche with spathulate leaves *C. stagnalis*, every Callitriche with linear leaves *C. autumnalis* or *C. hamulata*, every small landform *C. palustris*. To continue, many authors consider *C. platycarpa*-plants as *C. palustris* (Hegelmaier) or determine *C. stagnalis*-plants as *C. platycarpa*, *C. truncata* as *C. autumnalis* (Lebel). Others consider every modification as a new variety at the very least.

In a situation so confused only a combination of various research methods can procure some light, and lead to a justified nomenclature. Therefore it would undoubtedly have been desirable to commence a research after e.g. the manner of the Silene-investigations by MARSDEN-JONES and TURRILL, in which next to herbarium- and literature-studies attention is paid to geography, ecology, hybridization, anatomy, cytology and modifications.

When being put into practice, such an experimental taxonomic investigation encounters difficulties however. It is a very lengthy affair and in reality only fit for teamwork. Moreover in studying the Callitrichaceae difficulties arise, which do not, or hardly, occur in the case of terrestrial plants.

We here mention a.o. the following subjects:

1) The cultivation. This makes special demands on the control of environmental conditions and is rather complicated. It is owing to special circumstances at the botanical garden "de Wolf"—we, in this instance, think of e.g. the presence of running water—that here at long last all species could be grown marvellously, in various modifications.
2) The gathering of the seeds. The plants often suffer too much if one regularly pulls up the rather fragile stems from the water to take away the ripe seeds. This is the only way in which one can have at one's disposal a sufficient quantity of seeds: having the use of extensive field-cultures where parts may be sacrificed to the harvesting of seed.
3) The raising of seedlings. This can practically only be done in field cultures under special conditions. It was only in 1953 that this could be started in the botanical garden "de Wolf".
4) Hybridization. The difference in pollination and reproduction is the reason that hybridizations can only be made in 3 out of the 5 species treated here. The structure of the very tiny flowers and their position in the axils of the leaves make it extremely difficult not to damage the rosette in case of castration. Besides, this action must be repeated about 5 times a day to flourishing stems.
5) The study of meiosis. The ♂ flowers each consist only of 1 stamen and their number on one stem is small. Moreover the stems will not tolerate a regular investigation as to the presence of anthers, they break or become too dry. So one can use each stem only once and it requires very much material before one has gathered a number of good stages.

On account of the above mentioned facts the working-program necessarily had to be curtailed.

The investigation now comprises the 5 Dutch species of the section Eu-callitriche, viz. *C. hamulata*, *C. obtusangula*, *C. stagnalis*, *C. platycarpa* and *C. palustris*. The following subjects arise:

In Ch. I a description is given of the cultures indoors and in the field.

Ch. II treats of cytology and especially mitosis. The great differences in chromosome sets proved a fit basis for the limiting of the species. In *C. palustris*, apogamous as landform, meiosis was studied and a start was made with the cytology of the ovule.

In Ch. III the most striking modifications are described.

Ch. IV gives a description of the pollination of the various species.

Ch. V gives a survey of the geographical distribution of the species in the Netherlands and in Europe and gives data about pH, salinity, vegetation etc. of various Dutch Callitriche-localities.

In connection with the sometimes striking distribution areas the germination of the seeds in solutions of various salt concentrations was studied (Ch. VI).

The nomenclature is discussed in Ch. VII, and in Ch. VIII a description is given of each species, after which there follows a key to the species.

As to *Callitriche hermaphroditica*—probably the only Dutch representative of the section Pseudo-callitriche—only herbarium material could be studied. The data about this species will be published elsewhere (Acta Botanica Neerlandica, in preparation).

ACKNOWLEDGEMENTS

I am highly indebted to the Netherlands Organization for Pure Research (Z.W.O.) which offered me a grant enabling the publication of the illustrations.

I am specially indebted to Mr. L. Alkema, who bestowed so much care upon the photographs. My thanks are due to Miss dr Ch. H. Andreas for her interest and stimulation, to Miss M. C. Buyze for her valuable help and careful typing, to Miss A. Zeven, especially for her valuable assistance in composing the lists of geographical distribution, to dr G. F. Wilmink and his laboratory for analysing the water of the localities and to all who sent me living plants and herbarium material.

Finally I must record a special debt to Mr. E. Laarman for his interest and valuable help and to the gardeners, Mr. Medendorp, Mr. Blom, Mr. Lindeman, Mr. Lok, Mr. Robertus, Mr. Visser Sr and Mr. Visser Jr for their help in the field cultures.

LIST OF ABBREVIATIONS

Herbarium Amsterdam	h.AMD
„ Barbey-Boissier, Genève	h.B-B.

Herbarium	Clason (Groningen)	h.Clas.
,,	Copenhague	h.C.
,,	Delessert, Genève	h.D.
,,	Groningen	h.GRO
,,	Kern & Reichgelt (Nijmegen)	h.K. & R.
,,	Leiden	h.L. (NBV incl.)
,,	Lousley (London)	h.Ly.
,,	Schotsman (Groningen)	h.Sch.
,,	Zürich	h.Z.
living plants		x
vice county		v.c.

Chapter I

CULTURES

In the literature on this subject we find but spare data about the cultivating of Callitriche.

Askenasy (1872), Clarke (1859) and Jörgensen (1925) cultivated the plants in moist mud in flowerpots and in that manner also transferred waterforms into landforms. The plants remained alive but flowered only little and hardly set any fruit. Watercultures in glass jars gave many difficulties on account of abundant growth of algae. A rather dark place, to repress this growth, did not prove to promote the wellbeing of the Callitriches, so that none of those methods led to a useful result.

Perhaps Kirchner, Loew and Schröter (1932) experienced the same disappointments. They entirely agree with Jörgensen's information, that the Callitriches scarcely flower in cultures and hardly set any fruit.

Glück (1924) had slightly more success. He, anyway, succeeded in transferring landforms into waterforms in an unheated hothouse and to get *C. hamulata* to flower and fructification. Besides, he kept *C. obtusangula*, originating from Cambridge, alive from Oct. 1911 - June 1912. This plant developed good rosettes in the spring of 1912 and also flowered.

From the facts mentioned, it however becomes apparent that the cultures can never comprise a sufficient number of plants and that they survive only a few months.

As it is necessary for the study of lifecycles, modifications, cytological peculiarities etc. to have at one's disposal numerous plants, an investigation into fitting circumstances of cultures proved desirable in the first place.

I. Indoor Cultures

A. Waterforms. These cultures were started in Oct. 1948. In the beginning experiments were only made with *C. hamulata* (from Haren, prov. of Groningen), *C. platycarpa* (Haren, prov. of Groningen), and *C. obtusangula* (from the island of Texel). The plants were cultivated in glass jars and placed in an unheated room. As culture medium there were used: tapwater, rainwater and deep-wellwater from the pond of the botanical garden "de Wolf" with and without soilmaterial. This soil consisted of sieved leafmould or boulderclay and was added unsterilized or sterilized. This addition of soil proved neither a success in sterilized nor in unsterilized form. In nearly all cases there occurred waterpollution after a few weeks with strong growth of Cyanophyceae and Proderma viridis, so that the Callitriches expired. Tapwater too was found to be unfit. The best result, ultimately, came from rainwater. In this medium *C. platycarpa* and especially *C. hamulata* grew well, without annoying development of algae, and formed a good number of roots.

In the spring the temperature became too high in the workroom of the laboratory on sunny days, which caused a speedily turning yellow and withering of the plants. So the cultures were transferred to a part of the barn of a farmhouse, belonging to the botanical garden. These cool rooms, situated N.W. proved very favourable for the cultures. Not only rainwater cultures of *C. hamulata*, *C. platycarpa* and *C. stagnalis* succeeded well here, but also the germination of the seeds, the cultivating of the landforms and experiments regarding the salt tolerance in various species gave a good result. Moreover *C. obtusangula* was kept alive in diluted sea-water during several months, while normal flowering and fructification occurred. To prevent frostdamage to the glass jars, a fire was lit to keep the temperature just above 0° C during frostperiods.

B. Landforms. Those may easily be grown in open petridishes and be brought to flower; they were placed in the same room. As substrate, the soilsubstance of the findspot was used as much as possible. For *C. hamulata* and *C. platycarpa* this was mostly dried ditchmud, for *C. palustris* and *C. stagnalis* loamy brooksoil. The substrate was regularly kept moist with rainwater.

II. Fieldcultures

1) *Valley of the experimental brook*

A. Waterforms. Though the cultures progressed well indoors, several drawbacks nevertheless proved to be connected. In the first place it was not possible to grow *C. platycarpa* from the quickly flowing brooks of Limburg in this manner. Also *C. palustris* as a waterform brought difficulties. Further in several species—probably because temperature and light ratio are quite different indoors from those in the field—a diverging habit occurred and other forms of leaves. *C. hamulata* e.g. lives for years in cultures, whereas this species is a winter annual in our country. If certain observations are solely made from indoor cultures, then one soon draws conclusions that do not tally with the behaviour of the plants in the field.

To abolish the drawbacks mentioned, possibilities were sought to grow the different species in the open air, under circumstances as much as possible similar to those of the natural place of growth. This could only be realized after the watersupply of the botanical garden "de Wolf" was greatly improved in 1949. In that year a pump was set, bringing up water from a well, ± 70 m. deep, and propelling it into the brook through the arboretum and fields. In this way the water level remains up to the mark during the summer in the shallow places and moreover, in several slanting places in the brook, a fair current is caused. Because of the continuous supply of cool wellwater the temperature does not rise above 17° C in the unshaded parts; in the arboretum it is usually 15° C in summer. The growth of algae is especially inconsiderable in the arboretum, so that the botanical garden brook,—in the shady part as well as in the field part—forms an extremely fitting environment for the various species of Callitriche. The soil principally consists of sandy soils with a subsoil of boulder-clay. In the quiet parts *C. platycarpa*, *C. stagnalis*, *C. hamulata* have been grown for some years, while in the quickly flowing parts the Limburg brookform of *C. platycarpa* comes to abundant development. *C. obtusangula*, which originally would not keep for more than a few months, neither indoors, nor in the field, proved to have at last found a good place in a part of the brook covered by a thick layer of ashes. Since its having been planted in the autumn of 1951 it spreads into thick placcards of a few metres, flowers and fructificates and during the mild winters remains in good condition as well.

B. Landforms. Along the banks of the brook landforms of *C. platycarpa* and *C. hamulata* are being cultivated. Moreover *C. platycarpa* forms a vegetation continuously becoming more dense along a moist shady path between *Juncus bufonius* and a few Gramineae.

2) *"Cowpuddle" cultures*

In the marshy grasslands along the brooks of Drenthe we in summer find a bumpy piece of land, with more or less deep little hollows and cavities, caused by the cows grazing there and continually sinking their legs into the marshy soil. Henceforward these hollows will be called "cowpuddles". In these "cowpuddles", in which there is generally some water, we find a typical vegetation, consisting a.o. of land—and sometimes small waterforms of *C. stagnalis* and *C. palustris* (cf. for further peculiarities of this vegetation Ch. V).

As it was no success originally to cultivate *C. palustris* especially as a waterform, in an entirely satisfying way, the natural environment of these plants was imitated in a swampy strip of land looking suitable, along the brook, through the meadows in the botanical garden "de Wolf". At distance of a few dm. small hollows were dug of about 15 cm. diameter and about 20 cm. deep. During the winter the hollows are all full of water, in summer there is a possibility of letting some run dry. The environing vegetation (principally Gramineae and *Lotus uliginosus*) shields the plants from too strong a radiation of the sun. *C. palustris* and also *C. stagnalis*, when sown, grow into sturdy land- and waterforms. How exactly this area complies with the demands that *C. palustris* makes on its environment, appears from the spontaneous growth of scores of fructificating *C. palustris*-plants during the summer of 1953.

Also for the cultivation of seedlings the "cowpuddles" proved very efficient. In indoor cultures the seedlings rarely grow any higher than a few cm., while in the brook they usually are washed away. By means of the regulable waterlevel the transition from land- to waterform, and the other way round, can easily be studied in the "cowpuddles" without the tiresome transplanting.

Chapter II

KARYOLOGY

I. Literature

Only two authors studied karyology in some species of the section Eu-callitriche, namely Jörgensen and Sokolovskaja.

Jörgensen (1925) investigated meiosis in Danish plants and mentions a.o.: *C. hamulata*, *C. stagnalis* and *C. verna* (nomencl. Jörgensen). In the former species he found $n = 19$, in *C. stagnalis* $n = 5$ and $n = 10$, in *C. verna* $n = 10$. Moreover he studied various stages of the development of the ovules in these species. This investigation is most exhaustive in *C. autumnalis* (nomencl. Jörgensen, syn. *C. hermaphroditica* Juslen.), a species of the section Pseudo-callitriche. Probably the development in both species is rather analogous. According to Jörgensen the ovule of *C. autumnalis* shows a linear tetrad of which the chalazal megaspore forms the eight-nucleate embryosac. Also in *C. verna* he observed an eight-nucleate embryosac. In *C. autumnalis* he found after fecondation a cellular endosperm with a micropylar haustorium and a chalazal haustorium. The germ possesses a suspensor and lies in the central part of the endosperm.

In Jörgensen's article good descriptions of the species are lacking. Consequently one can not trace with certainty which species he studied. Therefore it is impossible to decide whether his *C. stagnalis* includes *C. platycarpa* or not. Also the limitation of his *C. verna* is uncertain.

Sokolovskaja (1932) has examined Russian plants. She counted the number of chromosomes in the roottips of *C. verna* (nomencl. Sokolovskaja) and *C. stagnalis* and gave a chromosome picture of both species with a table of the size of the chromosomes. She found in *C. verna* $2n = 20$ and in *C. stagnalis* $2n = 10$. Of both species—especially of *C. verna*—Sokolovskaja mentioned some clear characters. It is almost certain that her *C. verna* is morphologically identical with our *C. palustris*.

II. Material and Methods

For studying mitosis in *C. hamulata*, *C. obtusangula*, *C. platycarpa*, *C. stagnalis* and *C. palustris* Feulgen squashes of young roottips were made. The roots must be taken from waterforms; staining of landform-roots proved to be generally impossible.

Especially in *C. palustris*, mostly occurring as a landform, this fact gave rise to many difficulties. The small plants have scanty and very thin roots with a few divisions only. In the summer of 1953 however, we succeeded in obtaining well-stained clear preparations of *C. palustris*. The roots were coming from waterforms of an inundated brookvalley and from cultures in the botanical garden "de Wolf".

As to *C. hamulata* the roots were generally gathered in autumn, a period of intense vegetative growth. For *C. obtusangula*, *C. platycarpa* and *C. stagnalis* spring and early summer proved the most successful time.

The procedure adopted for making the Feulgen squashes was as follows:

1) Pre-treatment in 0.129 mol. α-8-hydroxychinoline solution for 2-4 hours.
2) Fix in Carnoy for $\frac{3}{4}$ hours.
3) Transfer to 100 % alcohol for 12 to 24 hours.
4) Hydrolyse in 0.1 *n* HCl at 60° C for 8 to 10 minutes.
5) Stain by Feulgen (basic fuchsin).
6) Transfer to water for 30 minutes.
7) Transfer to 45 % acetic acid on a slide, cover, tease out and squash.

The procedure for making preparations permanent was as follows:

1) Dissolve the cover slip by immersing the preparation in Carnoy.
2) Pass through absolute alcohol.
3) Mount in "euparal".

Meiosis and the development of the ovule were studied in *C. palustris*. As this species is rare in the Netherlands, we had only the disposal of a small number of anthers and ovules. Most of the material came from our own cultures in the botanical garden "de Wolf".

The anthers and ovules were fixed in Randolph's modification of Navashin, embedded in paraffin, sectioned 7 μ and stained with crystal violet.

The chromosome pictures were drawn after metaphase-chromosomes with the aid of a drawing-prism. In various metaphaseplates of one roottip the length of corresponding chromosomes may be different, so there can not be attached absolute value to the length of the chromosomes in a chromosome picture. A picture gives an impression only of the relative ratio of length of the chromosomes in one set and of the place of the centromeres.

For a good comparison of the sets of the various species it is necessary to choose the possibly most corresponding stages. Nevertheless exact comparison is out of the question.

III. OBSERVATIONS

A. Mitosis

1. **C. hamulata** (h.Sch. 51104, 52147, 5340)

The number of chromosomes is $2n = 38$ (plate 1). This number is quite in agreement with the statement of JÖRGENSEN (1925). We found that the chromosomes normally—without cold treatment—are heterochromatic. The other species show this phenomenon as well, especially it is very clear in *C. stagnalis* (plate 2*b*).

The chromosomes are of different length and possess median, submedian or subterminal centromeres. The latter type is the most frequent (17 pairs). In a few chromosomes the short arm is very small. There is only one pair of long chromosomes with a median centromere, and one pair with submedian (fig. 1*e*). Generally the former chromosomes are V-shaped, sometimes the arms are in prolongation of one another (plate 2*e*).

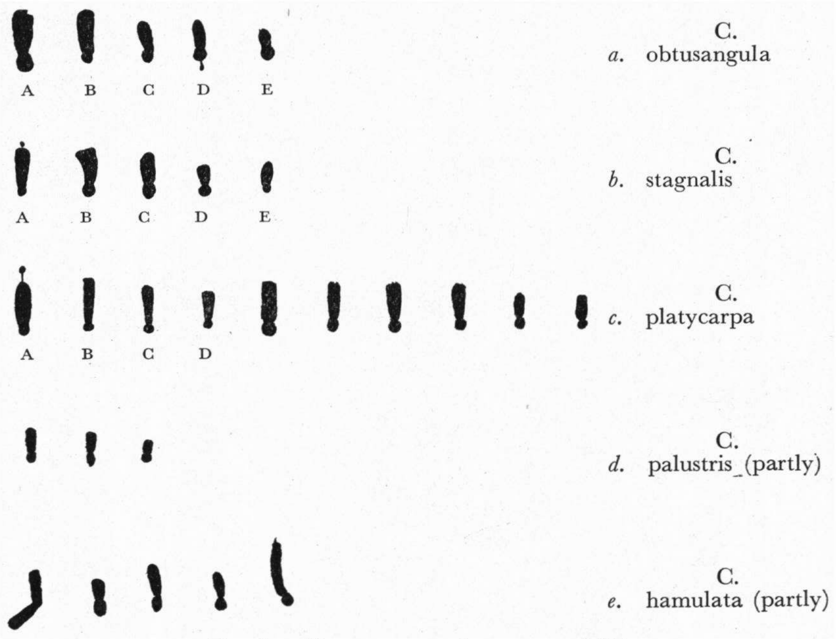

Fig. 1. Chromosome pictures. × 2400.

In the section Eu-callitriche *C. hamulata* is the only European species possessing chromosomes with median centromeres.

2. **C. obtusangula** (plants from the Isle of Texel: h.Sch. 51292, 51293; plants from the prov. of Zeeland: h.Sch. 5301)

This species has $2n = 10$ (plate 3*d*). In the haploid set one long chromosome can be observed, possessing a subterminal centromere (fig. 1*a*, chr. A). Chromosome B (fig. 1*a*) is somewhat smaller and shows a subterminal centromere as well. The short arm of this chromosome is very small. Moreover there are two medium-sized chromosomes with subterminal centromeres (fig. 1*a*, chr. C, D) and one small chromosome with a submedian constriction (fig. 1*a*, chr. E). All chromosomes are heterochromatic.

It is a striking fact that in this species we meet with plants having

0 or 2 SAT-chromosomes. The former type occurs in the island of Texel, whereas plants with 2 SAT-chromosomes are to be found in the province of Zeeland (plate 3*e*).

The satellites are small, nearly globular and connected with the short arms of one pair of medium-sized chromosomes (fig. 1*a*, chr. D). For more details concerning the structure of the satellite cf. *C. stagnalis*.

3. **C. platycarpa** (h.Sch. 5130, 5133, 5140, 52130)

This species has $2n = 20$ (plate 2*a*). The chromosomes are heterochromatic and all of them possess a subterminal centromere (fig. 1*c*). They are of different size. 4 Pairs of chromosomes are striking by their very small arms (fig. 1*c*, chr. A, B, C, D).

In *C. platycarpa* we found plants with 0, 1 or 2 SAT-chromosomes. When 2 SAT-chromosomes are present, two different possibilities arise. The satellites may occur either on 2 homologous chromosomes or on 2 chromosomes of different length. In the first case they are connected with a pair of long chromosomes, in the second case one short chromosome and one long chromosome possess a satellite.

When only one satellite is present, it is attached to the long chromosome (plate 2*d*).

Sometimes in one locality only one type was found, sometimes plants with 0, 1 or 2 SAT-chromosomes occur together. Only once the above mentioned case of two non-homologous SAT-chromosomes was observed (viz. Haren, prov. of Groningen; plate 2*c*, fig. 2).

The satellites are small, more or less globular and always attached to the long arms of the chromosomes. The satellite of the short chromosome appears to be somewhat longer than that of the long chromosome (plate 2*c*, fig. 2).

Fig. 2. Explanatory diagram of the left part of plate 2c.

4. **C. stagnalis** (h.Sch. 51109)

The number of chromosomes is $2n = 10$ (plate 3*a*). All chromosomes have a subterminal centromere; they are heterochromatic (plate 2*b*). Three pairs of long chromosomes show about the same length. The first pair (fig. 1*b*, chr. A) is clearly distinguishable from the others by the very small short arm, the second and third pair mutually are nearly analogous (fig. 1*b*, chr. B and C). The fourth and fifth pair are much smaller, resembling each other in total length, but there is a clear difference in the position of the centromere (fig. 1*b*, chr. D and E).

In this species we meet with plants having 0, 1 or 2 SAT-chromosomes (plate 3*a*, *b*, *c*). No morphological differences between the plants could be observed. In some localities only one type was found (a.o. in Middachten, prov. of Gelderland, 2 SAT-chrom.); in Schipborg (prov. of Drenthe), however, the three types occur together.

Only the pair of long chromosomes with the most terminally placed centromere possesses the satellites (fig. 1*b*, chr. A).

It should be emphasized, that in the case of only one SAT-chromosome being present, the homologous chromosome does not possess a satellite.

The satellite is small, nearly globular and attached to the long arm of the chromosome. It has been proved that each satellite in the prophase consists of 2 markedly defined parts, connected with each other by a threadlike connection (plate 4*a*, *b*). In the centre of this connection ("thread") a small thickening is visible (plate 4*c*, *d*). In this stage the satellite has removed from its chromosome over a distance as long as the chromosome itself, and an extremely thin connective "thread" is seen between the one part of the satellite and the end of the chromosome (plate 4*a*-*d*). Later on the two parts of the satellite approach each other more and more (plate 4*e*, *f*) until they form a whole. The threadlike connection between the chromosome and its satellite shortens so that in the metaphase the satellite gets very close to the chromosome.

Gosselin (1946) observed that the satellites of *Anthurium*, *Xanthosoma*, *Washingtonia*, and *Hedychium* in the prophase consist of two parts as well, one of them being connected with the end of the chromosome.

According to Gosselin however this latter part, called by him "chromocentre", disappears into the chromosome as "un bouchon dans le goulot d'une bouteille", whereas the other part remains out of the chromosome.

So Gosselin considered the satellite visible in the metaphase as one of the two parts mentioned. Unfortunately his pictures do not clearly demonstrate his theory.

Anyhow Gosselin's description of the behaviour of the parts of the satellites during the prophase and metaphase is quite different from our observations in Callitriche. We never observed one of the two parts disappearing into the chromosomes. Always both parts approach each other until they have united and as a result of proceeding contraction the satellite as a whole is coming close to the chromosome.

In *C. obtusangula* this phenomenon could be observed as well. Up till now we did not meet with *C. stagnalis*-plants with $2n = 20$, such as Jörgensen mentions. It may be possible that this number has reference to *C. platycarpa*, with which *C. stagnalis* often has been confused. In the absence of a good description of Jörgensen's material, this cannot be decided.

The chromosome set as we found this in Dutch plants is different from the set, pictured by Sokolovskaja (cf. fig. 1*b* with fig. 3). The small chromosomes D and E—very striking in our plants—are lacking in the picture given by Sokolovskaja. Her figure shows only one somewhat smaller chromosome, nearly as long as the others (chr. I). In the Dutch material, however, the 2 small chromosomes are about half as long as the other ones.

Besides Sokolovskaja found 2 chromosomes with a very short arm, being nearly similar in size (chr. IV, V). We too, found 2 chromosomes with a very short arm, however greatly differing in size; one belongs to the long chromosomes, the other to the short ones (fig. 1*b*, chr. A and E).

Sokolovskaja did not pre-treat her material, so it is not quite comparable with ours. We, however, compared the sets of untreated and pre-treated roots in *C. obtusangula* with each other. From this it may be concluded that the mutual ratio of length of the chromosomes does not change by the treatment, while the chromosomes contract proportionally. Also in the chromosome picture given by Sokolovskaja we should expect the two small chromosomes D and E to attract our attention, while the two chromosomes with a short arm should markedly differ in length. This, however, is not so. The difference in picture could possibly be explained on the assumption that Sokolovskaja found great difficulty in observing the chromosome lenghts in her material being untreated. For only rarely a chromosome in the equatorial plate is uncoiled and in its entirety visible. Pre-treated material certainly provides a more reliable result in determining the mutual ratio of length. It may, however, be possible that the Russian specimens possess a chromosome set different from that of our Dutch plants.

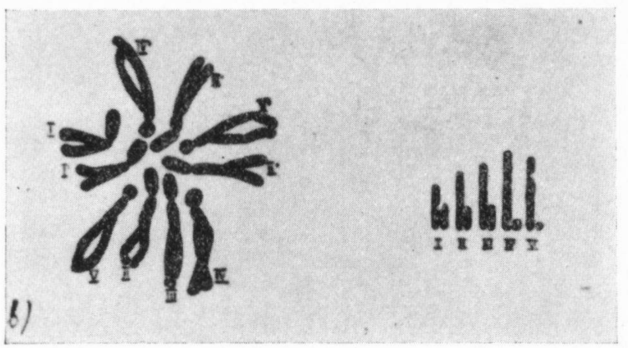

Fig. 3. C. stagnalis. After Sokolovskaja (1928). For explanation see text.

5. **C. palustris** (h.Sch. 5349)

The number of chromosomes is $2n = 20$ (plate 3*f*). They are all heterochromatic and have a subterminal centromere. As to the smallest pair we might speak of a submedian centromere, but because of the very small size it is difficult to decide between the two types.

The chromosome set pictured by Sokolovskaja, is different from the set we found (cf. fig. 4). Several chromosomes of Sokolovskaja's *C. verna* (= our *C. palustris*) are of the same size as the longest in *C. stagnalis*, but according to our observations the longest chromosomes of *C. palustris* are only somewhat larger than the smallest ones of *C. stagnalis* (fig. 1*d*).

Of all species in the section Eu-callitriche *C. palustris* possesses the smallest chromosomes. In this species again we meet with plants, having 0 or 2 SAT-chromosomes (plate 3*f*, *g*).

The satellites are very small and are connected with the short arms of two homologous chromosomes.

It is a striking fact that several chromosomes in the metaphase are connected with each other by more or less broad, stained "threads" (plate 6*a*, *b*). Mostly the short arms of the chromosomes are attached to each other, but sometimes the short arm of one chromosome is joined to the long arm of another. The total number of joined chromosomes ranges from 6 to 18; they are generally divided into two or more groups. So it should be emphasized that not only homologous chromosomes are connected.

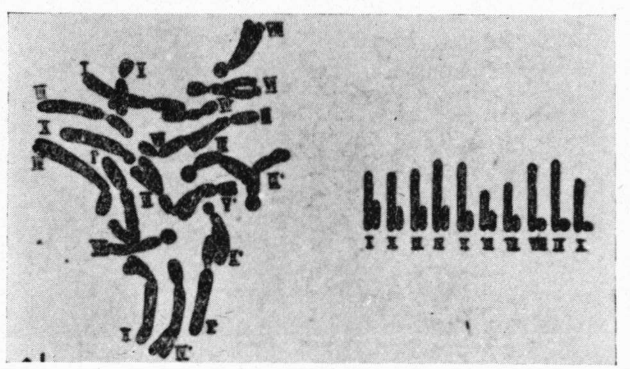

Fig. 4. C. palustris. After SOKOLOVSKAJA (1928). For explanation see text.

B. Meiosis

C. palustris (h.Sch. 5349)

In the waterforms, possessing well developed stamens, the meiotic division generally is entirely normal. Pairing is regular, ten bivalents are formed and consequently M_I and M_{II} are quite normal (plate 2*f*, *g*).

In several anthers, however, we meet with irregularities in the meiosis of the exterior PMC's; the chromosomes become more or less sticky. Hence in many ripe, apparently well developed anthers only the central pollengrains are normal in size and shape. In the landforms the stamens at best develop into a clavate body, showing in the upper part a few PMC's. In this case, however, a regular meiosis was never observed, the chromosomes being very sticky. Sometimes in older stages a few pollengrains have been seen, which are always shrunken.

C. Development of the ovule

C. palustris

The pistils of the investigated landforms all show abortive stigmata.

The ovules are anatropous. The first stages in the development are quite normal. The large EMC in prophase, dyads and especially the T-shaped tetrad (different from the linear tetrad Jörgensen mentions in *C. autumnalis*) have been seen several times (plate 5*a*). The number of chromosomes in the tetrad—when it could be counted —was 10.

Various times we observed a large cell lying below or somewhat at the side of the chalazal part of the tetrad (plate 5*b*, *c*). This cell, forming part of the surrounding tissue of the nucellus, must possess 20 chromosomes. To all appearance the tetrad is crushed by the development of this cell. In further stages remains of the four cells of the tetrad could be observed, lying above the enlarged somatic cell. Because the chromosomes in the observed metaphase plates always are very close together, only 17 chromosomes could be well counted (plate 5*b*, *c*).

The first divisions of the somatic cell were not observed, but in some ovules a large embryosac was seen with again a crushed mass of cells above it.

The chalazal part of this embryosac has a granulous content, the upper part is transparent. The border-line runs nearly across the middle. In the earliest stage of development observed, a large dividing nucleus was visible on either side of the border-line. Three antipods occur on the chalazal side. On the micropylar side only one nucleus could be distinguished, so either the embryosac is six-nucleate or the one or two present synergids soon disappear.

In older ovules a normally developed cellular endosperm is present. The germ lies in the centre of the endosperm, provided with a short suspensor. The chalazal haustorium is well developed and consists of 4 elongated cells (plate 6*c*). The apical haustorium is not clearly distinguishable. In the endospermcells about 20 chromosomes were counted.

CHAPTER III

MODIFICATIONS

The genus Callitriche shows a great variety of forms, just like many other waterplants. This is apparent principally in the vegetative organs.

The most remarkable thing in this respect is the difference between the land- and waterforms of one and the same species, but also the waterforms of one species can appear to us in manifold shapes, because the depth of the water, the speed of the current, the change of the seasons and the lightratio are of great influence on habit and leafshape.

So far as we know KÜTZING was the first to assemble a wide variety of forms of growth. The country round Schleusingen near Coburg, whence he gathered his material, was apparently a varied land, where *C. hamulata*, *C. platycarpa*, *C. stagnalis* and *C. palustris* grew in innumerable modifications. From the herbarium material collected by him (coll. Rijksherbarium, Leiden) the many drawings in Reichenbach's Iconografia botanica, and from his extensive systematical arrangement of the forms it becomes clear how intensely his attention was drawn to the polymorphy of Callitriche. In his field observations he remarks a.o. that when the environment dries up, waterforms can change into plants with quite a different habit. After Kützing several authors paid attention to the variation in habit and leafshape in Callitriche, as e.g. HEGELMAIER (1864).

Further some people tried to transform different forms of growth to each other by changing the environments. CLARKE (1859), ASKENASY (1872) and later JÖRGENSEN (1925) cultivated originally submerged plants in flowerpots and in this way obtained some landforms.

GLÜCK (1924) at last, gave a good survey of the influence of the depth of the water on the shape of the leaves and the lengths of the plants, based on numerous field observations. His data on *C. hamulata*, *C. obtusangula* and *C. verna* (*C. palustris*) can nearly all be checked. He, however, also considered *C. platycarpa*-plants as *C. stagnalis*, and this confusion makes his table and description of *C. stagnalis* practically useless.

To get a better survey of the richness in shape of the various species *C. hamulata*, *C. platycarpa*, *C. obtusangula*, *C. stagnalis* and *C. palustris* were observed during some years in the botanical garden "de Wolf" under varying circumstances. Of waterforms separated parts of homogeneous placcards were planted, of landforms as many cuttings of one plant as possible were planted in the several environments. Only for *C. palustris* separate plants had to be used as those are thin and little branched.

The plants were set in almost stagnant water of various depths, in running water, in moist soil, in "cowpuddles" shaded by the surrounding vegetation and in "cowpuddles" without surrounding vegetation. By altering the waterlevel, waterforms could on the spot grow into landforms and the other way round. Moreover, the habit and the leafshape during the seasons were observed.

As *C. obtusangula* in "de Wolf" only develops properly on a layer of ashes, so on a substrate diverging from the natural one, the habit- and leafchanges of this species were, during the years of observation, continually compared to those of specimina in the island of Texel. As far as it was possible the forms of growth in the cultures were also compared to those in the corresponding spots in nature for the other species.

In the survey following below only the most characteristic modifications are described, and we must always remember that the descriptions are only valid for certain plants under certain circumstances. We may, it is true, expect a fairly general validity supported by many fieldobservations, but this does not alter the fact that these extremely variable plants can place us face to face with surprises, again and again.

1. **C. hamulata** All plants from the village of Haren (prov. of Groningen)

a) In the several seasons

The plants lived in water of 30-40 cm. deep, with but very little current. This generally winterannual species forms exclusively linear leaves after having germinated in the autumn. The plants, growing quickly and branching, remain below the surface. In spring, at the beginning of the flowering period, the rosettes, floating on the surface, composed of spathulate leaves, appear after a few elliptic leaves (plate 7*a*).

During spring and summer spathulate leaves are formed, so that by the time the plants wither, the stems, reaching as high as the waterlevel, carry mostly spathulate leaves.

b) In water of about 20, 40, and 60 cm. deep

The plants in the spots 20 cm. and 40 cm. deep form rosettes floating on the surface with spathulate leaves, during the flowering period.

In deeper water the stems generally remain submerged, with only linear leaves. Sometimes slightly broader leaves are formed, close to the surface. Wholly submerged plants also flower and fructify amply (cf. pollination Ch. IV).

c) As landform

When the hollows, in which waterforms grow, are laid dry, the greater part of the stems perish. New, prostrate or ascendent shoots appear, with small elliptic leaves. Usually the landforms fructify abundantly (cf. Ch. IV).

A remarkable phenomenon was the growth of stalked fruits in some landforms. This was observed in the fields a.o. in a vegetation near Haren (1950) and along the rim of a cattlepond in Texel (1953).

In 1953 numerous landforms grew with stalked fruits in the cultures in "de Wolf". In November 1952 young waterforms had been brought to some "cowpuddles". The depth of the water was about 15 cm. during the wintermonths. The plants were offspring of a spontaneously grown *C. hamulata*-vegetation which, for a few consecutive years, occurred in two ditches in the botanical garden. The fruits of these plants were always sessile. During spring and early summer of 1953 flowering and fructification were abundant. The fruits were sessile, as before. In June the hollows were laid dry. The original stems withered and new shoots formed a patch of flowering landforms, in which about the middle of July numerous stalked fruits could be observed. The stalks had a maximum length of about 1 cm. The fruits principally grew on the branches lying flat on the substrate. The ascending stem-parts in the dense parts of the vegetation showed mostly sessile fruits. Sometimes non-stalked and stalked fruits alternated (plate 13*a*).

It will have to be examined more closely whether the possibility of forming stalked fruits is characteristic for all *C. hamulata*-plants under certain circumstances, or whether it is a hereditary trait of some individuals.

d) In quickly running water of about 20 cm. deep

In quickly running water floating stems, sometimes more than

½ m. long, are formed with only linear leaves. Those can grow to a length of about 4 cm. Rosettes do not occur in this habitat. Flowering and fructification proceed as usual (vide Ch. IV).

e) In sun and shade, waterdepth about 30 cm., with little current
In sunny places the manner of growing of this species is approximately the same as in shady ones. The leaves of the rosettes usually become yellow in the sun however, and the plants die sooner than in the shady habitats. By continually supplying cool wellwater the difference in temperature between the two places was but small.

2. C. obtusangula

a) In the various seasons
Plants from the island of Texel
Plants in running and almost stagnant water of about 30 cm. deep. *C. obtusangula* is a perennial, bearing full, floating rosettes in spring and summer during the flowering period, the leaves being rhombic (plate 8*a*). About October-November linear leaves are formed at last, after pairs of narrower leaves (plate 11). The many branches, growing in this period, all show the same type of leaf too. The species hibernates in more or less dense patches of branched stems, mostly remaining entirely submerged (plate 10).

b) In water of various depths
Plants from the island of Texel
In water only a few cm. to 30 cm. deep the stems form well developed floating rosettes on the surface. As this species was hard to grow outside the layer of ashes, observations in deeper water are missing. One plant having spontaneously come up in 1952 in the test-area, in about 60 cm. deep water, reached the surface with the tops of its stems in June 1953 and formed a few small rosettes with tiny lightgreen rhombshaped leaves. The stemleaves were linear. A few flowers did appear but fructification was not observed.

c) As landform
Plants from the island of Texel
The landforms show great likeness to the waterforms. When the habitat is laid dry during the flowering period, the original stems do not perish, so that the rosettes usually remain clearly visible during some dry weeks. Growth is very tardy. New leaves in the rosettes are usually narrower than the rhombshaped ones of the waterforms, those of new shoots are narrow elliptic. The colour turns a yellowish green. *C. obtusangula* is probably, also on account of the somewhat fleshy leaf better able to stand drought than the other species. Waterforms often remained lying on the dry soil for months without showing much change. Also in very sunny habitats e.g. in dried up cattleponds in Texel they maintained themselves excellently.

Plants from the province of Zeeland
For this type the same holds good. The stems and compact rosettes

with the firm, circular, sometimes truncated leaves are well proof against desiccation.

d) In quickly running water, depth about 30 cm.

As cultivating this species in the botanical garden is possible only in the presence of a layer of ashes, and this is entirely lacking in quickly running parts of the brook, it was not possible to follow the behaviour of *C. obtusangula* sufficiently. Anyhow specimina were found in Texel during April and May in a swiftly flowing watercourse from the dunes. A rosette was not formed, the topmost leaves were narrow elliptical to narrow rhombshaped. Flowers were not found.

e) In sun and shade

Plants from the island of Texel in 20 cm. deep water with little current

No clear difference was to be observed between the two forms, the rosettes remained a fresh green.

3. **C. platycarpa**

a. In the course of the seasons

1) Plants from Haren (prov. of Groningen) and Arcen (prov. of Limburg). In 30-40 cm. deep water with very little current. During the winter one generally sees stems with linear leaves, as well in old hibernating plants as in young specimina germinated in autumn. In spring, after a few narrowly elliptical leaves floating rosettes with nearly elliptical leaves are found (plate 12).
2) In quickly flowing water of about 20 cm. deep. Plants from Haren (prov. of Groningen) and Arcen (prov. of Limburg). During the whole year elliptical leaves are seen on these plants. Sometimes young sidebranches originally bear linear leaves, but only a few pair of them.

b. In water of various depths

Plants from Haren (prov. of Groningen), Arcen (prov. of Limburg) and Winterswijk (prov. of Gelderland)

Up to a depth of 40 cm. the plants form floating rosettes on the surface (plate 7*b*). At greater depth they remain submerged. The leaves are then linear and fructification does not occur (cf. Ch. IV).

c. As landform (plate 13*b*)

Plants from Haren (prov. of Groningen)

The landform of this species sometimes is very similar in habit to that of *C. hamulata* or of *C. stagnalis*. The creeping or ascendent stems bear small, more or less broad elliptical leaves and there is no rosette. Sometimes the seeds turn a lighter shade than those of the waterform and the wings somewhat broader. On account of this fact they have a tendency to resemble the fruits and seeds of *C. stagnalis*.

d. In a swift current

Plants from Haren (prov. of Groningen) and Arcen (prov. of Limburg)

The stems become floating, quite ½ m. long, limp, with large, elliptical, somewhat flabby leaves. A floating rosette is not formed, on account of the continuous movement of the water the leaves are nearly all submerged. Sometimes a few flowers appear, but owing to the fact that no pollination can take place under water, no fructification occurs.

e. In sun and shade
Plants from Haren (prov. of Groningen). Sunny habitat about 30 cm. deep with little current. Shady habitat: "cowpuddles" with about 15 cm. of water.
The rosette leaves of the plants in the sunny habitat usually turn yellowish, rather small and a little hard. The leaves of the shadeforms are big, limp and fresh green. In the "cowpuddles" shaded by grass sometimes rosettes developed with nearly circular leaves. These plants have therefore become vegetatively greatly similar to *C. stagnalis.*

4. **C. stagnalis** Plants from Schipborg (prov. of Drenthe)

a. During the seasons
In the "cowpuddles" *C. stagnalis* usually perishes in winter. Neither in the brookvalleys of Drenthe is this plant to be found during this period. Now and then a few specimina remain alive in the "cowpuddles" of the botanical garden "de Wolf", but in running water they hibernated exceptionally well. The leaves, in summer broad elliptical to nearly circular (plate 9*a*), grow slightly narrower in winter, but linear leaves I never observed on *C. stagnalis.* Compared to the other species *C. stagnalis* remains almost constant in habit and leafshape all the year round and under all sorts of conditions, which already struck Kützing.

b. In various depths of water
This species changes but little, up to a depth of about 35 cm. In the deeper parts the plants did not remain alive long. The forming of linear leaves was never observed.

c. As landform
The leaves are smaller in size than in the case of the waterforms, but remain nearly circular.

d. In flowing water
This species is not subject to any essential change of leafshape and habit. The ♀ flowers—perhaps because they are not fertilized—present longer stigmas than the plants in quieter water. Besides, the stigmas generally do not bend down, but remain a little patulous, on account of which they begin to resemble the flowers of *C. platycarpa.*

e. In sun and shade
No distinct differences could be ascertained.

5. **C. palustris.** Plants from Schipborg (prov. of Drenthe)

a. During the seasons

Plants in "cowpuddles" with about 10 cm. of water and as landform. This plant, a summer annual in our country, forms pairs of leaves after germination in spring, with linear leaves. When the tops of the stems reach the surface, floating rosettes with spathulated leaves are formed (plate 9*b*). Trying to make this species hibernate never met with any success. Also the landforms perished in autumn, in all cases.

b. In various depths of water

This frail, delicate plant only grows as a waterform in stagnant water of about 20 cm. depth and then forms rosette-bearing stems. The flowers are usually of normal structure in this form (cf. Ch. IV).

It proved impossible to grow *C. palustris* at greater depth. Plants with lengths of more than about 25 cm. are therefore an exception. Only once a very sturdy specimen was found in herbarium material, viz. from Maikeniemenjoki (Finl.). Its length was about 60 cm.

c. As landform

C. palustris mostly occurs as landform. The plants are very small, with tiny, narrowly elliptical or obtuse-linear leaves. Vegetatively they can resemble small landforms of *C. hamulata* and *C. platycarpa*. The flowers are greatly reduced (cf. Ch. IV).

d. In swiftly flowing water

It proved impossible to cultivate this species in the flowing current of the experimental brook. The fragile stems with their frail habit do not seem able to stand a strong movement of the water. In his investigation along the skaror-coast of Finland, LUTHER (1951) observed that *C. palustris* always grows in places out of reach of the wash of the waves.

The species only grows in small, shallow quantities of water (cf. Ch. V).

e. In sun and shade

No distinct differences could be observed.

CHAPTER IV

POLLINATION AND REPRODUCTION

Most species of the section Eu-callitriche show a normal sexual reproduction, only *C. palustris*—when a landform—is an apogamous species.

In the species, showing a normal reproduction, two different manners of pollination occur: in *C. obtusangula*, *C. platycarpa* and *C. stagnalis* pollination is aerial, in *C. hamulata* it is submerged.

1. C. obtusangula, C. platycarpa and C. stagnalis

As for the aerial pollination: already older authors, as Ruprecht and Lebel had observed this fairly accurately, so that we can be short on this subject. The stamina rise above the floating rosette. When the anthers dehisce, the yellow pollengrains are strewn over the surface of the water and remain floating there. The stigmas, emerging partly from the water, in this way easily come into contact with the pollengrains. Sometimes the pollen drops straight on to the stigmas of a neighbouring flower. No sign of entomophily, as LUDWIG (1881) suggested, was seen.

After fertilization the overblown flowers gradually submerge owing to the further development of the rosette, and so the fruits ripen under water. The pollengrains of this species are provided with a distinct exine, covered with little warts. The shape differs as to the species. In this way *C. obtusangula* has ellipsoidal pollengrains and *C. stagnalis* nearly globular ones, whilst those of *C. platycarpa* show a great variety of shape. Some are nearly globular, others rounded tetrahedral or short-ellipsoidal.

In the case of landforms we also find normal pollination and fructification.

2. C. hamulata

In *C. hamulata* the situation is quite different. This species does form rosettes on the surface in not too deep, quiet water, but the occurrence of well developed flowers is not restricted to the occurrence of rosettes, as in the case of *C. obtusangula*, *C. stagnalis* and *C. platycarpa.* The first flowers of *C. hamulata* appear in the axils of the lower pairs of leaves. In the leafaxils higher up we gradually find younger stages of development of the flowers.

In the rosettes as well flowers at last appear, but their position and structure is always such as to make them quite submerged.

Ruprecht and Lebel also knew of the developing of flowers under water, and had at the same time observed the always abundant fructification.

BEGER (1932) considers the occurring of submerged flowers a characteristic, specific for *C. hamulata*, and—taking into consideration the abundant fructification—he suggests submerged pollination, but the observation of this event was still lacking. And yet KÜTZING (1832) and HEGELMAIER (1867), about a hundred years ago, were very close to solving the enigma of the submerged pollination. Kützing gave an excellent—though very short—description of the flowers in Linnaea. The position of the threadlike stigmata in regard to the stamen and also the bending of the stamen towards one of the stigmata at the time of pollination, was observed by him quite accurately. Therefore it is remarkable that the position of the styles in this flower was misdrawn in Reichenbach's Iconographia botanica as well as in the Icones.

Hegelmaier also distinguished the existence of entirely submerged flowers in *C. hamulata* and even found anthers in which there occurred pollengrains with a "farblose und glatte Aussenhaut" and specimina for which he "die Anwesenheit einer Exine nicht konstatieren konnte". He imagined however that this pollen was not yet ripe and then he comes to the conclusion in 1867 that he is convinced by his observations that *C. hamulata* has yellow pollen and that the normal pollination is aerial.

Let us study the flowers of *C. hamulata* closer after these data from literature.

The nearly sessile ovary bears at the top 2 transverse threadshaped stigmata, directly reflexed at the base. They are directed obliquely backwards, so that on either side of the stem they protrude slightly under the leafaxil with the ♂ flower (plate 14*a*). The small stamen, originally visible as a green sessile little globe, possesses a quickly growing filament which soon bends towards one of the stigmata, so that the reniform unilocular anther comes to rest against that stigma (fig. 5).

Against the time that the anthers are going to dehisce, the wall is coloured light yellow. The pollination now proceeds as follows: at the top of the ripe anthers there appears a longitudinal rent and a colourless very coherent mass of pollengrains becomes visible. These pollengrains are globular and very thin-walled. Neither of an exine, nor of a walldesign anything can be seen. They are nearly full of starchgrains (blue with KJ). Not long after the grains have come into contact with the surrounding water, the pollentubes begin to develop (fig. 5). Within a few hours there appear long winding tubes, forcing their way into the stigmatic tissue. The transition from style to stigma is not quite clear in Callitriche; most probably the whole organ works as a stigma, as at the base germinating grains were observed as well.

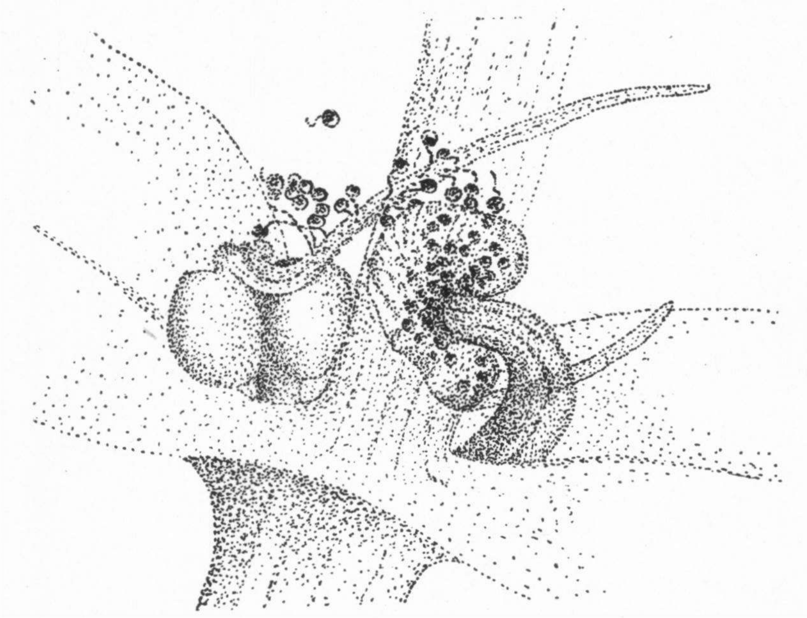
Fig. 5. C. hamulata. Submerged pollination.

Usually the mass of pollen in an anther remains very coherent, sometimes also smaller or larger ball-like groups of germinated pollengrains detach themselves and remain suspended in the water.

Landforms too usually fructify well. Often we can find little drops (usually due to dew or rain) in leafaxils, in which pollengrains have germinated.

The colourless pollen without exine also occurs in other waterplants, for which it has been stated that the pollination is submerged. In *Zannichellia* and *Najas* the grains are globular as in *C. hamulata*, in *Zostera*, *Posidonia*, *Halophila* and *Cymodocea* the pollen is confervoid (ROSE 1887, CLAVAUD 1878).

As for *Najas*, JÖNSSON (1883) mentions that the pollen is "helt fullpropade med stärkelse korn", while HOFMEISTER (1852) and MAGNUS (1894) saw that it already germinates before it becomes detached from the anthers. So these data show much resemblance to what was observed for *C. hamulata.*

3. C. palustris

In the waterform of *C. palustris* we usually find fairly normally built flowers in the rosettes. The ♂ and ♀ flowers nearly always develop together in one leafaxil in this species (plate 14*c*; fig. 11*d*).

The stamina are small, but usually well developed, though the anthers do not always dehisce. The small globular pollengrains are also generally wellshaped for the greater part. The stigmata are erect-patulous, several times longer than the ovary, sometimes nonequal in size. As *C. palustris* generally habitates in places exposed to varying waterdepths and especially dessication, outspoken waterforms do not occur so often in nature. As a rule, after a longer or a shorter period transition- and landforms develop.

In the landforms the stigmata of the ♀ flowers are reduced to short stubs (plate 14*b*); the stamina are sometimes still extant, more or less clavate, in which yet a few shrivelled pollengrains may develop (plate 14*c*). Generally also this remainder is missing. Nevertheless fructification is abundant.

In literature we found the reduction of the ♀ flowers mentioned in "Flora des Puschlav" by BROCKMANN-JEROSCH (1907) only. The author found *C. palustris*-plants in the Puschlav area with "abortierten Narben", which however fructificated excellently.

Even if in well developed waterforms normal pollination is perhaps possible, in the landforms this way of reproduction must be considered out of the question owing to the reduction of stamens and stigmata. By anatomic and cytological investigation of the ovule it proved probable that in this landform apospory exists (cf. Ch. II).

CHAPTER V

GEOGRAPHY AND ECOLOGY

1. **C. hamulata**

DISTRIBUTION (cf. appendix I, 1)

The Netherlands

According to the Dutch distribution map (map 1) *C. hamulata* is best represented in the provinces of Drenthe, Overijssel, the eastern part of Utrecht, Gelderland, N. Brabant and in a few Northsea-isles. This area seemingly shows but few peculiarities. If, however, we compare this map to a soilmap of the Netherlands (map 2), then it is striking that the localities of *C. hamulata* are situated on pleistocene sandy soils. Even in smaller, isolated pleistocene areas, as e.g. Vollenhove, Hippolytushoef, the country south of Nijmegen, the species occurs. In the province of Groningen, where we made many an investigation for *Callitriche*, it is only known to us from Marum, also

Map 1. C. hamulata. Distribution in the Netherlands (cf. app. I, 1).
• herb. specimens + living plants

Map 2. Sandy soils in the Netherlands (⁙). (Partly after MÖRZER BRUYNS and WESTHOFF, 1951).

situated in the pleistocene sandy part, and further from many finds to the south of the town of Groningen, all situated on the north elevations of the Hondsrug. In Drenthe *C. hamulata* a.o. occurs on the eastern slope of the Hondsrug. As for the provinces of North- and South-Holland we only know *C. hamulata* from the row of dunes of a few Northsea-isles and also from Loosduinen and Oegstgeest. These last localities are situated on sandy soil of the old dune landscape. In South-Limburg and on river clay soils and marine clay soils the species is entirely missing.

The water of these soils is generally neutral to slightly acid. The pH's of the localities reflect this (cf. appendix II, table I). The content of chloride is in most cases below 100 mg/L. Only a few findspots in Texel have a slightly higher percentage. Hippolytushoef forms an exception with 825 mg Cl′/L (cf. appendix II, table I). The extensive vegetation existing there makes us suppose that *C. hamulata* can also develop in oligohalinic water, though the germination of seeds in water of such Cl′ content did not succeed so far (cf. Ch. VI). The soils in which *C. hamulata* occurs are poor in lime.

Outside the Netherlands

As for the distribution abroad (map 6) there are several localities in Gr. Britain, France, Germany and Denmark. From Sweden we saw only a few herbarium specimina. According to Samuelsson—who described and determined *Callitriche hamulata* well—the species is especially common in the south, while he also gives several localities along the southern part of Norway's Westcoast.

From the Faer-Oer, Iceland, Finland, West-, South- and East-Greenland we saw several plants in the Copenhague herbarium. In Greenland *C. hamulata* occurs as far north as 68° 42″ N.L.

From Italy and Switzerland the materials were very scarce, while Poland, Austria and Czecho-Slovakia were not represented. Samuelsson too mentions but few localities in these countries. As the most easterly findspot of *C. hamulata*'s area he considers the Bohemian Wood. The plant found there is probably the specimen from the herbarium Delessert, which bears the determinationlabel of Samuelsson. Recapitulating we may say with Samuelsson that the European region—in so far as it is known at present—has a somewhat atlantic tendency. In the central European provinces it practically entirely confines itself to the western and northwestern part of the baltic sector. In the alpine sector there are only few localities.

Taking into consideration the existence in the continental parts of Scandinavia (Samuelsson), in Greenland and in Iceland, we certainly do not have to deal with a typical atlantic plant. From its appearing there it also becomes clear that *C. hamulata* is not limited to a climate with mild winters. Also in our country the species, usually a winter-annual, is very frostresisting. During a few consecutive years we observed that plants, grown into a layer of ice,—also floating—appeared fresh and green after the thaw had set in and normally went on growing.

As for the geological structure of the soil of the foreign localities we have at our disposal only a few data, noted down on herbarium labels. Thus *C. hamulata* specimina come from the Vosges, out of brooks across granite (e.g. the specimen from Gerardmer, dep. Vosges, h.Del.), which we observed in that country as well. Specimina from the Bohemian Wood (h.Del.) grew on gneiss, the plants in the Regnitz near Bamberg (a.o. h.Del.) on sandy soil. In Denmark the species occurs on pleistocene sandy soil. If we study the whole distribution area, it makes the impression that *C. hamulata* has a preference for poor soils. Calcareous soils it seems to avoid. So Samuelsson informs us that *C. hamulata,* in South-Sweden, is lacking in the calcareous cultural areas, as well as in the calcareous parts round the Oslofjord. In South-Limburg (cretaceous district) it was not seen either.

It moreover entirely tallies with our observations in the botanical garden "de Wolf" during the period from November 1952-August 1953, when it proved that as well land- as waterforms of *C. hamulata* developed badly in hollows with lime-marl. Most plants withered, a few remained very small with yellow leaves, while the plants in the neighbouring "cowpuddles" did very well in the normal soil or on a layer of peat. *C. stagnalis* and *C. platycarpa* showed a normal development on the marl.

ENVIRONMENT AND VEGETATION

The Netherlands

C. hamulata is found in the Netherlands mostly on a clean sandy soil in brooks (Arcen, Wolfheze, Loenen, Drenthe). Also in a swift current the plants can form dense vegetations with long floating stems. Sometimes we find *C. hamulata* in the brooks together with *C. platycarpa.* On the island of Texel we saw *C. hamulata* in flowing water in or along the dunes. It was further found in a few cattleponds with clear wellwater, not used as such however. In all this as good as oligotrophic water no other waterplants were found. In one cattlepond it grew together with *C. obtusangula* and *C. platycarpa* as landforms.

On the borders of the pleistocene, where the oligotrophic water mixes with the more eutrophic of the neighbouring area (Drenthe, eastern slope Hondsrug) we find *C. hamulata* in ditches with gently flowing to nearly stagnant water. Here the species grows in small clumps amidst an often dense vegetation of *Elisma natans* and *Hottonia,* sometimes with *Elodea* and *Menyanthes* along the edge. We may ask whether in this case instead of *C. palustris* from the Hottonietum palustris (WESTHOFF, 1946), not *C. hamulata* is meant. *C. palustris* in this association certainly never occurs. This biotically weak species requires quite a different kind of environment (cf. sub 5 of this chapter). In so far as we are now able to ascertain, the species *C. hamulata,* however, may be called characteristic for the Hottonietum.

In the botanical garden "de Wolf" *C. hamulata* occurred spontaneously and in great quantities during some years in two ditches with rainwater, not communicating with other watercourses. After the eutrophic water had however been drained off from the pond through these two ditches (1950) a quickly spreading vegetation of *Myriophyllum spicatum* appeared, while *C. hamulata* lost ground. Continually removing the *Myriophyllum*-plants was not able to prevent *C. hamulata* from disappearing nearly entirely from these ditches. Seeing that *C. hamulata* occurs in oligotrophic-mesotrophic water, the affluence of eutrophic water was probably primary for its vanishing, while moreover the species could not hold out against *Myriophyllum.*

C. hamulata is the only species of the Dutch Callitriche's that can live for years in water, poor in nutrients. In our indoor-cultures the plants proved to keep for years in rainwater, without its being refreshed. In these circumstances *C. hamulata* becomes perennial, so does not die in late summer, neither does it flower, but it remains a fresh green and grows on very slowly. Thus specimina, gathered in 1950 and in 1951, are still in our possession.

Outside the Netherlands

From abroad only a few data about the accompanying vegetation of *C. hamulata* are at our disposal. Moreover, it is often hard to discern whether the *Callitriche* was rightly determined, so that making use of such data might give rise to incorrect conclusions. Fairly reliable we consider the report of Nordhagen, mentioned by Samuelsson, concerning lower lake Sikkisdale on the western border of Central Norway. In this lake, situated at the height of 1000 m. in the birch-zone, *C. hamulata* occurred together with *Isoëtes lacustris, Sparganium affine* (sterile), *Potamogeton alpinus, Juncus supinus, Utricularia minor* and *Myriophyllum alterniflorum.*

Another, also oligotrophic community IVERSEN (1929) mentions from Praestesø, a "Heidesee", to the west of Varde in western Jutland. As became apparent from herbarium investigations *C. hamulata* is common in the surroundings of Varde. Besides this plant Iversen found in Praestesø: *Isoëtes lacustris, Sparganium affine, Scirpus fluitans, Juncus supinus, Elatine hexandra, Myriophyllum alterniflorum, Lobelia dortmanna, Littorella uniflora, Helosciadium inundatum, Potamogeton filiformis* and *Potamogeton crispus.* The water was neutral according to Iversen.

2. **C. obtusangula**

DISTRIBUTION (cf. appendix I, 2)

The Netherlands

From the distribution map of the Netherlands (map 3) it appears that *C. obtusangula* only occurs in the wadden district, the haff district and the river district (map 4). In this last area it is especially found in the province of Zeeland; only here and there along the rivers are localities (Zwolle, Leersum, Ooypolder near Nijmegen, Amby, Roermond).

Outside the Netherlands

When studying the European herbarium data more closely we come to the conclusion, together with Samuelsson, that the geographical distribution is a mediterranean-atlantic one, radiating to the area round Geneva (map 5). That *C. obtusangula* also occurs in the cantons Geneva and Wallis, need not cause any surprise, as more mediterranean plants have forced their way into this country through the entrancegateway of the Rhonevalley (Weiss, 1934).

Map 3. C. obtusangula. Distribution in the Netherlands (cf. app. 1, 2)
• herb. specimens + living plants

Map 4. River-, haff-, wadden- and dunedistrict in the Netherlands (after Van Soest, Heukels en Wachter, Schoolflora v. Nederland).
░ River district ▨ Haff district
■ Wadden district ☰ Dune district

From N.W. Germany no localities are known to us, and in the herbarium at Copenhague no *C. obtusangula* from Denmark was present, so that we must take it for granted the species does not exist there.

In the northeast of the area, the northern Netherlands will form the boundary; to the west, in Great Britain, it is possible that it grows at a latitude yet a little heigher, in view of the data, giving a reliable-looking impression, in the British flora of Clapham, Tutin and Warburg (1952) where they mention as localities a.o. Lancashire and York. We have however not yet seen herbarium specimens of this area.

C. obtusangula is a perennial. It continues to grow in winter with the aid of the submerged stems and continuously enlarges its area during this period.

In the mild rainy wintermonths of the area only a few days occur with a temperature below 0° C and it was to be taken for granted that this outspoken mediterranean-atlantic plant would not prove very frostresistant. Now the Groningen localities lie in an area with more than 11-12 icy days a year, while the frostperiod in Denmark averages about two months. It is very well possible that this lengthy frostperiod is the cause that *C. obtusangula* is absent from Denmark.

An indication that *C. obtusangula* is indeed susceptible to temperatures below 0° C, is to be found in the following observations in the botanical garden "de Wolf" during the winter 1952/1953. [1])

In the experimental brook there were also a.o. several extensive vegetations of *C. obtusangula* of Texel, the stems of which almost reached the waterlevel in the shallow parts. Already after a few icy days it became apparent how much more these plants were suffering than e.g. the interlying specimina of *C. stagnalis* and *C. platycarpa.* All leaved parts, becoming frozen, rotted after the thaw had set in. The stems, creeping in the mud, having had no contact with the ice, sprouted again nicely after the period of frost. Much damage was done to the floating plants; owing to the fact that they were entirely crusted with ice the damage was much greater than in the case of the rooted plants. After having produced a hesitating sprout all the test-plants succumbed in the spring. If we freeze *C. obtusangula* overnight in the refrigerator and thaw it during the day very gradually, at a temperature of a few degrees above 0° C, then we see a similar spectacle: the plants are quite black and limp after this has been done once or twice.

It is remarkable that *C. obtusangula* from Rottum (prov. of Groningen) showed hardly any frostdamage. The plants at issue were growing in two identical "cowpuddles" and quite filled them. Eight specimina from Texel grew under quite the same circumstances in the same area. On account of the shallowness of the water (about 10 cm.) the whole plant was sometimes almost covered by ice and this caused the already mentioned symptoms of perishing in nearly all specimina from Texel, after the thaw had set in. In the plants from Rottum, however, practically no damage could be found, nearly all the leaves remained a fresh green. Whether we have here a race with greater frostresistance or that an unknown incidental circumstance played us parts will have to be ascertained by further observations.

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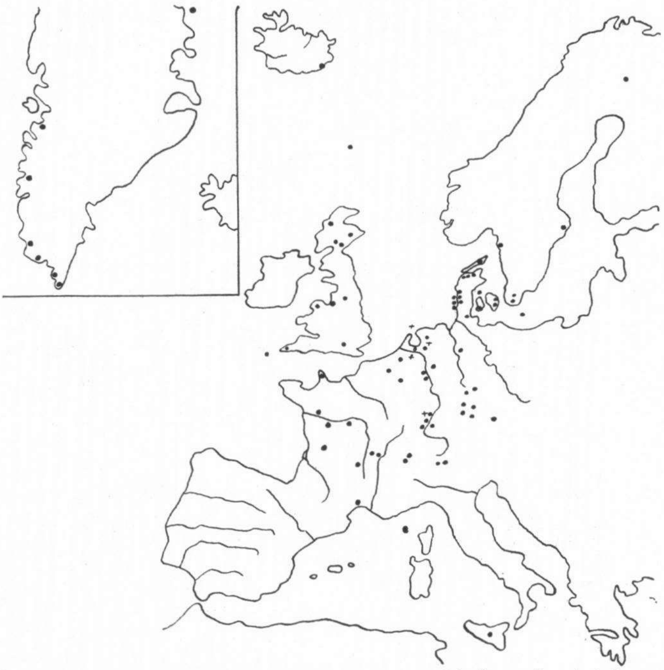
[1] In the winter of 1953/1954, when the frost penetrated to the bottom of the experimental brook, nearly the whole culture perished.

Map 5. C. obtusangula. Distribution in Europe and on the north coast of Africa (cf. app. I, 2). • herb. specimens + living plants



Map 6. C. hamulata. Distribution in Europe and Greenland (cf. app. I, 1). • herb. specimens + living plants

As was already observed (Ch. III) *C. obtusangula* resists desiccation much better than the other species. It maintains itself in the Netherlands as a landform, also in very sunny habitats. But data about its conduct during the dry warm summermonths in the mediterranean area are entirely wanting.

Environment and Vegetation

The Netherlands

In the ditches, in which we find *C. obtusangula* in the haff district of the Netherlands (prov. of Groningen, marine clay soils on the isle of Texel), we usually also find *Potamogeton pectinatus*, *Zannichellia palustris* ssp. *pedicellata*, *Enteromorpha intestinalis*, further *Lemna minor* and *L. trisulca*, *Phragmites*. In dried up mud of such ditches (a.o. the watercourse to the Slufter, Texel) there moreover often occurs a rich vegetation of *Scirpus maritimus* and *Schoenoplectus tabernaemontani*, between which a good sized vegetation of *C. obtusangula* landforms is to be found. Near den Hoorn on Texel, *C. obtusangula* was found in the spring of 1951 together with a smallflowering "Batrachium", which we identified as *Ranunculus tripartitus* DC. In the dune area of Texel we sometimes find *C. obtusangula* together with quite different plants, viz. *Hydrocotyle*, *Mentha aquatica*, *Echinodorus ranunculoides* etc.

The occurrence together with plants characteristic for brackish water, like *Zannichellia*, *Enteromorpha* (characteristic species of the alliance of Ruppion Maritimae Br-Bl) and *Scirpus maritimus* (characteristic species of Scirpetum maritimi Tx), besides the distribution in haff- and wadden district and the Zeeland part of the fluviatile area gave rise to the suggestion, that *C. obtusangula* is fairly salt-tolerant. Remarkable in this respect is the isolated locality Hoogkerk (prov. of Groningen) where in summer so much salt groundwater is present that a saltwater swimmingbath could be made and the cattleponds in the surroundings become unfit for use.

The water of the localities have a Cl′ content from 100 to about 2000 mg/L (cf. appendix II, table II). In ditches in or near the dune area of Texel the content of chloride may be less than 100 mg/L (samples 12, 18, 19). So these localities may be considered as appertaining to fresh water. From these facts we can gather that *C. obtusangula* is especially a plant of oligo-mesohalinic water. In the mesohalinic area it occurs together with *Zannichellia palustris* ssp. *pedicellata*, *Scirpus maritimus* etc.; in more oligohalinic water it can grow together with *Echinodorus*, *Hydrocotyle*, *Mentha aquatica*.

From the germination tests as well, described in Ch. VI, it appears that with a Cl′content of about 3000 mg/L the percentage of the germinating seeds is still high (71-88 %). Less common seems to be *C. obtusangula* in fresh water. It then principally remains restricted to the dune areas. In the freshwater cultures obstacles presented themselves. Only in a thick layer of ashes in the brook of the botanical garden "de Wolf" an abundant vegetation occurred.

The water of the localities is generally neutral-slightly alcalic (cf. appendix II, table II). *C. obtusangula* growing in Zuid-Beveland (prov. of Zeeland) differs from the other specimina found in the Netherlands in leafshape and in the presence of 2 SAT-chromosomes; it is stated in an environment richer in Cl′ than the plants from Texel and Groningen. According to VAN 'T LEVEN (1952 unpubl.) the Cl′ content can rise as high as 5000 mg/L in Zuid-Beveland. Also in cultures it is distinctly more salt-tolerant than *C. obtusangula* from Texel (cf. Ch. VI). We only call to mind here the fact that the seeds of the plants from Texel do not germinate in sol. 10 (6750 mg Cl/L). The seeds of the Zeeland plants however germinate abundantly in it.

Outside the Netherlands

In the west of France too and in the mediterranean area *C. obtusangula* grows in places comparable as for the vegetation with our brackish-water areas. In the department Morbihan e.g., where *C. obtusangula* was first described, grow a.o. *Triglochin barrelieri, Potamogeton pectinatus, Ruppia rostellata, Zannichellia dentata, Zostera nana,* further *Statice* sp., *Sonchus maritimus, Polygonum maritimum* etc. (LE-GALL, 1852).

3. **C. platycarpa**

DISTRIBUTION (cf. appendix I, 3)

The Netherlands

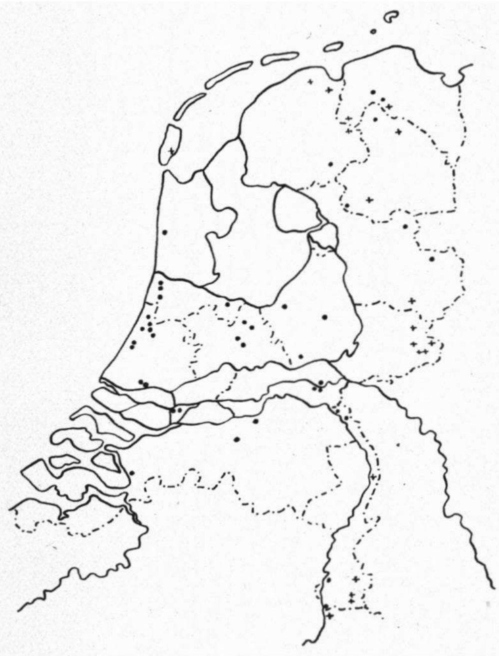
This species, new to the Netherlands, is remarkably enough the most common in the low lands. It occurs—except in Zeeland— in all provinces (map 7).

Because *C. platycarpa* is often gathered in sterile condition or with unripe fruits, numerous herbarium specimina cannot be identified with sufficient certainty. This is especially a handicap when fixing the foreign regions, for which one has entirely to rely on herbarium data. The temptation exists that one starts to identify plants solely by habit and leafshape—a temptation which some authors have not quite been able to resist—but, taking into consideration the great variability this cannot be justified for any specimen. Added to this is the drawback that in France plants, in all probability belonging to waterforms of *C. platycarpa*, show similarities with *C. stagnalis* in fruitform and sometimes also in habit. Samuelsson met with the same difficulty in his researches. It is very well possible that other climatological circumstances and other soil structure cause such a modification, but it is just as well possible that here a genetically differing form is concerned, which can only be stated by cytological research and culture experiments. As this was not possible so far, these dubious plants were not noted down on the distribution list.

Outside the Netherlands

Most findspots out of the Netherlands lie in Germany and Denmark. Further *C. platycarpa* occurs in Sweden, here and there in Switzerland and Czecho-Slovakia. From Finland, western Russia and a few

Balkan countries there were some plants in herbaria. In the Iceland and the Greenland herbarium material *C. platycarpa* was not found. Neither in the higher parts of the Alps does it seem to grow, which Samuelsson also tells us. It gives an impression that it habitates the lower regions in Europe (map 8).



Map 7. C. platycarpa. Distribution in the Netherlands (cf. app. I, 3).
• herb. specimens + living plants

Map 8. C. platycarpa. Distribution in Europe (cf. app. I, 3).
• herb. specimens + living plants

ENVIRONMENT

The Netherlands

In the Netherlands we find *C. platycarpa* in stagnant water and in flowing, on sandy soils, clay soils and on the calcareous soils of Zuid-Limburg. In the field it is a freshwater plant, also in the coastal range it rarely occurs in water which a Cl′ content higher than 100 mg/L (cf. appendix II, table III). In that case it sometimes grows together with *C. obtusangula* (Haarlem, Dokkum, Oude Schild in Texel). The species is missing from Zeeland and from the typical brackish parts of the haff- and wadden district.

The pH in the series of samples varied from slightly acid to slightly alcalic (cf. appendix II, table III).

As to the richness in nutrients of the water, we find *C. platycarpa* mostly in mesotrophic-eutrophic water, together with *Elodea, Ceratophyllum submersum* (shallow water) and sometimes with *Myriophyllum* *spicatum*, *Potamogeton natans* and *Nymphaea alba* (at the edge of deeper water). Even in polluted water *C. platycarpa* can subsist (ditches along farmhouses). Nevertheless the species is also found in oligotrophic water on clean sandy soils (a few places near Haren, eastern part of Gelderland, the Veluwe and northern Limburg). It may then grow together with *C. hamulata.* Also in calcareous areas we can find *C. platycarpa* (Zuid-Limburg, Belgian side of Sint Pietersberg).

Whether the specimina from brooks (only to be cultivated further in flowing water) represent another ecotype, must be investigated more closely.

Resuming we may say that *C. platycarpa* gives an impression of being a freshwater plant in the lower regions of Europe, where it proves to be fairly ubiquist.

4. **C. stagnalis**

Distribution (cf. appendix I, 4)

The Netherlands

This species does not seem to be very common in our country. We found it in the brookvalley area near Schipborg (prov. of Drenthe) and near Lieveren (ib.). Further living material was produced from the Biesbos (prov. of Zuid-Holland and Noord-Brabant). From the surroundings of this latter area there were also several herbarium plants. The other herbarium data originate principally from brookvalley areas (Coevorden, de Lutte, Renkum, Ruurlo) and from places along the big rivers (Utrecht, Vreeswijk, Nijmegen, Middachten, Leiden, map 9). From the marine clay areas, from peat soils and from Limburg no findspots are known. Interesting is the recent find of Reichgelt in Terschelling, one of the very scarce *C. stagnalis* localities on our Northsea-islands. It was to be expected there, as *C. stagnalis* is common on Denmark's westcoast and also occurs in Borkum, but neither in Texel nor in Ameland did we succeed in finding specimina of the species.

Outside the Netherlands

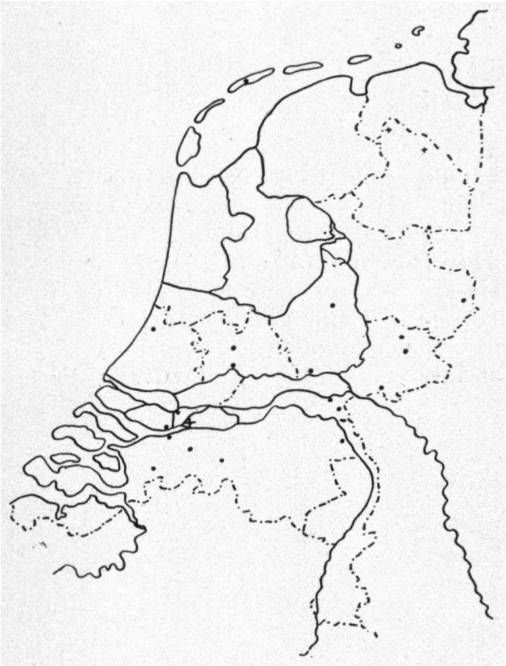
As for the other countries of Europe, we saw herbarium material from Sweden, Norway, S.W. Iceland, the Faer-Oer, Great Britain, France, Portugal, Spain, Italy, Switzerland and Germany (map 10).

Also in those countries *C. stagnalis* often occurs along the coast or near estuaries (Trondheim, Göteborg, Rörvig, coast of Jylland, Manche, Nantes, Vendée, Oléron, Bordeaux, Bastia, Ajaccio, Espinho, N. coast of Spain, Minorca, Venice, Messina, Bremen, Rügen, Borkum, Cumberland and Somerset, coast Faer-Oer, S.W. coast of Iceland). Inland it occurs in rivervalleys (Paris, Epinal, Toulouse, Coimbra, Rheinfelden, Cleve, Padova), in brookvalleys (Schleusingen). Here and there it occurs at greater height, as in the Haute Savoie and in Switzerland, but principally along the lakes there (Lac Majeur, Lac de Muzzano, the Lake of Geneva).

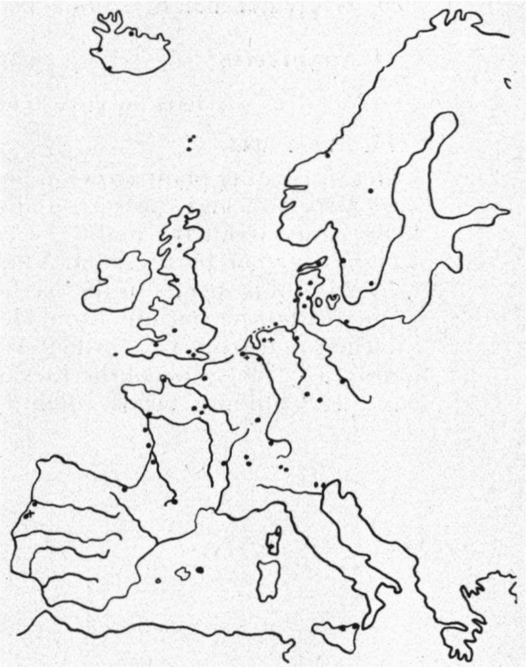
ENVIRONMENT AND VEGETATION

About the factors of the environment of the habitats of *C. stagnalis* little is as yet known, the same holding good for the accompanying vegetation of plants.

In the Biesbos it grows in the mud of creekbanks in the "kleine kreekoever gezelschap"1) belonging to the Sparganion. It further grows in tidal woods (Alnion).1) In a few cases it appears here together with *C. obtusangula*. In France and Great Britain this is the case too.



Map 9. C. stagnalis. Distribution in the Netherlands (cf. app. I, 4).
• herb. specimens + living plants



Map 10. C. stagnalis. Distribution in Europe (cf. app. I, 4).
• herb. specimens + living plants

In the brookvalley area in Drenthe *C. stagnalis* was found in the "cowpuddles" and furrows together with *C. palustris*, *Stellaria uliginosa* etc. (cf. vegetation-description *C. palustris*). Once a rich vegetation was found in a dystrophic ditch in the brookvalley near Schipborg, while *C. stagnalis* also flourished on a damp path near Lieveren. In Terschelling it appears in brackish water with *Zannichellia palustris* ssp. *pedicellata* (in sched. Reichgelt, 1951).

As regards the distribution of plants differing in cytological respect, we still have at our disposal too few data. It could be ascertained that the plants, found in Lieveren, have 2 SAT-chromosomes just

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[1] Ir S. Sonneveld by letter.

like those from Middachten. In Schipborg plants occur with 0,1 or 2 SAT-chromosomes.

C. stagnalis, and *C. obtusangula* likewise, proves much more salt-tolerant than *C. hamulata* and *C. platycarpa*, which tallies with its appearance along the coast. Of the seeds from Coimbra even 100 % germinated in solution 3 (cf. Ch. VI). Generally speaking *C. stagnalis* seems to us a plant especially occurring in rivervalleys, estuaries and—at greater height—along lakes.

5. **C. palustris**

DISTRIBUTION (cf. appendix I, 5)

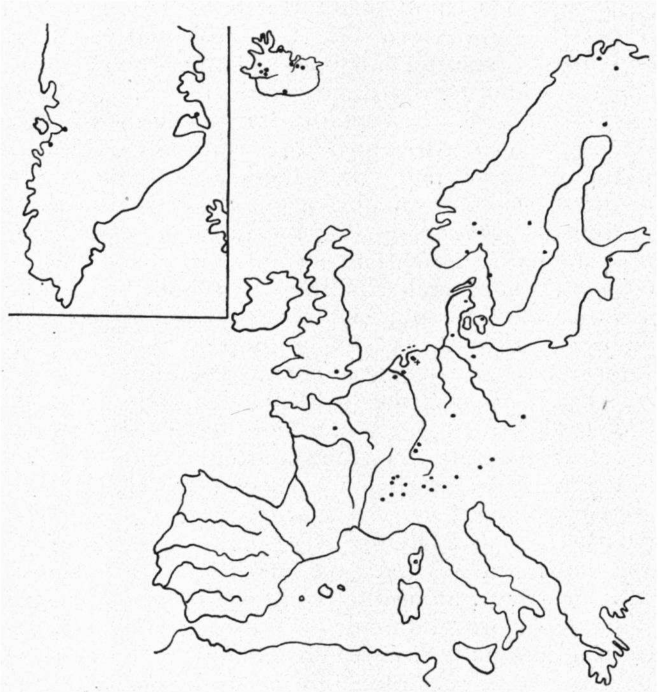
The Netherlands

This interesting plant grows in only a few places in the Netherlands. From Berlicum and the surroundings of 's Hertogenbosch (prov. of N. Brabant) about the middle of last century extensive material was brought together by a certain Van Hoven, which is among the best gathered of this species in the Netherlands. Further there were plants in the Leiden herbarium from Heikop near Vianen, Persinge near Nijmegen and from Coevorden. We ourselves found a few scattered landforms in the valley of the Lieveren brook and a fairly rich habitat near the Schipborg brook (map 11).

Map 11. C. palustris. Distribution in the Netherlands (cf. app. I, 5).
• herb. specimens + living plants

Outside the Netherlands

In the lower regions of France, Germany and Switzerland the species also occurs sporadically: in Denmark, Sweden and Finland it neither seems to be common. Especially the Alpine sector, however, is remarkably abundant in finds, just as Iceland and Greenland (map 12). As for the former area, we mention, in France, the departments Doubs, Isère and especially Savoie and Haute Savoie; in Switzerland the cantons Vaud, Valais, Graubünden, Tessin and Bern have many localities, while there were herbarium specimina from Linz, Salzburg and Tirol in Austria. In Italy *C. palustris* occurs in the alpine part (Alpes bergamasques etc.).



Map 12. C. palustris. Distribution in Europe and Greenland (cf. app. I, 5).
• herb. material + living plants

Often it grows at great height. Thus *C. palustris* rises above 2500 m. in the Alps (Braun-Blanquet, in sched.).

In Iceland too *C. palustris*—considered the numerous specimina in the Copenhague herbarium—is fairly frequent. The same holds good for Greenland. The most northern findspot lies here at 71° N.L.

The area of *C. palustris*, however, is not limited to the above-mentioned arctic-alpine area. SOKOLOVSKAJA (1932) gives us several localities in Russia, among which the Caucasus is well represented. In Asia *C. palustris* is especially found in the mountains about the 50th degree of latitude, between about 60° and 110° N.Longitude (a.o. the Altairegion). We ourselves saw Asian herbarium plants from Siberia, Kashmir (N.W. Himalaya), Yunnan, the upper course of the Amur, Japan, Corea and Taiwan (Formosa). Also in N. America *C. palustris* occurs (a.o. Labrador). As in Eastern Europe and Asia plants occur with slightly diverging fruitform (PETROV, 1928) we shall not treat this part of the area further.

ENVIRONMENT AND VEGETATION

The Netherlands

The growth of *C. palustris* is restricted to very special conditions of environment. On account of its frail habit it cannot stand swift watermovement as waterform, as also appeared from transplant experiments in the experimental brook of the botanical garden "de Wolf" (Ch. III). The stems are short and the branching is but little, it does not form any dense vegetation of quickgrowing clumps, like some of the other species. Its appearance is usually of an ephemerous character, though in a single case a dense vegetation may occur by an accrescence of seed on a small plot. As it proved from cultures and fieldobservations, *C. palustris* as waterform depends on scarce, shallow quantities of stagnant water. The germination of the seeds too takes place exclusively under such conditions; probably in shallow water the temperature can rise quickly in spring to the value necessary for germination (about 20° C, exper. unpubl.).

As landform it rarely forms a dense vegetation, contrary to *C. platycarpa* and *C. hamulata*; the little plants usually grow scattered. Owing to its frail growth it is much more dependent than the other species on a clear substrate when germinating and for further development, where—at least during its vegetation period—no coarse, quickly growing plants occur.

In the Netherlands *C. palustris* occurs only in the brookvalleys of Drenthe in "cowpuddles" and tiny furrows in the marshy strip of land, flooded in winter, along the banks of the brooks. Usually these strips are used as pasture, and many parts are mown as well. According to the waterlevel the plant occurs here as land- or waterform, usually accompanied by *C. stagnalis* and small herbs like *Stellaria alsine*, *Peplis portula* and sometimes by *Montia*. In a few cases a specimen of *C. hamulata* and *C. platycarpa* is found. Further we meet in this vegetation here and there, *Ranunculus flammula*, *Myosotis palustris*, *Galium palustre*, *Alopecurus geniculatus* and *Rorippa islandica*.

At the end of *C. palustris*' vegetation period a Polygoneto-Bidentetum cernui develops in late summer in many places, in which especially *Polygonum hydropiper* and *Bidens tripartitus* occur. Perhaps the disappearance of *C. palustris* is somewhat hastened by this compact, quickly growing vegetation, though also in areas free of rivalry most *C. palustris*-plants perish about August-September.

If an important change in waterlevel or growth of plants takes place, the development of *C. palustris* is immediately hampered. Such a case occurred in 1953 near the Schipborg brook. Owing to the quantity of rain the area along the brook remained flooded nearly all summer. In the localities of the foregoing years the water reached to more than half a meter high, so that pasturing was not possible. Neither could the grass be mown, so that a dense vegetation of Gramineae with long leaves, decaying here and there, filled the former furrows and "cowpuddles". Only in the shallow zone, in a few small plots with a clean substrate a few *C. palustris*-plants appeared; in the deeper parts nothing could be discovered. The thick growth of grass and the deep water—owing to which the temperature remained too low on the bottom—had most probably already prevented the germination of the seeds.

In N. Brabant *C. palustris* occurred according to Van Hoven (in sched. 1847) along the Dommel and in the hollows along the river A, near 's Hertogenbosch. It is remarkable that the species appeared spontaneously and abundantly in the botanical garden "de Wolf", where "cowpuddles" had been artificially made in the marshy area along the experimental brook in the spring of 1953 and in a shallow little pool.

All Dutch localities lie in freshwater regions. As the species occurs but rarely, we have a wateranalysis of but one locality, besides that of the habitat in the botanical garden "de Wolf". (cf. appendix II, table IV).

Outside the Netherlands

An environment analogous to the "cowpuddles" in the brookvalleys described above, is found in Finland. In his interesting ecological study about the South Finnish skaror area LUTHER (1951) relates that *C. palustris* occurs here in "Hufspuren", "Ruderstrassen" and "Bootufer". The "Hufspuren" are here situated along the edges of the swampy meadows, adjoining the reedborder along the coast. On the landing-places and in the paths the boats have forced through the reed vegetation—where the bottom is practically clean—*C. palustris* principally grows together with other biotic weak species, as *Subularia aquatica*, *Ranunculus confervoides*, *Crassula aquatica*, *Elatine hydropiper* and *triandra*, *Limosella aquatica* and some *Chara*- and *Nitella*species.

As well from the Dutch observations as from Luther's description it becomes apparent that the existence of *C. palustris* in culture areas is strongly dependent on human influence. It can only maintain itself in habitats, where on account of the continuous eliminating of the existent vegetation small areas with clean substrates originate. It is probable that also in the marshy hayfields in Iceland *C. palustris* grows under analogous circumstances.

In rocky regions (a.o. in Finland) and in mountain areas *C. palustris* is especially a plant of "Felstümpel", puddles in drying river beds, glacier regions (Rhoneglacier) etc.

In the Alps it sometimes forms a "Verlandungspioniergesellschaft" with *Sparganium affine*, *Rorippa islandica*, *Ranunculus flaccida* and *Alopecurus aequalis*, in drying puddles (Braun-Blanquet in sched.). In Iceland it grows a.o. on the "hraun" (lava) in and near the brooks and besides in the Geysir together with Cyanophyceae (h.C.).

CHAPTER VI

INFLUENCE OF SALTISH WATER ON THE GERMINATION OF THE SEEDS

For *C. hamulata*, *C. obtusangula*, *C. platycarpa*, and *C. stagnalis* the germinative power in saltish water was studied. The seeds were sown in petridishes, in artificially composed diluted seawater of different strenghts (BAKKER 1951).

The solutions contain per 1:

sol. 1 = 1 g NaCl + 0.12 g $MgCl_2$ + 0.08 g $MgSO_4$ + 0.05 g $CaSO_4$ + 0.02 g KCl.
sol. 2 = 3 g NaCl + 0.36 g $MgCl_2$ + 0.24 g $MgSO_4$ + 0.15 g $CaSO_4$ + 0.06 g KCl.
sol. 3 = 5 g NaCl + 0.60 g $MgCl_2$ + 0.41 g $MgSO_4$ + 0.24 g $CaSO_4$ + 0.11 g KCl.
sol. 4 = 10 g NaCl + 1.20 g $MgCl_2$ + 0.82 g $MgSO_4$ + 0.49 g $CaSO_4$ + 0.22 g KCl.

The Cl′content is as follows (analysed in the same way as the field samples, Ch. V):

TABLE V

Sol. nr.	Content of Cl′ in mgr/L
1	680
2	1970
3	3400
4	6750

1. C. hamulata

Seeds from plants growing at Haren (Gr.)
No germination occurred for this species in the solutions used.

2. C. obtusangula

A. Seeds from plants growing in Texel

The tables indicate the percentage of germinated seeds, a fortnight after having been sown.

TABLE VI
Sown 29-7-’53. Number of seeds for every solution 25.

Sol. nr.	Perc. of germ. seeds
1	95
2	96
3	88
4	—

TABLE VII
Sown 10-8-'53.
Number of seeds for every solution 25.

Sol. nr.	Perc. of germ. seeds
1	96
2	81
3	71
4	—

TABLE VIII
Sown 10-8-'53.
Number of seeds for every solution 100.

Sol. nr.	Perc. of germ. seeds
1	97
2	81
3	77
4	—

B. Seeds from plants growing in Zuid-Beveland (Zeeland)

TABLE IX
Sown 29-8-'53.
Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	98
2	99
3	97
4	97

TABLE X
Sown 15-9-'53.
Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	99
2	98
3	99
4	95

3. **C. platycarpa**

Seeds from plants growing at Haren (Gr.)

As *C. platycarpa* germinates best in fresh water after the seeds have been subject to a low temperature during a short period (experiments unpubl.), the sowing experiment was made in salt solutions at different temperatures.

The tables indicate the percentage of germinated seeds, a fortnight after having been sown.

TABLE XI
Sown 9-10-'53. Temp. 12° C.
Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	14
2	2
3	2
4	—

TABLE XII
Sown 9-10-'53. The seeds were stored at a temperature of 12° C. After having been sown in the petridishes, these were placed in a room at a temperature of 25° C. Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	46
2	0
3	2
4	1

TABLE XIII
Sown 9-10-'53. The seeds were put in the refrigerator for 1 week at a temperature of —4° C. After having been sown in the petridishes, these were put in a room at a temperature of 25° C. The table indicates the percentage of germinated seeds after 1 week. Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	99
2	17
3	1
4	—

4. C. stagnalis

As the number of seeds from Dutch material at our disposal was too small, seeds of plants from the botanical garden of Coimbra (Portugal) were used.

In each solution 50 seeds were sown.

TABLE XIV
Sown 15-5-'53.

Sol. nr.	Perc. of germ. seeds		
	24 May	25 June	1 July
1	100	100	100
2	100	100	100
3	0	61	100
4	0	9	died

TABLE XV
Sown 26-6-'53.

Sol. nr.	Perc. of germ. seeds		
	2 July	12 July	25 July
1	99	100	100
2	100	100	100
3	0	24	100
4	0	2	died

5. C. palustris

As too few seeds were at our disposal, no experiments were made for this species.

From the aforegiven tables it becomes clear that the germination may, for some species, take place in a much higher saltconcentration than for others. Thus the germination-percentage in sol. 3 is still very high for *C. stagnalis* and *C. obtusangula* (material from Texel), while for *C. platycarpa* only in sol. 1 a high percentage is reached under the most favourable circumstances.

For *C. hamulata* the seeds did not germinate even in sol. 1, while in rainwater always abundant germination occurred.

With a view to the germination *C. hamulata* is therefore probably the least salt tolerant of the species mentioned above, which tallies with the data about the Dutch distribution area, from which it proved that *C. hamulata* grows in fresh water (cf. Ch. V).

C. platycarpa can stand a higher saltconcentration, but as in sol. 2 only 17 % of the seeds germinated, the normal development will take place up to a value of a Cl′ content of ± 1000 mg/L.

From the distribution in the Netherlands it appeared that *C. platycarpa* also is predominantly a freshwater plant. In the wadden- and haff districts it occurs in oligohalinic water at best.

As regards the germination of the seeds of *C. obtusangula*, there is a distinct difference between the material from Zeeland and that from Texel. If we compare the tables VI, VII, and VIII (Texel) with IX and X (Zeeland) then we see that in the first three cases in sol. 3 the percentage of germinated seeds is a little lower than in sol. 1 and 2, while in sol. 4 no germination occurs anymore. The seeds of the Zeeland plants on the contrary germinate also in sol. 4 in a percentage nearly as high as in the other solutions.

C. obtusangula growing in Zeeland is therefore clearly more salt-tolerant than the plants from Texel, which also manifests itself in the Cl′ content of the findspots, lying much higher in Zuid-Beveland than in Texel (cf. Ch. V).

In *C. stagnalis* (Coimbra) all seeds still germinate in sol. 3, according to tables XIV and XV. So it can stand a Cl′ content of 3400 mg/L quite well and will still be able to develop well in brackish water. That is what its occurrence along the coasts and in the estuaries point to (cf. Ch. V).

CHAPTER VII

NOMENCLATURE

1. **C. hamulata** Ktzg

This name dates from 1837 and was published by KÜTZING, in KOCH (1837). In REICHENBACH (1841) some clear reproductions were given.

He had already earlier given good descriptions and reproductions of the species (1831 and 1832), under the name of *C. autumnalis* L. however. He thought that forms of his new species were part of *C. autumnalis* L. and he obviously wished to make a division, giving the name *C. autumnalis* L. to his species, while he started indicating the rest of the original species of Linné by the name of *C. virens* Goldbach. According to Kützing *C. autumnalis* L. sensu L. therefore comprised, besides *C. autumnalis* L. sensu Ktzg (the later *C. hamulata*), also *C. virens* Goldbach (*C. autumnalis* L., *C. hermaphroditica* Juslen., cf. sub 5).

In 1837 Kützing changed the nomenclature, originally chosen by him, in this sense that he again connected the name *C. autumnalis* to that part of the Linnean species that we even now know as *C. autumnalis* L. (*C. hermaphroditica* Juslen.), while he gave the rest, corresponding with his own species, the new name *C. hamulata* Ktzg.

In literature we sometimes find as a synonym for *C. hamulata* Ktzg the name *C. intermedia* Hoffm. (not intermedia Schkuhr, as WAHLENBERG mentions in his Flora Lapponica, 1812). *C. hamulata* is also sometimes considered as a variety of *C. intermedia* Hoffm. (a.o. in the British flora by CLAPHAM, TUTIN and WARBURG, 1952).

C. intermedia was described by HOFFMANN in the "Bot. Taschenb. f. d. Jahr 1791". Here the author refers to SCHKUHR, Bot. Handb. t. 1 (1791) fig. e. This fig. e refers to a twig of *Callitriche* that Schkuhr indicates by the name *C. autumnalis* (in his text; below the picture, only *C. verna* is mentioned accidentally; fig. 6).

This twig surely does not represent *C. hamulata*, but it is quite a different *Callitriche* which becomes apparent from the upright stamens in the rosettes. Such stamens do not occur in *C. hamulata* (cf. Ch. IV).

Therefore *C. intermedia* Hoffm. should in no way be connected with *C. hamulata* Ktzg.

2. **C. obtusangula** Legall

In his "Flore du Morbihan" of 1852 LEGALL mentions a new *Callitriche* he had found in the departments Ille-et-Vilaine and Morbihan. According to him the plant resembles the "Callitric des étangs (C. stagnalis), mais il en diffère par le fruit dont les loges ne sont point en carène ailée, mais présentent un dos très obtus. C. obtusangula N."

The description is not extensive, but by the characteristics mentioned of the fruit, the plant is well designated, so that it is quite clear which *Callitriche* Legall meant. His localities as well fit in perfectly with the area as we know it now for the *C. obtusangula.*

Fig. 6. After SCHKUHR (1791). On the left Hoffmann's C. intermedia. For explanation see text.

About the taxonomic rank which the new *Callitriche* would have to occupy, Legall probably was still somewhat uncertain, as becomes clear from the sentence: "c'est au moins une var. fort remarquable du Callitric des étangs."

He however used the name obtusangula as a specific epithet in the diagnosis and this fact seems sufficient for us to consider the specific name *C. obtusangula* Legall as validly published.

3. **C. platycarpa** Ktzg

In 1831 KÜTZING described a new species of *Callitriche*, common in Germany, which he gave the name *C. platycarpa.* This species, according to him, somewhat resembles *C. stagnalis* but diverges vegetatively by the linear young leaves, linear stem leaves and the absence of branches directly under the rosette. Kützing most emphatically states here that *C. stagnalis* remains the most constant in leafshape of all species under varying conditions and never shows linear leaves.

Further, according to the description, the fruits of *C. platycarpa* are a little smaller than those of *C. stagnalis* and the carpels are less divergent. If we study the reproductions in REICHENBACH's Iconogr. bot. 1831 (tab. DCCCLXXXIII-DCCCLXXXIX), in Ic. fl. germ. 1841 (tab. CXXIX, fig. 4748) and the herbarium material collected by Kützing (h.L.), then there is no doubt but that Kützing meant by *C. platycarpa* the species, also most common in the Netherlands. As Kützing's *C. platycarpa* is the oldest validly published name for this species the Callitriche at issue will have to bear the specific epithet platycarpa. This species is new for the Netherlands.

From the beginning there has been great confusion roundabout *C. platycarpa* in Europe. By some authors (a.o. Lebel) the name *C. platycarpa* was used for *C. stagnalis*-plants, others considered *C. platycarpa* as *C. verna* L. or distinguished a variety platycarpa of *C. stagnalis*; also for *C. platycarpa* pro parte the name *C. polymorpha* Lönnr. was used. This was first done by SAMUELSSON (1925), who tried to escape from the confusion by entirely rejecting the name platycarpa. He was of opinion that Kützing had not rigthly outlined his species: *C. platycarpa* was thought to be composed of a heterogeneous group of bigfruited and smallfruited plants. Now Samuelsson regarded all bigfruited specimens as belonging to *C. stagnalis*, for the smallfruited plants he used the name *C. polymorpha* Lönnr.

The problem, however, was not solved in this way. In the first place the above-mentioned changing of nomenclature is not permitted according to int. code nom. 1952, art. 63. In the second place it does not show either in Kützing's descriptions, or in his reproductions, that he really brought together plants with very different-sized fruits in the species *C. platycarpa*. Now, what must we understand by *C. polymorpha* Lönnr. mentioned by Samuelsson? Is it indeed identical with the smallfruited *C. platycarpa* growing under special circumstances?

C. polymorpha was described in 1854 by LÖNNROTH and was common in Sweden. If we compare the diagnosis with that of the *C. platycarpa* Ktzg, then it proves that there exists an important difference in the size of the fruits. Also the width of the wings is different.

Lönnroth says of his plants: that the fruit is "aequi longi, ac fructus (sunt) C. vernae, paullo latiores et crassiores, . . . marginibus carpellorum . . . obtusis, vix alatis." Kützing, however, describes the fruits of his *C. platycarpa* as being somewhat smaller than those of *C. stagnalis*.

Lönnroth, acquainted with Kützing's description, was also struck by this fact. He says a.o.: ". . . C. platycarpa Kütz., cujus formam typicam Reich. icon. 1189-90 exprimunt, fructibus differt multo maioribus, cartilagineo alatis, longitudine paene latioribus." Lönnroth considered his plants, a.o. owing to the fruitshape, as a species different from *C. platycarpa*.

In Swedish herbarium material we indeed found plants as described by Lönnroth (a.o. ex. herb. Svanlund, h.G.). In the Netherlands such plants were not observed thus far. In the very variable *C. platycarpa* under certain circumstances specimina occur with fruits smaller than normal, while also the width of the wings may vary. But they are too different from the Swedish plants for us to call the *C. polymorpha* a mere modification or var. of *C. platycarpa.*

Only by cytological investigations and culture experiments we shall be able to ascertain whether *C. polymorpha* is a species or a—perhaps northern—form or variety of *C. platycarpa.*

The chromosome number $2n = 12$ (*C. platycarpa* has $2n = 20$), stated by Löve and Löve (1948), might perhaps point towards a species. The analogy in habit and pollen shape may speak for the second possibility.

4. **C. stagnalis** Scop.

C. stagnalis was described in 1772 by Scopoli in his "Flora carniolica" as follows: "Folia ovata. Flores polygami. Habitat in fossis circa Tergestum, aqua marina plenis." He further refers to Stellaria 3 in Haller's Enumeratio (1742), where we find the following words: "3 Stellaria foliis omnibus subrotundis".

Though both diagnoses are not very ample, it is sufficiently clear which species Scopoli meant. The "foliis omnibus subrotundis" from Haller's diagnosis is characteristic for this species, the only one in Europe that never bears linear leaves (cf. Ch. III and VIII). Further, the findspot Triëst, as well as the occurrence of the plant in salt water there, is quite in accordance with our data about the distribution area and the salt tolerance (cf. Ch. V and VI).

The mentioning of "Flores polygami" (so unisexual as well as hermaphrodite flowers) moreover indicates that Scopoli has very accurately observed that in his species a ♂ and a ♀ flower may occur together in one leafaxil. He, however, apparently considered the two flowers as one hermaphrodite flower, as was done by many authors.

5. **C. palustris** L.

The nomenclature of this species has given rise to much misunderstanding. The cause of this is, among other things, the fact that in the days of Linné the nomenclature of *Callitriche* was changed three times in the course of a few years, while the descriptions were little accurate.

If we trace the nomenclature of Linné and his pupils chronologically, then we get the following survey.

In Spec. pl. ed. I 1753 Linné describes one species, viz. *C. palustris,* with the varieties minima, β bifida and γ natans.

In 1754 Grufberg (Fl. angl.) and Hedenberg (Stat. Plant.) also speak of *C. palustris.* In February 1755 the Cent. I Plant. of Juslenius appeared, in which he describes 2 Callitriche species viz. *C. androgyna* and *C. hermaphroditica.* Paying attention to the references in the descriptions we presume that *C. hermaphroditica* took the place of *C. palustris β bifida,* while *C. androgyna* is probably *C. palustris* (α) *minima* and *C. palustris γ natans,* joined together. In October of the same year we find in the 2nd ed. of the Flora suecica, two other names. Linné now distinguishes *C. verna* and *C. autumnalis,* the description of which nearly entirely falls in with resp. *C. androgyna* and *C. hermaphroditica* of Juslenius. Why he changed Juslenius' nomenclature he doesn't say. In the following years NATHORST (1756) uses the names of Juslenius, while HOLM (1757) again takes the names *C. verna* and *C. autumnalis,* curiously enough with the indication "N".

In the Spec. pl. ed. II, 1762 (citation) and in ed. III, 1764 LINNÉ maintains his *C. verna* and *C. autumnalis,* and also uses this nomenclature in his herbarium.

Now, which Callitriche's were indicated by the names mentioned above? The descriptions do not make us much wiser and therefore SAMUELSSON (1925) presumed that by *C. hermaphroditica* (*C. autumnalis*) only submerged Callitriche's were meant and by *C. androgyna* (*C. verna*) landforms and rosette-bearing plants. If, however, we study the herbarium of Linné, then it does not seem improbable that by his *C. verna* and *C. autumnalis* he most certainly meant two definite species.

On the first sheet (plate 15) we find, below an undetermined, sterile *Callitriche* two specimina, indicated by the name *C. autumnalis.* Both indeed belong to the species of the section Pseudo-callitriche, which we nowadays indicate by that name or by *C. hermaphroditica.* Samuelsson's supposition that Linné meant another Callitriche by *C. autumnalis* and did not know this Pseudo-callitriche, proved wrong, on account of the existence of these two plants.

Further three waterforms have been gathered under the name of *C. verna,* while under the same name, on a second sheet, six small landforms are present. All these specimina with their conspicuous small fruits belong to one species, which—outlined more or less exactly—is now indicated by most authors by this name (or by *C. vernalis* Ktzg,[1]) *C. androgyna* Juslen., *C. palustris* L.).

That Linné did not provide the topmost Callitriche on the first sheet with a name, might also show that the division C. *verna* - *C. autumnalis* is not only based on modifications, as Samuelsson suggested. If this were the case, this specimen would probably have been classed with one of the two species.

As for the nomenclature, the following remarks may serve. The two younger epithets verna and autumnalis of Linné for androgyna and hermaphroditica of Juslenius are superfluous names and may as such be considered illegitimate.

When dividing *C. palustris* into two species, *C. androgyna* Juslen. and *C. hermaphroditica* Juslen., the name *C. palustris* L. must be conferred on one of the two species, according to the rules of nomenclature. According to those rules the name palustris would have to be used for the part comprising the type. As no herbarium material of *C. palustris* is known, and so no type can be pointed out, the name may be given to either species mentioned, at will. As the name *C. herma-*

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[1] By KOCH (1857) erroneously attributed to Kützing. In fact Kützing mentioned *C. verna.*

phroditica (*C. autumnalis*) has always been used for the species of the section Pseudo-callitriche, it is the best solution to replace *C. androgyna* Juslen. (*C. verna* L.) by *C. palustris* L., as was done by Druce (cf. Mansfeld, 1940).

Chapter VIII

DESCRIPTION OF THE SPECIES

In the species of the section Eu-callitriche we meet with a great number of modifications in the vegetative parts, especially in the size and shape of the leaves. Only *C. stagnalis* is more uniform under various conditions. The phenomenon of producing so many forms makes it impossible to give a description of a species including every form the species may develop. The numerous "formae" distinguished by several authors (Kützing a.o.) have no taxonomic value, whereas a division into varieties, which also has been tried, is not justified either, because of the fact that those varieties generally arise owing to the action of external conditions and thus do not rest on genetical factors.

In the following descriptions of the species therefore, we do not give but the theme; as to the variations be referred to Ch. III.

The descriptions have been made of plants in their optimal stage of development, that is to say with very well developed vegetative parts, flowering and fruiting abundantly.

Some remarks may follow.

The flowers are borne without any perianth in the axils of the foliage leaves. The male flower consists of one stamen, mostly provided with two transverse, falcate or more crescent-shaped membranaceous prophylla at its base.

The female flower consists of one pistil, mostly provided with two prophylla as well.

The male and female flowers of *C. obtusangula*, *C. platycarpa* and *C. hamulata* generally occur separately, rarely we meet with two flowers in one axil. In *C. stagnalis* and *C. palustris*, however, the latter situation is the most common. Here an anterior female flower and a posterior male one are borne in one leaf axil. Many authors considered both flowers to be parts of one hermaphrodite flower. This opinion is incorrect, for both, male and female flower are bearing their own two membranaceous prophylla.

As to the shape of the fruits we can say that in nearly all literature we meet with the opinion that the fruits of the species in the section Eu-callitriche—*C. obtusangula* excepted—are winged on the four angles. This, however, is not the case. The seeds, not the fruits, do possess a wing on their dorsal side or at their top. In this connection it may be emphasized that only Wahlenberg (1812) mentions winged seeds, in contrast with various other authors.

Near to the seedwings the walls of the fruits are thin and their cells are transparent. From this and in the side view one gets the impression that the fruits themselves are winged. In transverse section however (fig. 8) it is clear that such wings in reality are lacking. We can only say that the fruits are more or less keeled.

1. **C. hamulata** Ktzg. Plants from the village of Haren (prov. of Groningen)

a. *Waterform.* Plant generally winter annual, rooted in the mud. Stems branched, terete, — 40 cm. long, ca 3/4 mm. thick. Young stems with pluricellular disc-shaped glands which are composed of about 12 to 18 radiate cells (fig. 7).

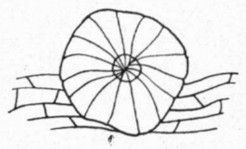

Fig. 7. C. hamulata. Gland of young stem. × 100.

Stem leaves opposite, linear, with a slightly widened and deeply emarginated apex (bicycle spanner), 1-nerved, green above, silvery greyish green beneath, 1-3 cm. long, ca 1 mm. broad. Floating rosettes tenuous, cup-shaped, composed of about 10 leaves (plate 7a). Lower leaves of the rosettes spathulate, about 1 cm. long; petiole light green, ca 1 mm. broad; lamina gradually tapering into the petiole, elliptical-obovate, with slightly emarginated apex, green above, greyish green beneath, with small disc-shaped glands on both sides, ca 6 mm. long, ca 3 mm. broad. Male and female flowers single in the axils of stem-leaves and lower rosette leaves, sessile, wholly submerged (plate 14a).

Prophylla—when present—small, narrowly falcate, membranaceous, white, to 1/2 mm. long.

Male flower: stamen small, at first erect, at time of pollination recurved towards one of the stigmata, ca 1 mm. long; filament white; anther reniform, rather colourless, ca 1/2 mm. broad. Pollen globular, colourless, without exine.

Female flower: stigmata thread-shaped, transverse, reflexed at base, turned backwards, colourless, at time of pollination from 1 1/2 to 2 mm. long (plate 14a).

Fruit sessile, in side view nearly circular, ca 1 1/4 mm. across; basal rests of reflexed stigmata pressed close to the sides of the fruit. (Transverse section see fig. 8c).

Seed nearly bean-shaped, with narrow dorsal wing, darkbrown, 1 mm. long, ca 1/2 mm. broad (plate 16b).

Submerged pollination. Flowering time April-June. Common in ditches and brooklets on pleistocene sandy soils and dune soils (map 1, 2; p. 336).

b. Landform. Stems prostrate or ascendent, rooting at the nodes, branched, slender, bearing no rosette at the top, from 5 to 15 cm. long, 1/2 mm. thick. Leaves opposite, elliptical, ca 5 mm. long, 2 mm.

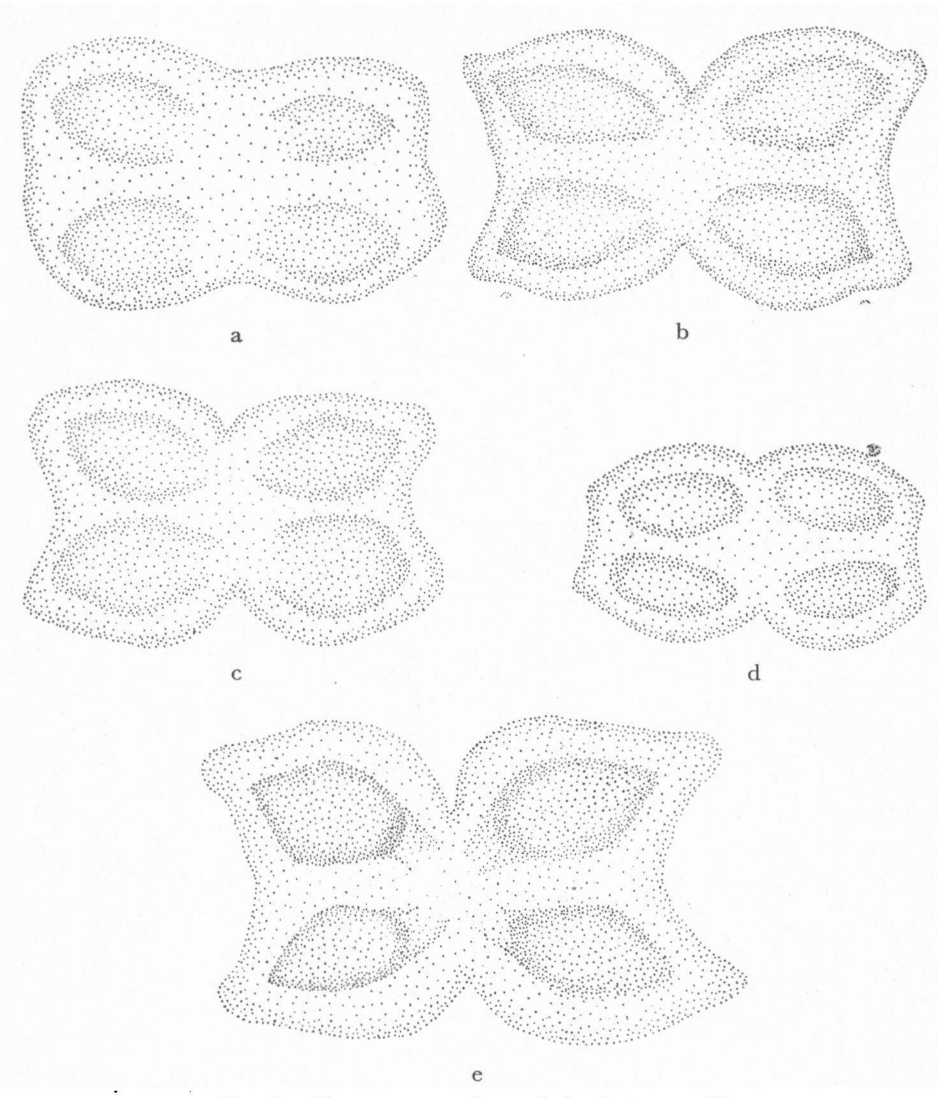

Fig. 8. Transverse sections of the fruits. × 27.
a. C. obtusangula, b. C. platycarpa, c. C. hamulata, d. C. palustris, e. C. stagnalis.

broad. Fruits sessile, sometimes stalked (plate 13a); stalks to ca 1 cm. long.

2 **C. obtusangula** Legall. Plants from the Island of Texel
a. Waterform. Plant perennial, rooted in the mud. Stems branched, terete, palish green, to 1 ½ mm. thick. Young stems glandulous. Glands irregularly disc-shaped, composed of about 8 radiate cells (fig. 9).

Stem leaves opposite, the lower ones of the main stems linear, emarginated at the apex, the upper elliptical or more or less rhomb-shaped.

Floating rosettes dense, composed of about 20 leaves, ca 2½ cm. across (plate 8a). Lower rosette leaves spathulate, thick, to 1½ cm. long; petiole markedly light coloured, to 7 mm. long, 1½ mm. broad; lamina rather abruptly tapering into the petiole, rhomb-shaped, somewhat emarginated at the apex, with small disc-shaped glands on both sides, green above, greyish green beneath, ca 8 mm. long, 6½ mm. broad; nerves 3-5, somewhat prominent above. Male and female flowers generally solitary, sessile, in the axils of rosette leaves only, each of them with 2 crescent-shaped prophylla at its base, partly raised above the water surface. After pollination the continued unfolding of the rosette brings the flowers down into the water.

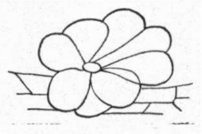

Fig. 9. C. obtusangula. Gland of young stem. × 100.

Male flower: stamen erect, ca 5 mm. long, after dehiscence recurvated and elongated; filament thread-shaped, white; anther reniform, yellow, to 1½ mm. broad. Pollen yellow, ellipsoidal, with well developed exine (fig. 10).

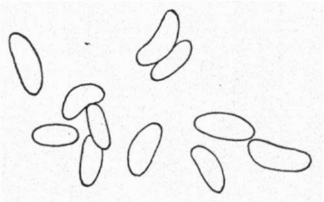

Fig. 10. C. obtusangula. Pollengrains. × 100.

Female flower (fig. 11c): stigmata 2, transverse, thread-shaped, divergent, at time of pollination ca 4 mm. long, after pollination nearly horizontally spread out, elongated. Fruit generally with erect short stigma rests, brown, in side view elliptical, longer than broad, 1½ mm. high, 1 mm. broad, in transverse section rounded rectangular (fig. 8a); median and lateral furrows very shallow.

Seed longly bean-shaped, unwinged, light brown, 1½ mm. long, ½ mm. broad (plate 16a). Air pollination. Flowering time May-autumn. In ditches and small streams near the coast (Haff-, Wadden-, Dune- and River district; map 3, 4; p. 340). Especially frequent in brackish water.

b. *Landform.* Stems prostrate or ascendent, rooting in the lower nodes, branched, generally bearing a rosette at the top, palish green, to ca 10 cm. long, 1 mm. thick. Young stems with disc-shaped glands. Stem leaves elliptical or narrowly rhomb-shaped. Rosettes composed of about 8 leaves. Rosette leaves more or less rhomb-shaped.

In 1953 we have grown *C. obtusangula* from the province of Zeeland (Netherlands). These plants were differing from the other *C. obtusangula*-specimens by their smaller, dark green rosettes and circular or obovate leaves with truncated apex (plate 8b).

For other differences cf. Ch. II and VI.

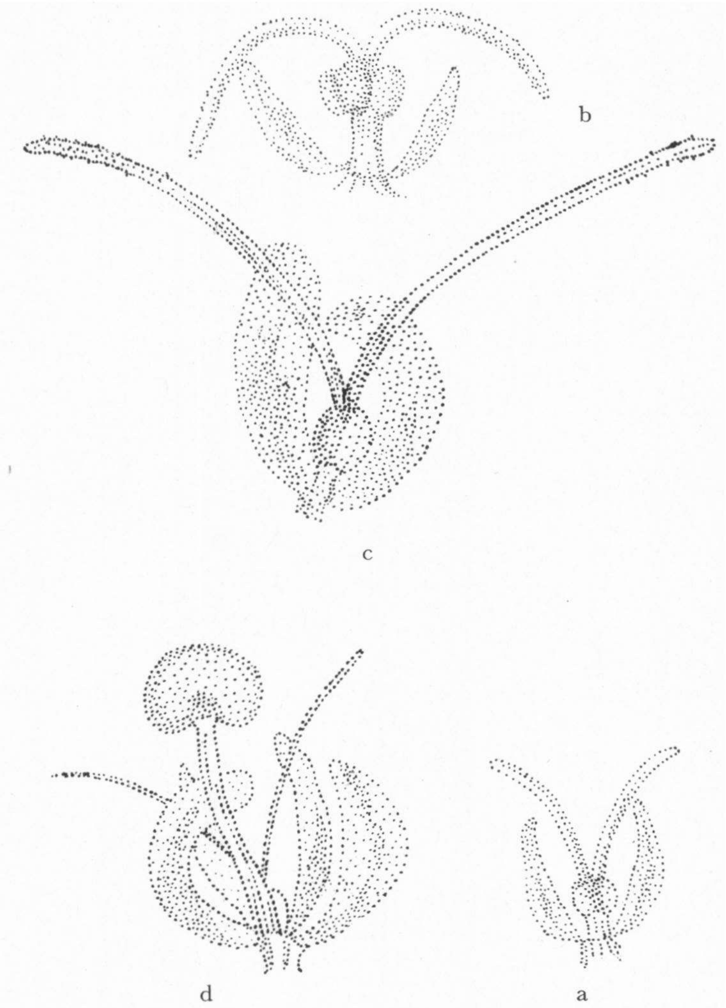

Fig. 11. Flowers. × 12½. a. C. stagnalis. Waterform. Young female flower. b. C. stagnalis. Waterform. Female flower at pollination time. c. C. obtusangula. Waterform. Female flower at pollination time, d. C. palustris. Well developed waterform. Male and female flower in one leafaxil, each of them with 2 prophylla.

3. **C. platycarpa** Ktzg. Plants from the village of Haren (prov. of Groningen)

a. *Waterform.* Plant perennial (generally about 2 years), rooted in the mud. Stems branched, terete, ca ¾ mm. thick. Young stems glandulous. Glands irregularly disc-shaped, composed of about 8 radiate cells. Leaves opposite. Lower stem leaves generally linear or narrowly elliptical, emarginated at the apex. Floating rosettes composed of about 12 leaves (plate 7b). Lower rosette leaves spathulate, ca 1 ½ cm. long; petiole ca 8 mm. long, to 1 ½ mm. broad, light green; lamina more or less broad elliptical, more or less gradually tapering into the petiole, slightly emarginated at the apex, with small disc-shaped glands on both sides, green or glaucous, ca 1 cm. long, 7 mm. broad; nerves 3-5, somewhat prominent beneath.

Male and female flowers generally single, in the leaf axils of rosette leaves only, sessile, each of them with two crescent-shaped membranaceous prophylla, partly raised above the water surface, after pollination submerged.

Male flower: stamen ca 4 mm. long, with white thread-shaped filament, after dehiscence recurved and elongated; anther reniform, yellow, from ¾ to 1 mm. broad. Pollen of various shape, globular, ellipsoidal, etc., yellow, with well developed exine (fig. 12).

Female flower: stigmata 2, transverse, thread-shaped, erect or patulous, 3-4 mm. long, after pollination widely spread out or somewhat recurved, elongated.

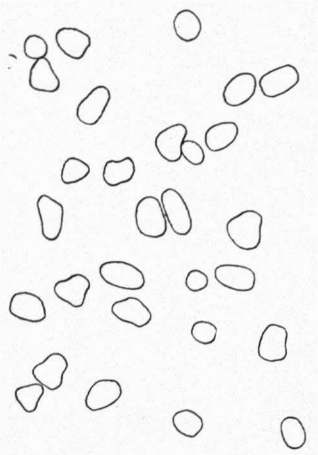

Fig. 12. C. platycarpa. Pollengrains. × 100.

Fruit sometimes with short, erect stigma-rests, carinated, in side view circular or shortly elliptical, from 1 ½ to 1¾ mm. high, from 1 ¼ to 1 ½ mm. broad; median furrows in transverse section (fig. 8b) crescent-shaped, lateral furrows rather deep. Seeds in a transverse section of the fruit never divergent, but parallel.

Seeds somewhat bean-shaped, with dorsal wing, brown, 1¾ mm. long, ca ¾ mm. broad (plate 16c). Often 1-3 seeds do not develop.

Air pollination. Flowering time May-autumn. Common in ditches and brooklets. In fresh water (map 7, p. 345).

b. *Landform* (plate 13b)

Stems prostrate or ascendent, branched, with opposite, elliptical leaves. No well-marked rosettes. Prophylla small or lacking. Anthers generally smaller than those of the waterforms. Fruits commonly conspicuously keeled, light brown or brown. Seeds commonly with broader wings than those of the waterform, and more lightly coloured. Resembles in the vegetative parts sometimes *C. stagnalis* or *C. hamulata.*

4. **C. stagnalis** Scop. Plants from Schipborg (prov. of Drenthe)

a. *Waterform.* Plant annual or perennial.

Stems branched up to the top, rooting at many nodes, terete, to 3/4 mm. thick, green. Young stems glandulous. Glands disc-shaped, composed of about 8 radiate cells. Stem leaves opposite, the lower ones elliptical or spathulate, slightly emarginated at the top, never linear. Floating rosettes composed of 6 to 8 opposite leaves (plate 9a). Lower rosette leaves spathulate, ca 15 mm. long; lamina broadly elliptical or circular, rather abruptly tapering into the petiole, very slightly emarginated at the top, generally 5-nerved, with small disc-shaped glands on both sides, bright green, ca 12 mm. long, ca 8 mm. broad.

Male and female flowers single or together in the leaf axils, each of them with two slightly crescent-shaped prophylla, partly raised above the water-surface, after pollination submerged.

Male flower: stamen erect, ca 2 mm. long, after dehiscence somewhat recurved and elongated; anther reniform, yellow, ca 1 1/2 mm. broad. Pollen globular, yellow, with exine (fig. 13).

Female flower stalked; stigmata two, transverse, thread-shaped, generally arcuate-recurved, ca 2 mm. long (fig. 11a, b). Fruit conspicuously keeled, light brown, in side view nearly circular, commonly somewhat broader than long, ca 1 3/4-2 mm. high, to 2 mm. broad; median furrows in transverse section deeply crescent-shaped, lateral furrows deep (fig. 8e).

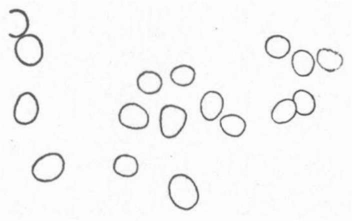

Fig. 13. C. stagnalis. Pollengrains. × 100.

Seeds in a transverse section of the fruit divergent (fig. 8e). Seeds broadly bean-shaped or somewhat reniform, broadly winged, light brown, from 1 1/2-1 3/4 mm. long, 3/4 mm. broad (plate 16e). Air pollination. Flowering time May-autumn. Estuaries, ditches and pools, in brook- and rivervalleys. In fresh and brackish water. Rare in the Wadden isles (map 9, p. 347).

b. *Landform.* Repent plants with branched stems, rooting at the nodes, with broadly elliptical or nearly circular leaves.

5. **C. palustris** L. Plants from Schipborg (prov. of Drenthe)
a. *Waterform.* Plant summer annual, with only a few roots. Stem unbranched or with some branches, terete, glabrous or with scattered disc-shaped glands near the top, to 25 cm. long, ca 3/4 mm. thick. Glands composed of about 12-15 radiate cells (fig. 14). Stemleaves opposite, the lower ones mostly linear with emarginated apex, ca 3 cm. long, 1 mm. broad. Floating rosettes composed of ca 10 leaves, ca 1 1/2 cm across (plate 9b). Lower rosette leaves spathulate, thin, 3-nerved, light green; lamina more or less gradually tapering into the petiole, broadly elliptical or nearly circular, ca 1 cm. long, ca 4 mm. broad.

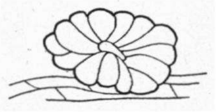

Fig. 14. C. palustris. Gland of young stem. × 100.

Male and female flowers commonly together in one leaf axil (fig. 11d), each of them with two rather straight membranaceous prophylla, partly raised above the water surface. Rarely one male flower and 2 female flowers in one leaf axil.

Male flower posterior; stamen rarely normally developed, generally more or less reduced, in well developed stage erect, ca 2 mm. long; anther small, yellow. Act of dehiscence often lacking.

Female flower sessile; stigmata erect-patulous, thread-shaped, in well developed condition ca 1 1/2 mm. long, often more or less reduced, sometimes unequal in length.

Fruits small, narrowed in the lower half, in side view obovate, without stigma-rests, dark brown or blackish, 1 mm. long, at the top 3/4 mm. broad; median and lateral furrows shallow. Seeds in a transverse section of the fruit slightly convergent (fig. 8d).

Seed narrowed towards the base, with small wing along the top, blackish, 1 mm. long, 1/3 mm. broad (plate 16d).

Apogamous, only in well developed conditions perhaps airpollination. Flowering time June-August. In "cowpuddles", in marshy brookvalleys. Rare (map 11, p. 348).

b. *Landform.* Small repent plants, glabrous or with a few disc-shaped glands. Leaves shortly linear or narrowly elliptical, to 4 mm. long, 2 mm. broad.

Male flowers rudimental, generally wholly disappeared (plate 14c). Stigmata of female flowers nearly entirely reduced (plate 14b).

KEY TO THE SPECIES

Only reliable for well developed, flowering and fruiting plants.

A. Waterforms

1*a*. Leaves all linear, with widened and deeply emarginated apex. Basal rests of the reflexed stigmata pressed close to the lateral sides of the fruit . . . . **C. hamulata**

b. Upper leaves spathulate, forming a well-marked floating rosette 2

2*a*. Rosette composed of about 20 rhomboid thick leaves. Fruit with rounded edges and very shallow median and lateral furrows, in side view elliptical, longer than broad. Seed unwinged. Pollen ellipsoidal . . . . **C. obtusangula**

Plants with almost circular leaves with truncated apex were found in the province of Zeeland.

b. Rosette composed of about 8-14 elliptical, circular or obovate leaves. Fruit more or less keeled. Seed winged 3

3*a*. Fruit small (1 mm. long), narrowed in the lower half, in side view obovate, blackish. Seed winged at the top . . . . **C. palustris**

b. Fruit larger, in side view circular or almost circular. Seed with dorsal wing 4

4*a*. Rosette cup-shaped. Stamens and stigmata wholly submerged. Anthers small, rather colourless. Pollen colourless. Stigmata reflexed at base. Basal rests of stigmata pressed close to the lateral sides of the fruit. . . . **C. hamulata**

b. Rosette more or less convex. Stamens and stigmata above the watersurface. Anthers yellow. Pollen yellow. Stigmata erect or recurved 5

5*a*. Rosette leaves generally elliptical. Pollen of various shape. Stigmata erect or spreading, to 5 mm. long. Seeds in transverse section of the fruit parallel . . **C. platycarpa**

b. Rosette leaves generally almost circular. Pollen globular. Stigmata generally arcuate-recurved, 2-3 mm. long. Seeds in transverse section of the fruit divergent . **C. stagnalis**

B. Landforms

1a. Pistil with very reduced stigmata. Stamen reduced, generally entirely lacking. Fruit small (1 mm.), narrowed in the lower half, in side view obovate, blackish. Seed winged at the top . . . . **C. palustris**

b. Pistil with well developed, thread-shaped stigmata. Fruit larger, in side view circular or elliptical 2

2*a*. Fruit with rounded edges and very shallow furrows, in side view elliptical, longer than broad. Seed unwinged. Pollen ellipsoidal. . . . . **C. obtusangula**

b. Fruit keeled. Seed with dorsal wing 3

3*a*. Stigmata reflexed at base. Rests of the stigmata pressed close to the lateral sides of the fruit. . . . **C. hamulata** *b*. Stigmata erect or recurved 4

4*a*. Stigmata erect - patulous. Seeds in transverse section of the fruit parallel. Leaves generally elliptical **C. platycarpa**

b. Stigmata arcuate - recurved. Seeds in transverse section of the fruit divergent. Leaves generally almost circular . . . . **C. stagnalis**

SUMMARY

For the study of the section Eu-callitriche in the Netherlands the cytological investigations formed the base for the outlines of the species. Owing to the chromosome sets, very different among themselves, the section might be split up into 5 fractions. This division proved to be consolidated as well by morphological, geographical and ecological characteristics and by the differences in the lifecycles. The combination of these characteristics at last led to a division into 5 species: *C. hamulata* Ktzg, *C. obtusangula* Legall, *C. platycarpa* Ktzg, *C. stagnalis* Scop. and *C. palustris* L.

While cultivating under various conditions we saw that—*C. stagnalis* excepted, being little variable—all species are very variable, especially in the vegetative parts. Many varieties, described in literature, must therefore be considered as modifications. Also *C. pedunculata* DC., described as a species, is probably a modification, and in that case belongs to *C. hamulata.*

Only a few varieties in ecological and morphological qualities are probably founded on hereditary factors (different leafshape and larger salt tolerance in *C. obtusangula* from the province of Zeeland, the brookform of *C. platycarpa*). For the time being no further systematic division was based on these characteristics.

In the species *C. obtusangula*, *C. stagnalis*, *C. palustris* and *C. platycarpa* plants occur with and without SAT-chromosomes. Between the two types of one species no further differences were observed, only in the case of *C. obtusangula* the existence of SAT-chromosomes proved to coincide with a differing leafshape and larger salt tolerance.

When studying the early stages in the mitosis, it became apparent that each satellite is composed of 2 parts, which unite before the metaphase into one (plate 4).

Most species show a clear preference for a certain environment, which also appears from the distribution regions.

In order to unravel the nomenclature, the knowledge of morphology, distribution etc. proved to be an aid. Thus e.g. *C. intermedia* Hoffm. must be rejected as a synonym for *C. hamulata* Ktzg, because of the quite different structure of flower.

A short survey of the principal data follows below.

C. hamulata Ktzg.

In several respects this species occupies a place of its own in the section. It deviates in the number of chromosomes ($2n = 38$; see plate 1) from the other species which have $2n = 10$ or $2n = 20$.

The chromosome set must be considered as the most asymmetrical; the lengths of the chromosomes are very different and as for the position of the centromeres, we find transitions from median to subterminal centromeres (fig. 1e). In contrast to the other species of the section no plants with SAT-chromosomes were observed.

Also in the structure of the flowers and in the submerged pollination *C. hamulata* differs from the other species (plate 14a; fig. 5). Because of its submerged pollination it is the only species able to fructify in deep water and in swiftly flowing water.

With regards to the distribution it is, for the Netherlands, typically a plant of sandy soils (pleistocene soils and dune soils, see map 1, 2; p. 336) where it grows in slightly acid - neutral water (cf. app. II, table I). *C. hamulata* is the only winterannual species.

By the fruit, with reflexed stigmata rests, laterally pressed close to it, it may easily be distinguished in any habit from other species.

C. obtusangula Legall has $2n = 10$ chromosomes (plate 3d). Some chromosomes belong to the longest of this section. The position of the centromeres is submedian - subterminal (fig. 1a). This salt tolerant species occurs in Europe in the mediterranean-atlantic coastal areas (map 5, p. 342). In the Netherlands we especially find it in oligohalinic-mesohalinic water of the wadden-, dune-, haff- and fluviatile districts (map 3, 4; p. 340). The water is neutral to slightly alcalic (cf. app. II, table II).

Well developed waterforms may be recognized by the dense rosette with rhombic, thick leaves (plate 8a), the fruit with rounded edges (fig. 8a), the non-winged seeds (plate 16a) and the ellipsoidal pollengrains (fig. 10). The species is a perennial.

A different form was found in the prov. of Zeeland. Those plants show an other leafshape (plate 8b), the seeds germinate in a higher salt concentration (cf. Ch. VI, table VI-X). The chromosome picture of these plants shows 2 SAT-chromosomes; the plants from Texel have no SAT-chromosomes. The satellite is connected to the small arm of the chromosome (plate 3e).

C. stagnalis Scop. also has $2n = 10$ chromosomes (plate 3a). But they are different in shape and size from those of *C. obtusangula.* All chromosomes have a subterminal centromere (fig. 1b). In this species plants were found with 0, 1 or 2 SAT-chromosomes (plate 3a, b, c). The satellite is connected to the long arm of the chromosome. The chromosome picture, observed by us, differs from that of the Russian plants of SOKOLOVSKAJA (1932); (cf. fig. 1*b*; fig. 3).

Just like *C. obtusangula C. stagnalis* is salttolerant (cf. Ch. VI, table XIV, XV) and occurs in coastal regions of Europe. However it also appears inland (map 10, p. 347). In the Netherlands (map 9, p. 347) we find it in the brookvalley areas and here and there along the coast (Biesbos). It is the only species that varies but little, and never forms linear leaves. The round rosette leaves (plate 9*a*), the globular pollen (fig. 13), the characters of the female flower (fig. 11a, b) and the broadly winged seeds (plate 16e) are characteristic for this species.

C. platycarpa Ktzg. The number of chromosomes is $2n = 20$ (plate 2a). All centromeres are subterminal (fig. 1c). Also in this species plants occur with 0 or 2 SAT-chromosomes (plate 2c, d; fig. 2). The satellite is connected to the long arm of the chromosome. *C. platycarpa* is an extremely variable species. In the Netherlands it proves to be the most common. It is much less restricted to special conditions of environment than the other species and occurs everywhere, except in brackish water (map 7, p. 345).

On account of its polymorphy and because it is often found in a sterile condition, this species often can be recognized as such after culture-experiments or cytological research only. That is probably the reason why it was not recognized thus far in our country.

C. palustris L., just like *C. platycarpa*, has $2n = 20$ chromosomes (plate 3f). They are smaller, however, and are nearly equal in size. (*C. palustris* has the smallest chromosomes of the 5 species of the section, fig. 1d).

Here we also find plants with 0 or 2 SAT-chromosomes (plate 3f, g). The satellite is connected to the small arm of the chromosome. For this species the connections between the metaphase-chromosomes in the mitosis are remarkable (plate 6a, b).

In habit *C. palustris* is the smallest of the 5 native Eu-callitriche species, the plants are tiny and little branched; as landform, the form in which it is mostly found, it is apogamous: the stigmata are abortive in these plants, while the stamens often have vanished altogether (plate 14b, c).

The embryosac probably develops from a somatic cell (plate 5).

The area of distribution is—so far as western Europe and Greenland are concerned—principally arctic-alpine (map 12, p. 349). In the intermediate regions it appears only rarely, and then only under very special environmental conditions ("cowpuddles"). Also in the Netherlands only few finding-places are known (map 11, p. 348). The species is a summerannual and well discernable by the very small dark fruit. The seeds are winged at the top only (plate 16d).

APPENDIX I

LOCALITIES OF THE FIVE SPECIES

1. *C. HAMULATA*

THE NETHERLANDS

Prov. of Drenthe: Koevorden 1859, h.L. 237, 251; Meppel, h.L. 91; Paterswolde 1855, h.G.; Peize, h.L. 39; Peize, h.G.; x Schipborg 1951; x Taarlo 1949; x Vosbergen, 1949; x Zuidlaren 1949, 1953.

Prov. of Friesland: Ameland (G 6. 51. 22) 1935, h.L. 112; Terschelling 1887, h.L. 139, 144, 537.

Prov. of Gelderland: Apeldoorn 1882, h.L. 926, 340-639; Apeldoorn 1892, h.L. 56; Cannenburgh near Vaassen 1874, h.L. 5; Cannenburgh near Vaassen 1885, h.L. 9; Harderwijk 1864, h.L. 130; Heelsum 1851, h.L. 335; Lent, h.L. 128; Loenen 1928, h.L. 937, 63-42; Malden 1924, h.K. & R.; Neerbos near Nijmegen 1865, h.L. 41, 42, 43, 44, 45, 47; Neerbos 1936, h.K. & R.; Neerbosser broek near Nijmegen, h.L. 6; Ooy 1938, h.K. & R.; Renkum, h.L. 336; Ruurlo 1882, h.L. 926, 340-580; Ruurlo 1886, h.L. 273; Ruurlo 1886, h.AMD 005005; Twello 1848, h.L. 101; Wolfheze, h.L. 394; x Wijchense ven 1949.

Prov. of Groningen: x Haren, Hortus „de Wolf" 1949-1951; Haren, Sassenhein 1951; x Haren Scharlakenhof 1949, 1951; Helpman, Groningen, h.L. 326; x Marum 1952.

Prov. of Limburg: x Arcen 1949, 1951.

Prov. of Noord-Brabant: Beugen (Q 6. 43. 32) 1933, h.L. 74; Berlicum, h.L. 77, 78; Boxmeer and Sambeek 1853, h.L. 81, 352; Boxmeer Zandbeek 1853, h.L. 81; Boxtelse heide 1847, h.L. 77, 80; Breda 1938, h.L. 935,5 - 58; Cromvoirt, h.L. 78; 's Hertogenbosch, h.L. 77, 78; Oeffelt, h.L. 73; Son 1850, h.L. 194, 203; Volkel (Q 5. 47. 41), h.L. 79.

Prov. of Noord-Holland: x Hippolytushoef 1953; x den Hoorn 1949; den Hoorn-den Burg 1921, h.GRO; x de Kooy 1949, 1951; Texel 1860, h.L. 276, 332; Texel 1895, h.L. 349.

Prov. of Overijsel: Delden 1870, h.L. 333; Denekamp, h.L. 246; Hardenberg 1892, h.L. 926, 340-611; Lattrop, Breklenkampse veld 1952, h.L. 95,372-711; Ootmarsum 1933, h.L. 393; Vollenhove 1898, h.L. 243.

Prov. of Utrecht: Beerschoten 1912, h.L. 942, 285-398; Blaauwkapel, h.L. 50, 231; de Bildt, h.L. 14, 15, 67; Eemnes 1895, h.L. 259; Rijzenburgse bos, h.L. 48, 49, 51, 52, 53, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 69, 264, 337, 345; Utrecht, h.L. 68, 265; Trajectum ad Rhenum (Utrecht), h.K.; Zeisterbos, h.L. 942, 285-134.

Prov. of Zuid-Holland: Endegeest, h.L. 355; Leiden 1820, h.B-B. 26; Loosduinen, h.L. 293.

OTHER COUNTRIES:

Belgium:
Casteau 1862, h.D.; Gedinne (Namur) 1866, h.L. 908, 281-381; 's Gravenwezel bij Antwerpen 1883, h.L. 908, 281-209.

Czechoslovakia:
Böhmerwald, h.D.

Denmark:
Bornholm: Olana 1850, h.C.; 1870, h.C.; 1876, h.C.

Jylland: Aalbaek 1872, h.C.; Blaavand 1899, h.C.; Blokhus 1888, h.C.; Esbjerg 1914 (distr. 27), h.C.; Fanö 1896, h.C.; Filsö 1950 (D 27), h.C.; Fyen, Fagsted mose 1926, h.C.; Holmslards Klut 1913, h.C.; Höve (Limfjord) 1864, h.C.; Höve 1868, h.C.; Hvidberg: Thy 1946 (D 7), h.C.; Lemvig 1874, h.C.; Mors 1901, h.C.; Ostbredden 1933 (D 52), h.C.; Römö, Kongsmark 1933, h.C.; Samsö 1890, h.C.; Samsö 1892, h.C.; Skjern 1932, h.C.; Skogens Nordstrand 1925, h.C.; Söndervig 1927, h.C.; Taasinge 1909, (D 32) h.C.; Torssö 1946, h.C.; Vinderup 1878, h.C.

Seeland: Furesöen Holte 1936, h.C.; Lac Dambusso près Copenhague 1866, h.L. 903, 364-1; Ravnsholt Hegn 1892, h.C.

Faroes:
Fuglö 1897, h.C.; Nolsö 1897, h.C.; Osterö, Göte, h.C.; Strömö 1897, h.C.; Syderö 1867, h.C; Syderö 1897, h.C.; Viderö 1897, h.C.

Finland:
Muonioalf (68°) 1915, h.K.

France:
Dep. Cantal: Auvergne Cantal, La Vigerie 1907, h.L. 911, 116-50.
Dep. Charente: Confolens 1879, h.Z. 65.
Dep. Eure-et-Loir: Dreux, h.D.
Dep. Haut-Rhin: Mulhouse 1851 h.D.; x Westhalten 1952.
Dep. Haute Saône: Champagney 1867, h.D.
Dep. Hérault: Gramont près Montpellier 1887, h.C.; Montpellier 1888, h.D.; Roquechanté 1896, h.Z. 66.
Dep. Indre-et-Loire: Landes de Bourgeuil 1873, h.Z. 70.
Dep. Loire: Montbrion 1887, h.D.
Dep. Loir-et-Cher: Romorantin 1862, h.D.
Dep. Maine-et-Loire: Angers, h.Z. 57.
Dep. Manche: Beaumont près Valognes 1861, h.L. 903, 364-34; 903, 364-35; 903, 364-36; h.D.; h.C.; h.B-B 29; Beaumont près Valognes, h.Z. 67; Cherbourg 1890, h.Z. 72; Tourneville 1891, h.D.; Valognes 1837, h.B-B 25; Valognes 1857, h.B-B 30; h.C.
Dep. Rhône: Charbonnière près Lyon 1852, h.D.
Dep. Seine-et-Marne: Fontainebleau 1829, h.D.; Fontainebleau, h.L. 903, 364-30; Fontainebleau, h.C.; h.D.; Fontainebleau 1853, h.Z. 229; Fontainebleau 1867, h.D.
Dep. Vosges: Epinal 1879, h.L. 909, 68-7; h.Z. 73; h.D.; Gérardmer 1849, h.D.; Huguemin, h.D.; Vogezen 1849, h.L. 903, 364-32.

Germany:
Bamberg 1905, h.D.; Bayreuth h.D.; Cleve 1871 h.Z. 68, 71; Cleve 1872, h.Z. 63; Coloniam (Köln), h.L. 903, 364-97; Flensburg 1878, h.D.; Freiburg 1900, h.Z. 60*a*; Hamm 1912, h.Z. 159; Hannover 1838, h.C.; Klein Wollmsdorf 1846, h.D.; h.Z. 4; Nürnberg 1856, h.L. 926, 156-488; Regnitz bei Bamberg 1904, h.C., h.B-B. 87, h.Z. 58, h.D.; Schleusingen, h.L. 910, 17-252; 910, 17-253; 910, 17-254; 910, 17-255; 910, 17-256; 910, 17-257; 910, 17-259; 910, 17-262; 910, 17-263; 910, 17-265; 910, 17-266; 910, 17-267; 910, 17-269. Schwarzwald, h.D., h.Z. 10; Tilleda 1878, h.Z. 64, h.D.; Waldmünchen, h.Z. 59; Wiesenthal 1863, h.Z. 52, 53.

Great Britain:
Clova, Angus, Scotl. 1935, v.c. 90, h.Ly.; W. Cornwall 1929, v.c. 1, h.Ly.; Dorset 1932, v.c. 9, h.Ly.; Farley 1926, v.c. 17, h.Ly.; Haroldwich, Shetland 1950, v.c. 112, h.Ly.; Isles of Scilly 1938, h.Ly.; Lancashire 1885, h.C.; Loch Ballates, S. Aberdeen 1934, v.c. 92, h.Ly.; Lyndhurst, Hants 1926, h.Ly.; Perthshire, Loch Acksay 1911, h.C.; Mid-Perthshire, Scotl. 1933, v.c. 88, h.Ly.; Scotland 1936, v.c. 105, h.Ly.; Sheffield 1944, v.c. 63, h.Ly.; Surrey 1945, v.c. 17, h.Ly.; Surrey, Mitcham Common, 1931, v.c. 17, h.Ly.; N. Wales 1931, v.c. 49, h.Ly.; Walton-on-Thames, h.Z. 56.

Greenland:
Amitsok 1883, h.C.; Amitsuarssuk 1937, h.C.; Arsukfjord (61° 15′ N) 1925, h.C.; Elv i Björnedal 1889, h.C.; Igalikofjord, h.C.; Julianehaab - Godthaab (60° 4′ - 64° 10′ N), h.C.; Nordkysten af Sargardsleg (68° 42′ N, 52° 30′ W) 1932, h.C.; Sukkertoppen 1884, h.C.; Tasermiutfjord (60° 16′ N) 1925, h.C.

Iceland:
Several localities: o.a. Hornafjord 1933, h.C. The other finding-places (h.C.) could not be located.

Italy:
Alpes bergamasques: Villasola, h.D.
W. Sicily: Ficuzza, Gurgo del Lupo 1856, h.Z. 46; h.D.; h.L. 903,364-115.

Spain:
Cerdagne, Llivia 1916, h.D.

Sweden:
Bohusia, Uddevalla in Ryån juxta Bräcke, h.C.; Längäsjö 1898, h.C.; Skåne: Eslöf 1885, h.K.; Svalöv 1928, h.D.; Småland 1849, h.C.; Upsala, h.L. 903, 364-13; Västmanland 1928, h.D.

Switzerland:
Canton Genève: Pinchat 1875, h.D.; Viry 1854, h.D.; Viry 1856, h.B-B 23; Bois de Viry 1860, h.B-B 5.
Canton Tessin: Lac majeur muralto 1903, h.D.
Canton Vaud: h.D.

2. *C. OBTUSANGULA*

THE NETHERLANDS

Prov. of Friesland: x Ameland (Buren) eendekooi 1952; Ameland (Nes), h.L. 233; Bolsward 1875, h.L. 909, 67-634; x Dokkum 1953; Leeuwarden, h.L. 921, 262-560.

Prov. of Gelderland: de Ooy, h.L. 251, 252.

Prov. of Groningen: x Delfzijl - Appingedam 1953; Hoogkerk h. Clas; x Rottum 1952; x Scheemda 1953.

Prov. of Limburg: Amby 1861, h.L. 329; Roermond (S 6. 54. 14), h.L. 399, 400.

Prov. of N. Brabant: Ulvenhouts Bos near Ginneken 1917, h.L. 928, 13-277.

Prov. of N. Holland: Alkmaar-Bergen 1878, h.L. 353; Diemerweg, h.L. 274; Haarlem 1877, h.L. 138; Haarlem, de Hout 1866, h.L. 226; Haarlem, de Hout 1871, h.L. 143; Hakkelaarsbrug near Naardermeer 1899, h.AMD 005004; Kraantje Lek 1872, h.L. 270; Naarden, h.L. 245; Schoten 1894, h.L. 933, 49–41; Schoten 1888, h.L. 347; Schoten 1870, h.L. 141; Sparendam 1888, h.L. 140; Texel 1895, h.L. 349, 350; x Texel, den Burg 1951; Texel, de Geul, (J 4. 52. 11) 1837, h.L. 940, 6–90; x Texel, de Cocksdorp, 1949, 1951, 1952, 1953; x Texel, den Hoorn 1949; x Texel, de Muy 1949, 1951; x Texel, Oosterend 1951; x Texel, Prins Hendrik Polder 1951; x Texel, Pijpersdijk 1949, 1951, 1952, 1953; Schelvisnol 1933, h. GRO; x Vogelenzang near Haarlem 1953; Wieringen 1856, h.L. 274.

Prov. of Overijsel: Kampen h.L. 326; Zwolle (L 6. 54. 44), h.L. 926, 340-597; Zwolle 1913, h.L. 40.

Prov. of Utrecht: Leersum 1919, h.L. 921, 61-148.

Prov. of Zeeland: Domburg, Duinvliet, 1877, h.L. 376; Domburg Oranjezon, 1839, h.L.; x Goes 1953; Haamstede 1844, h.L. 372; x Kapelle-Biezelinge 1953; Kapelle, h.L. 82, 328; Kapelle 1898, h.L. 398; Kloetinge, h.L. 88; Kloetinge 1886, h.L. 103; Kloetinge 1886, (R 2. 37. 2), h.L. 926, 340–612; x Kloetinge 1953; Kloosterzanden 1845, h.L. 371; Nieuwvliet 1877, h.L. 937, 351–362; Passegeule 1861, h.L. 237; id. bij Biervliet, h.L. 318; Tholen 1877, h.L. 86, 87; Walcheren, h.L. 236; Zuid-Beveland, h.L. 324; Zuid-Beveland 1839, h.L. 369; Zuid-Beveland 1840, h.L. 209; Zuid-Beveland 1840, h.L. 358; Zuid-Beveland 1843, h.L. 130.

Prov. of Z. Holland: Barendrecht 1939, h.L. 953, 178-351; x Biesbos 1953; Eindmeer (Rozenburg), h.L. 272; Hoek v. Holland 1879, h.L. 359; Hoek v. Holland 1900, h.L. 910, 286–704; Katwijk, h.L. 155; Katwijk 1894, h.L. 933, 49–39; Katwijk-Noordwijk 1897, h.L. 300, 301, 302; Katwijk, Leidse duinwater Mij 1952, h.L. 95, 372–330; Leiden, h.L. 356; Leiden 1847, h.L. 150; Leiden, Leidse vaart, 1867, h.L. 228; Lisse 1894, h.L. 933, 49–39; Noordwijk 1872, h.L. 147; Noordwijk 1891, h.L. 928, 13–276; Noordwijk-Voorhout 1939, h.L. 945, 256–232; Noordwijk 1939, h.L. 953, 178–354; Schiedam 1892, h.L. 228; Valkenburg, h.L. 187; Wassenaar 1897, h.L. 298; Zoeterwoudse weg, h.L. 23.

OTHER COUNTRIES:

France:
Dep. Alpes maritimes: Entre Juan-les-Pins et le Golfe Jouan 1912, h.Z. 160.
Dep. Charente-Inférieure: Saint Georges d'Oléron 1892, h.D.; Saint Georges d'Oléron 1892, h.B-B 37; id. 1890, h.B-B 34.
Dep. Eur-et-Loir: Dreux 1843, h.D.
Dep. Gironde: La Teste 1897, h.D.
Dep. Hérault: Montpellier 1881, h.C.; Montpellier 1851, h.Z. 118.
Dep. Manche: Yvetot près Valognes 1857, h.K.; Yvetot près Valognes 1857, h.B-B 36.
Dep. Orne: Flers 1890, h.D.
Dep. Sarthe: Le Mans 1897, h.D.
Dep. Vendée: Ile d'Elle, h.D.; Ile d'Elle 1883, h.C.; Luçon 1868, h.D.; Luçon 1903, h.D.; Vendée 1853, h.L. 903, 364–44.
Corsica: Ajaccio 1913, h.Z. 131, 132.

Great Britain:
Dorset 1928, v.c. 9, h.Ly.; Essex: Tilbury 1885, h.C.; Isles of Scilly 1940, no. 402, 409, h.Ly.; W. Kent 1923, 1943, v.c. 16, h.Ly.; Norfolk: Acle 1883, h.C.; h.Z. 88; Caiston-Yarmouth 1884, h.C.; Somerset 1930, 1931, v.c. 6, h.Ly.; E. Sussex: Broomhill 1932, v.c. 14, h.Ly.; E. Sussex: Iford 1931, v.c. 14, h.Ly.

Italy:
Napoli, h.L. 903, 364-93; Neapel h.C.; Pistoia 1886, h.B-B 58.
Sardiny: Orune, iter Sardoum 1899, h.D.
Sicily: Palermo 1841, h.D.; Palermo 1850, h.D.

North Africa:
Algiers: Algér, h.D.; Algers 1870, h.C.; Constantine 1888, h.D.; Constantine 1915, h.D.; Dj. Ouach près Constantine 1889, h.D.
Tunis: Aïn-Draham 1909, h.D.

Switzerland:
Canton Genève: Compesière 1848, h.D.; Etrambières 1872, h.B-B 45, 48; Genève 1793, h.D.; Puplinge 1879, h.D.; Puplinge 1880, h.D.; Roëllebot 1854, h.D.; Veyrier 1875, h.D.; Veyrier 1880, h.D.
Canton Valais: Valais 1771, h.D.

3. *C. PLATYCARPA*

THE NETHERLANDS

Prov. of Drenthe: x Anlo 1951; Meppel (K 6. 76. 21) 1930, h.L. 114; Peize, h.L. 128; x Ruiner Aa 1952.

Prov. of Friesland: x Bakkeveen 1953; x Kollum 1953; Oldeberkoop, h.L. 224.

Prov. of Gelderland: Apeldoorn 1883, h.L. 125, 378; Bennekom 1890, h.L. 93; Bennekom 1902, h.L. 928, 7–58; x Corle 1951; x Eibergen-Borculo 1951; Hees near Nijmegen 1851, h.L. 103, 218, 256; x Korenburgerveen 1951; Lent near Nijmegen, h.L. 219; x Lichtenvoorde 1951; Nijmegen, h.L. 247; Putten 1931, h.L. 388; x Ratum 1951; Ubbergen 1928, h.K. & R.; x Winterswijk 1951.

Prov. of Groningen: Dorkwerd, h.L. 232; Dorkwerd 1855, h.GRO; Groningen 1856, h.L. 116; h.GRO; x Haren 1951, 1952, 1953; x Leens 1951; x Marum 1952.

Prov. of Limburg: x Arcen 1949, 1951; Bunde 1904, h.L. 375; Eijsden near Oude Maas 1894, h.L. 215, 311; Eijserbos h.L. 954, 062-591; x Heerlen-Brunssum 1951; Mook (Q 6. 23. 33) 1938, h.L. 107; Plasmolen (Q 6. 23. 44) 1919, h.L. 923, 123-345; Plasmolen (Q 6. 23. 43) 1933, h.L. 106; Ottersum 1897, h.L. 214; x Kasteel Wittem 1951; x Wijlre-Mechelen 1951.

Prov. of Noord-Brabant: Bergen op Zoom, h.L. 196; Bergummerheide 1864, h.L. 909, 67 -630; 's Hertogenbosch, h.L. 196; Loon op Zand 1939, h.L. 942, 123-348.

Prov. of Noord-Holland: Alkmaar-Bergen 1878, h.L. 353; Haarlem, de Hout, h.L. 910, 283-633; Heemstede, h.L. 269; Naarden 1901, h.L. 279; Schoten 1894, h.L. 928, 13–261; Vogelenzang 1867, h.G.; Vogelenzang 1875, h.G.

Prov. of Overijsel: x Diepenheim-Goor 1951; Hardenberg 1892, h.L. 926, 340–627; h.L.926, 340–626; Ittersum near Zwolle 1894, h.L. 240; Ittersum near Zwolle (L 6. 65. 43) 1894, h.L. 926, 340–55; Tubbergen-Reutum 1935, h.L. 389.

Prov. of Utrecht: Amersfoort 1906, h.L. 928, 7-13; de Bilt 1930, h.L. 391; Bunnik 1912, h.L. 947, 334-312; Soesterveen 1925, h.L. 258.

Prov. of Zuid-Holland: Delfshaven near Rotterdam 1909, h.L. 934, 83-170; Dordrecht 1849, h.L. 317; Dubbeldam, h.L. 280; Dubbeldam 1848, h.L. 317; den Haag (N 3. 55. 24), h.L. 158; den Haag, Clingendaalse weg 1900, h.L. 354; den Haag 1933, h.L. 951, 159–124; Leiden, h.L. 356; Leiden 1847, h.L. 150; Leiden 1901, h.L. 315; Noordwijk, h.L. 98, 99; Noordwijk 1849, h.L. 101, 357; Noordwijk 1913, h.L. 928, 13–262; Rotterdam h.L. 292; Rotterdam 1850, h.L. 297; Rotterdam 1918, h.L. 923, 134–80; Rotterdam 1933, h.L. 934, 59–66; Rijnsburg 1845, h.L. 96; Rijnsburg, h.L. 338, 339, 340, 341, 342, 343, 344; Warmond 1841, h.L. 151; Zoeterwoudse weg, h.L. 23.

OTHER COUNTRIES:

Austria:
Austria superior: Aistersheim, h.L. 915, 150-252; Mannersdorf 1890, h.Z. 99.

Belgium:
x Lixhe 1949.

Czechoslovakia:
Prope Gratzen 1894, h.D.; h.Z. 102; Gratzen, h.D.; h.Z. 98; Wiesenbach bei Sonntag in Südböhmen 1884, h.Z. 101.

Denmark:
Jylland: Fur 1917, h.C.; Guden Aa ved Randers 1899, h.C.; Lustrup ved Ribe 1886, h.C.; Ribe 1887, h.C.; Tradsborg Baek 1886, h.C.
Seeland: Arrenaes (D 45) 1936, h.C.; Dyrehavn (D 45) 1867, h.C.; Hillerød E. of Store Lake Gribsø (D 45) 1946, h.C.; Hornbaek 1894, h.L. 950, 142-238; Lyngby in Dyrehavn (D 45) 1946, h.C.; Sondersoën 1885, h.C.; Töllöse (D 44) 1890, h.C.

Finland:
Prope Helsingfors 1884, h.Z. 106.

Germany:
Bamberg 1905, h.D.; Berlin 1895, h.Z. 94, 104, 187; Bremen 1894, h.Z. 103; Breslau 1872, h.D.; Eberswalde 1878, h.D.; Regnitzaltung Bamberg 1905, h.D.; Schleusingen, h.L. 910, 17-270; h.L. 910, 17-272; h.L. 910, 17-273; h.L. 910, 17-274; h.L. 910, 17-275; h.L. 910, 17-276; h.L. 910, 17-278; h.L. 910, 17-279; h.L. 910, 17-280; h.L. 910, 17-281; h.L. 910, 17-282; h.L. 910, 17-284; h.L. 910, 17-291; h.L. 910, 17-292; h.L. 910, 17-293.

Jugo-Slavia:
Bosnië 1848, h.D.

Roumania:
Transsilvanië, Retteg 1862, h.D.; Transsilvanië 1875, h.D.

Sweden:
Skåne: Bl. Lösen 1888, h.C.; Christianstad 1881, h.Z. 107; h.D.; Freuningen 1899, h.C.; Göteborg 1898, h.C.; Södermanland, par. Strängnäs, Eldsund 1924, h.D.

Switzerland:
Canton Valais: Col de Morgins 1868, h.D.; Lac du Golset près Morgins 1918, h.D.
Canton Vaud: Marais de la Dôle, h.D.

West Russia:
Lwow, h.Z. 105.

4. *C. STAGNALIS*

THE NETHERLANDS

Prov. of Drenthe: Havelte 1937, h.L. 953, 178-379; Lheeërzand 1948, h.AMD. 008604; Koevorden 1859, h.L. 237; x Roden-Lieveren 1951; x Schipborg 1949, 1950, 1951, 1952, 1953.

Prov. of Friesland: Terschelling, Midsland 1939, h.L. 953, 178–350; Terschelling 1950, h.K. & R.

Prov. of Gelderland: Epe 1890, h.L. 124 or 127; Groesbeek 1925, h.K. & R.; Groesbeek (Q 6. 23. 21) 1933, h.L. 123; Montferland near 's Heerenberg 1866, h.L. 230; Nijmegen, h.L. 247; Renkum 1897, h.L. 124; Ruurlo, h.L. 126; Wildenborgh 1833, h.L. 204.

Prov. of Noord-Brabant: Boxmeer 1853, h.L. 199, 205, 352; Breda-Terheyden 1916, h.L. 953, 222-960; Liesbos h.L. 188; Rozendaal 1860, h.L. 367; Tilburg 1940, h.L. 953, 222-929; Vliet, Moerdijk 1860, h.L. 367.

Prov. of Overijsel: de Lutte 1948, h.L. 948, 313-439.

Prov. of Utrecht: Utrecht, Ezelsdijk, h.L. 942, 285-404; Utrecht, h.L. 134; Vreeswijk, h.L. 135.

Prov. of Zuid-Holland: x Biesbos 1952; Dordrecht, Polder Jager 1838, h.L. 165; Dordrecht, Noordendijk 1850, h.L. 170, 202; Dordrecht, Noordendijk, h.L. 165; Leiden, h.L. 129; Moerdijkbrug 1938, h.L. 935, 5–56; Rotterdam, bij Nieuwe Maas 1908, h.GRO.

OTHER COUNTRIES:

Denmark:
Jylland: Astrap 1902, h.C.; Fanö 1880, h.C.; Fanö 1896, (Dist. 27) h.C.; Fanö 1899, h.C.; Fenshold, Stovskov 1913, h.C.; Filsö, (D. 27) 1950, h.C.; Heerup i Thy 1925, h.C.; Hirtshals 1898, h.C.; Hostrup sø ved Aabenraa 1934, h.C.; Colding Kirkeskov paa Vej 1927, h.C.; Kongshuvet 1913, h.C.; Lilleballe Skov ved Kolding, (D. 25) 1927, h.C.; Lustrup v. Ribe 1886, h.C; Moselud ved Teylgaards-vest, Viborg 1904, h.C.; Skibild 1872, h.C.; Silkeborg 1867, h.C.; Sondervig ved Ringkobing 1893, h.C.; Sondervig 1926, h.C.; Stogholmsö 1906, h.C.; Varde, Gröster ved Oxby 1899, h.C.; Varde, Trisvang 1950, (B.T.U. distr. 27) h.C.
Seeland: Mose ved Türesöen 1935, h.C.; Vallenzbaek Mose 1932, h.C.; Ved Rörvig 1899, h.C.

Faroes:
Kunö 1897, h.C.; Nolsö 1897, h.C.; Strömö, h.C.; Strömö, Thorshavn 1867, h.C.; Strömö, 1867, h.C.; Suderö 1897, h.C.; Viderö, Ostrig 1897, h.C.; Viderö, Krannasund 1897, h.C.

France:

Dep. Charente-Inférieure: La Matière-en-Oléron 1890, h.B-B 78; La Matière-en-Oléron 1892, h.D.; h.B-B 79.
Dep. Eur-et-Loir: Dreux, h.D.
Dep. Gironde: Arlac près Bordeaux 1842, h.D.; De la route de Casaux 1897, h.D.
Dep. Haute Garonne: Toulouse 1857, h.D.
Dep. Haute Savoie: Alpes d'Annecy (nr 4-9), h.B-B 88; Collet des Glisses, h.B-B 101.
Dep. Loire inférieure: Nantes 1829, h.D.
Dep. Manche: Herbeville près de Valognes 1863, h.L. 903, 364-49; h.C.; h.D.; Herbeville 1863, h.L. 903, 364-50.
Dep. Rhône: Arnas 1877, h.D.; h.L. 903, 364–45; h.L. 381; Arnas 1898, h.C.
Dep. Seine: Paris, h.D.
Dep. Seine-et-Marne: Fontainebleau, h.B-B 68, 83.
Dep. Somme: Le Eréport dans le Bresle 1892, h.D.
Dep. Vendée: Ile d'Elle 1898, h.C.
Dep. Vosges: Epinal, h.D.

Corsica:

Ajaccio 1849, h.D.; Bastia 1881, h.B-B 76.

Germany:

Bayreuth 1876, h.Z. 141; Borkum 1871, h.Z. 143, 144; Bremen, h.Z. 137; Cleve 1871, h.Z. 134; Cleve 1872, h.D.; Dresden, h.L. 903, 364–55; Immelborn 1876, h.Z. 140; Immelborn 1877, h.Z. 139; Immelborn 1879, h.Z. 138; h.D.; h.L. 944, 202–202; Schleusingen, h.L. 910, 17–283; 910, 17–285; 910, 17–286; 910, 17–290; Tiefendorf bei Annen 1874, h.Z. 150; Im Bache bei Dolgemost, Putbus 1855, h.L. 903, 364–60.

Great Britain:

Cumberland: Ardale 1911, h.C.; Isles of Scilly 1940, h.Ly.; Perthshire: Trossachs, Loch Ackray 1911, h.C.; Somersetshire: h.K.; Staffordshire: Kuypersley 1885, h.C.; E. Sussex 1936, v.c. 14, h.Ly.; Surrey: Ashstead 1894, h.D.; E. Sutherland: Loch Fleet 1936, v.c. 107, h.Ly.

Iceland:

Reykir (S. Isl.)' 1911, h.C.; Reykir 1934, h.C.; Reykjafors 1911 (S. Isl.), h.C.; Reykjavik 1876, h.K.; Ved Reykjavik 1884, h.K.; Reykjavik 1888, h.C.; Skribla 1876, h.C.; Vik (S. Isl.) 1933, h.C.

Italy:

Colico (Alpes bergamasques) 1912, h.D.; Padova, h.Z. 136; Venetië 1897, h.C.
Sicily: Caronia, h.Z. 145; Messina 1856, h.D.

Norway:

Nordre Throndhjemsamt, h.C.; Tilder Lerfossen 1926, h.C.; Ulvik 1904, h.B-B 63.

Portugal:

Coimbra, Baleia, h.Z. 126; Coimbra, Porto dos Bentos 1904, h.C.; x Coimbra 1949, 1952, 1953 (bot.garden); Douro litoral, Espinho Beira de ribeiro 1946, h.L. 950, 101-780; Terra de Nagueira 1909, h.D.

Spain:

Cerdagnes, Ur, 1927, h.D.; Guipuzcoa, Pasajes 1895, h.C.; Jerez 1883, h.C.; Merquita (Minorca, Baléaren) 1873, h.Z. 148.

Sweden:

Prov. Dalarna, par. Folkärna, prope Västansjö 1928, h.D.; Kronob(erg?) 1867, h.C.; Smaaland, Femsjö, h.C.; Smaaland, Langasjö 1897, h.C.; Smaaland, Langasjö 1898, h.C.; ved Nedsjön 1926, h.C.; Smaaland 1898, h.C.; Västergotland, Göteborg 1927, h.D.

Switzerland:

Canton Aargau: Frauenwald bei Rheinfelden, 1852, h.D.

Canton Genève: Bois de Viry 1840, h.B-B 63; Ecogia près Versoix, h.D.; Lancy Onex 1877, h.D.
Canton Tessin: Lac majeur, Muralto, h.D.; Lac de Muzzano, h.D.

5. *C. PALUSTRIS*

THE NETHERLANDS

Prov. of Drenthe: Koevorden 1859, h.L. 251; Koevorden 1859, h.L. 234.

Prov. of Gelderland: Hees near Nijmegen, h.L. 256; Nijmegen, h.L. 248, 249; Persinge, h.L. 250.

Prov. of Noord-Brabant: Berlicum 1847, h.L. 76, 191, 194, 195, 291, 317; 's Hertogenbosch 1847, h.L. 117, 169, 196; 's Hertogenbosch 1891, h.L. 941, 314–812.

Prov. of Zuid-Holland: Heikop near Vianen, h.L. 283; Vianen, h.L. 282.

OTHER COUNTRIES:

Austria:
Kreuzberg (Tirolia austr. orient) 1875, h.D.; Linz 1849, h.Z. 165; Salzburg 1904, h.Z. 186.

Denmark:
Hornbaek (Seeland) 1922, h.C.; Mariager (Jylland) 1942, h.C.; N. Jylland 1950, h.C.; Petersborg 1846, h.C.; Rostgaardsdam 1862, h.C.; Stensvod Mose (Seeland), h.C.; Tröbjerg 1913, h.C.; Tversted aa 1901, h.C.

England:
Petersham (Surrey) 1877, h.D.

Estonia:
Wormsi 1926, h.C.

Finland:
Maikoniemenjoki, Savonia borealis 1911, h.C.; Rovaniemi (66° 40′) 1930, h.C.

France:
Dep. Eur-et-Loir: Dreux, h.D.
Dep. Isère: Grenoble 1848, h.D.
Dep. Haute Savoie: Alpes d'Annecy 1909, h.B–B 84; Alpes d'Annecy 1912, h.B-B 84; Beaufort 1847, h.D.; Collet des Glisses 1900, h.B-B 101; Au dessus de Conflans 1897, or 1899, h.D.
Dep. Savoie: Albertville 1862, h.D.; Mont Cenis 1867, h.Z. 184; Mont Cenis 1894 (?), h.B-B 94; Sommet du Cormet 1861, h.D.; Lac de la Girottaz 1862, h.D.; Hauteluce 1861, h.D.; Au M^{e} Mirantin 1861, h.D.

Corsica:
Lago di nino 1932, h.Z. 164.

Germany:
Baden 1893, h.Z. 179; Hollingsted (Syd-Slesvig), h.C.; Schleusingen, h.L. 910, 17-287; h.L. 910, 17-289; Schwarzwald, h.Z. 178; Wittenburg 1849, h.Z. 180.

Greenland:
Cape Hedlund (72° 10′, 26° 10′) 1932, h.C.; Holstenborg 1886, h.C.; Igaliko 1828, h.C.; Igaliko 1888, h.C.; Jakobshavn 1892, h.C.; Jacobshavn 1891, h.C.; Kehestat (71°), h.C.; Kung Oskarshavn 1883, h.C.

Iceland: several localities, a.o.:
Breidamerkursandi (Syd Isl.) 1908, h.C.; Flateyr (N. Isl.) 1891, h.C.; Geysir (S.W. Isl.) h.C.; "Hraun i Fljotum" 1899, h.C.; "Hraun" (N. Isl.) 1899, h.C.; Langarvatn (S. Isl.) 1907, h.C.; Langarvatn 1911, h.C.; Myvatn 1928,

h.C.; Reykjalang i Olafsfirdi, h.C.; Reykjalang 1890, h.C.; Skagafjörd 1930, h.C.

Italy:
Alpes bergamasques 1912, h.D.; Bormio 1911, h.Z. 176, 177; Piémont 1880, h.Z. 181.

Norway:
Finmarken 1838, h.C.; Larvik, h.C.; Oystre Slidre, Kvithøvd 1930, h.C.; Rendalen ved Hornset 1899, h.C.

Poland:
Peilau 1887, h.Z. 172.

Sweden:
Gothenburg, h.C.; Lexssand (Dalarna) 1849, h.C.; Mälaren (Södermanland) 1924, h.D.

Switzerland:
Canton Genève: Alpes Léman., Mont de Granges 1920, h.D.; Alpes Léman., Plateau d'Avoria 1920, h.D.; Alpes Léman., Crète de Chaufleurie 1920, h.D.; Bois de Viry 1840, h.B-B 63.
Canton Graubunden: Lago di Lagalb 1905, h.D.; Lenzerheide, Crap la Pala, 1922, h.D.
Canton Tessin: Val Bavona 1904, h.D.; Frasco 1903, h.D.; Locarno 1900, h.D.; Prumogna 1905, h.D.
Canton Valais: Foret d'Aletsch 1934, h.D.; Vallée de Binn 1887, h.D.; Alpe de Louvie sur Fionnay 1917, h.D.; Près le Lancet 1900, h.B-B 84; Münster (Magordi), h.D.; Bourg. St. Pierre (route du Grand St. Bernard) 1919, h.B-B 85; Mares au glacier de Rhône 1895, h.D.; Sur le Simplon 1822, h.D.
Canton Vaud: Bex, h.B-B 80, 81; Alpes de Bex, h.B-B 90.

APPENDIX II

QUALITIES OF WATER IN DUTCH LOCALITIES

TABLE I
C. hamulata

Locality		pH	Content of Cl' in mgr/L
Arcen (prov. of Limburg)	running water	6.0	32
Marum (prov. of Groningen)	stagnant water	7.2	96
Bot. Garden „de Wolf"	„	7.2	36
Sassenhein (prov. of Groningen)	running water	6.2	67.5
Scharlakenhof „	„	5.8	trace
„ „	„	6.1	trace
Schipborg (prov. of Drenthe)	„	6.2	67
Hippolytushoef (prov. of N.-Holland)	stagnant water	6.7	852
"Oude Kamp" (Texel)	cattlepond	6.7	128
de Koog „	„	6.5	39
den Hoorn „	running water	7.7	64
de Dennen „	„	6.6	112
den Hoorn „	„	7.2	34
„ „	„	6.6	50
Ameland	„	7.1	71

TABLE II. *C. obtusangula*

Locality	pH	Content of Cl′ in mgr/L
1 Rottum (prov. of Groningen). . . .running water	9.0	1161
2 „ „ . . . . „	7.4	622
3 „ „ . . . . „	8.1	1995
4 „ „ . . . . „	8.0	1960
5 Dokkum (prov. of Friesland) . . . .stagnant water	7.2	114
6 Vuurtoren (Texel) . . . . .running water	8.0	710
7 „ „ . . . . „	7.8	1406
8 „ „ . . . . „	8.2	704
9 Bouwlust „ . . . . „	7.0	315
10 „ „ . . . . „	7.0	152
11 „ „ . . . . „	7.1	185
12 Duinweg Cocksdorp (Texel) . . . . „	7.6	96
13 Muysloot (Texel) . . . . „	7.6	604
14 „ „ . . . . „	7.8	614
15 Museum „ . . . . „	6.8	131
16 Cocksdorp „ . . . . „	7.8	220
17 Prins Hendrik polder (Texel). . . . „	7.8	554
18 den Hoorn (Texel) . . . . „	7.7	51
19 „ „ . . . . „	7.7	90.5
20 „ „ . . . . .cattle pond	6.7	128
21 Oosterend „ . . . . .running water	6.5	390
22 Oude Schild „ . . . . „	6.5	312
23 „ „ . . . . „	6.5	213
Cultures botanical garden “de Wolf”		
experimental brook (layer of ashes)	7.8	21
„ „	7.9	25

TABLE III. *C. platycarpa*

Locality	pH	Content of Cl′ in mgr/L
Marum (prov. of Groningen) . . . . .stagnant water	7.2	96
Wehe „	8.6	32
„ „ . . . . .stagnant water	7.0	130
Botanical Garden “de Wolf” . . . . . „	7.8	27
„ . . . . .running water	7.8	21
„ . . . . .stagnant water	7.6	29
Scharlakenhof (prov. of Groningen) . .running water	6.1	trace
Dokkum (prov. of Friesland) . . . . .stagnant water	7.2	114
den Hoorn (Texel). . . . . .cattle pond	6.7	128
Oude Schild (Texel) . . . . .running water	6.5	312
„ „ . . . . „	6.5	213
Goor (prov. of Overijsel) . . . . „	7.4	43
Corle (prov. of Gelderland) . . . . . . „	7.0	27
Winterswijk (prov. of Gelderland) . . .stagnant water	6.8	46
Arcen (prov. of Limburg) . . . . . . .running water	6.0	32
Kasteel Wittem (prov. of Limburg) . .stagnant water	7.0	12
Mechelen (prov. of Limburg) . . . . .running water	7.5	14
Brunssum „ . . . . . „	6.6	trace
Cultures botanical garden „de Wolf”		
“cowpuddles”.	7.9	35.5
experimental brook meadow.	7.8	21
„ arboretum.	7.8	27

TABLE IV
C. palustris

Locality	pH	Content of Cl′ in mgr/L
"Cowpuddles" brookvalley Schipborg (prov. of Drenthe)	6.2	67
"Cowpuddles" bot. garden "de Wolf"	7.9	35.5

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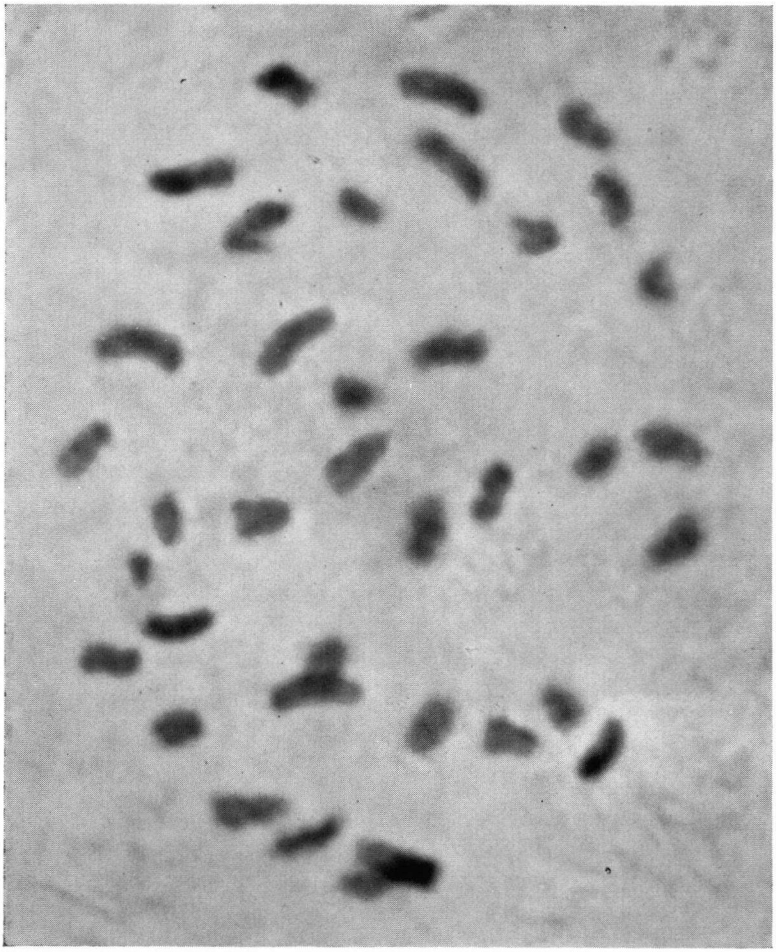


C. hamulata. Mitotic metaphase with $2n = 38$. Perm. Feulgen squash.

PLATE 2

a. C. platycarpa. Mitotic metaphase with $2n = 20$.
b. C. stagnalis. Mitotic metaphase with heterochromatic chromosomes. No cold pre-treatment.
c. C. platycarpa. Part of a metaphaseplate with 1 long and 1 small SAT-chromosome. For explanatory diagram see fig. 2.
d. C. platycarpa. Part of a metaphaseplate, with 1 long SAT-chromosome.
e. C. hamulata. Chromosome with median centromere.
f. C. palustris. First meiotic metaphase.
g. C. palustris. Second meiotic metaphase.
a-e. Perm. Feulgen squash.
f-g. From sections stained with crystal violet.

PLATE 2

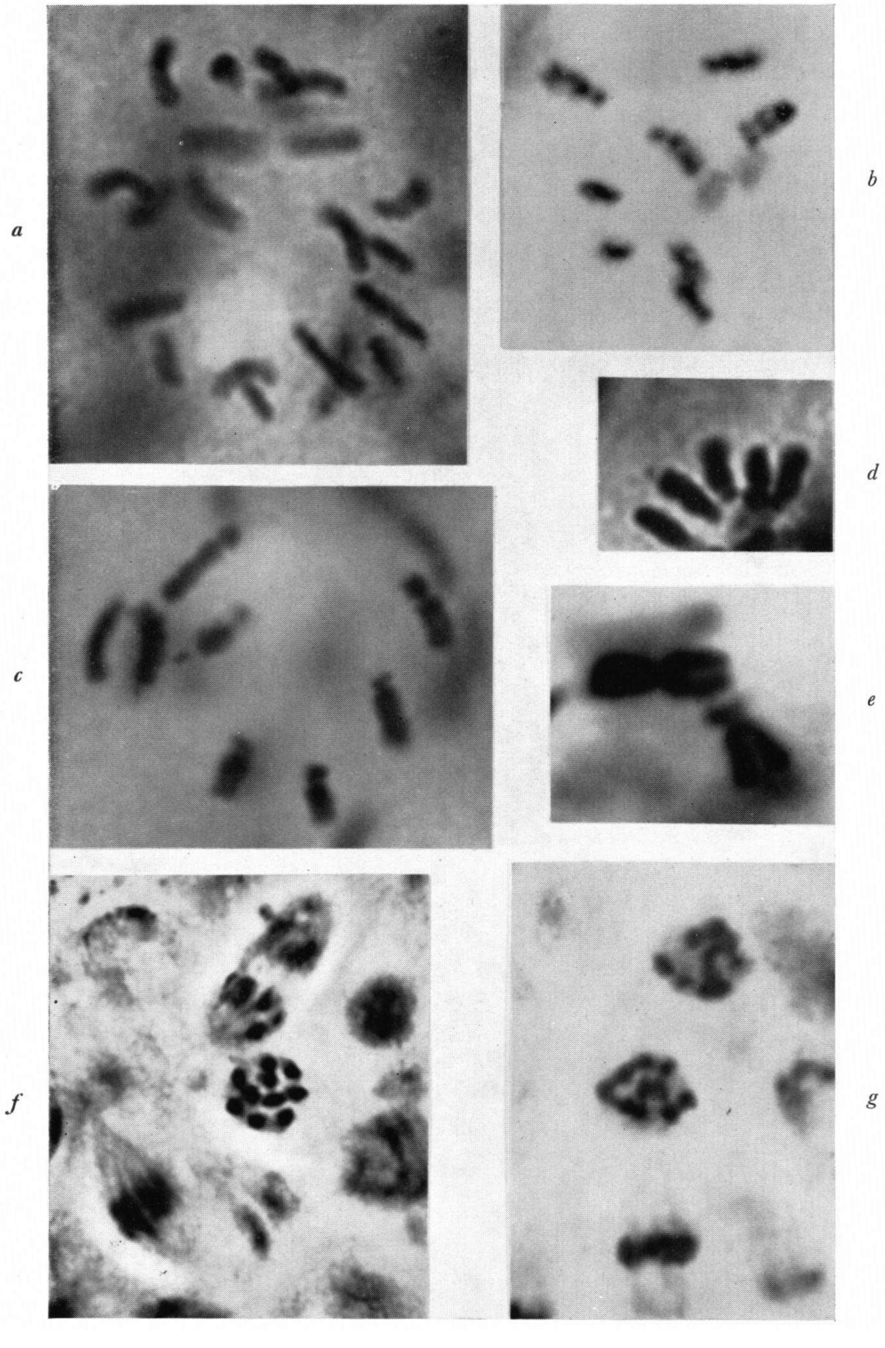


PLATE 3

- *a.* C. stagnalis. Mitotic metaphase with $2n = 10$. 0 SAT-chromosomes.
- *b.* C. stagnalis. The same with 1 SAT-chromosome.
- *c.* C. stagnalis. The same with 2 SAT-chromosomes.
- *d.* C. obtusangula from the Isle of Texel (Netherlands). Mitotic metaphase with $2n = 10$. 0 SAT-chromosomes.
- *e.* C. obtusangula from the prov. of Zeeland (Netherlands). Part of mitotic metaphase with 2 SAT-chromosomes.
- *f.* C. palustris. Mitotic metaphase with $2n = 20$. 0 SAT-chromosomes.
- *g.* C. palustris. The same with 2 SAT-chromosomes.

a-g. Perm. Feulgen squash.

PLATE 3

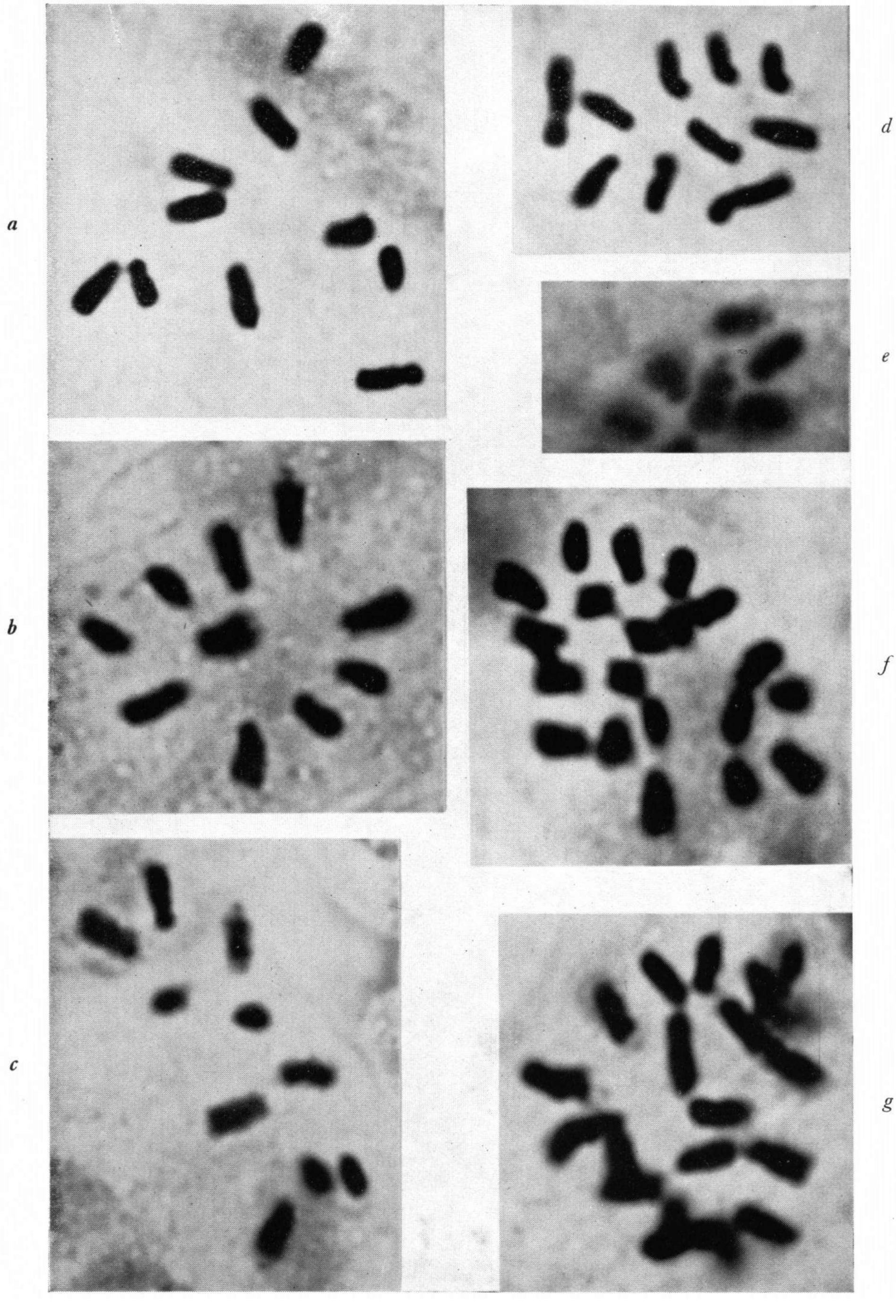


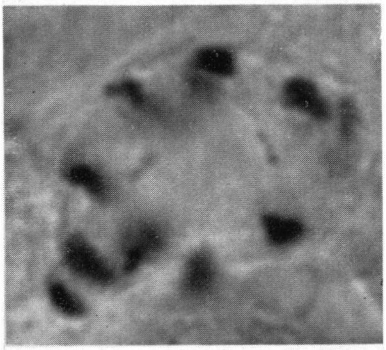
PLATE 4

a. C. stagnalis. Early mitotic prophase. The satellite consists of two parts. The connection with the end of the long arm of the chromosome is clearly visible.
b. Explanatory diagram of *a.*
c. C. stagnalis. The same as *a.* A small knob between the two parts of the satellites is visible.
d. Explanatory diagram of *c.*
e. C. obtusangula from the province of Zeeland (Netherlands). Late mitotic prophase. The two parts of the satellite just before joining.
f. Explanatory diagram of *e.*
a, c, e. Perm. Feulgen squash.

PLATE 4


a


b

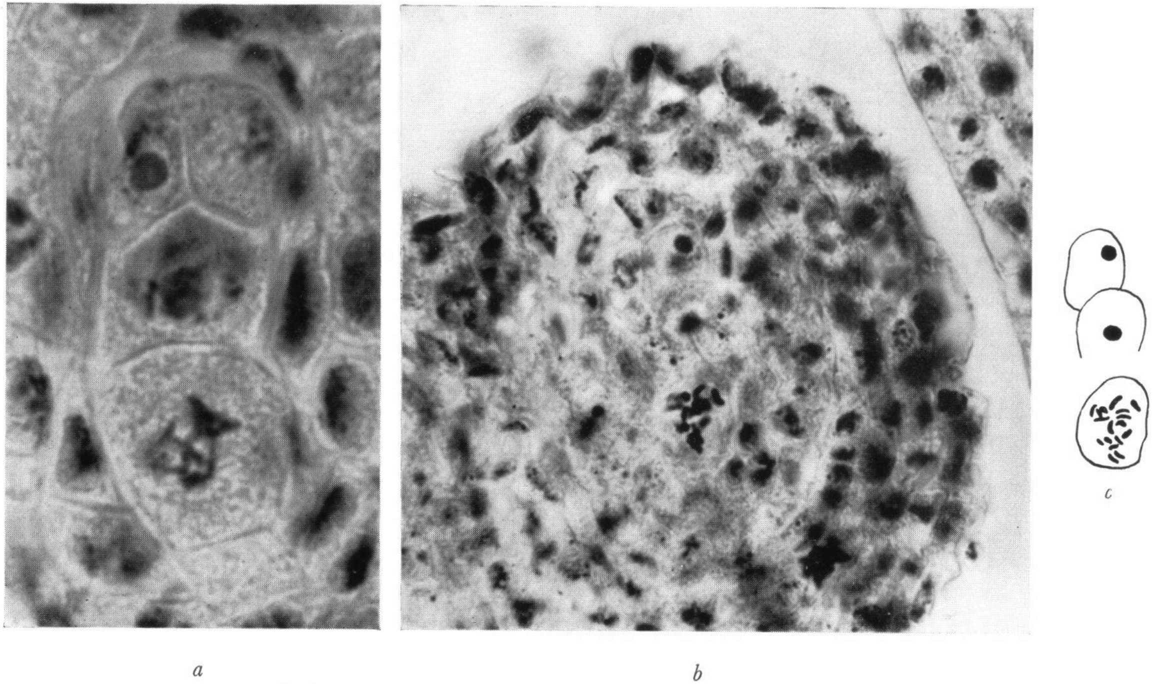

c


d


e

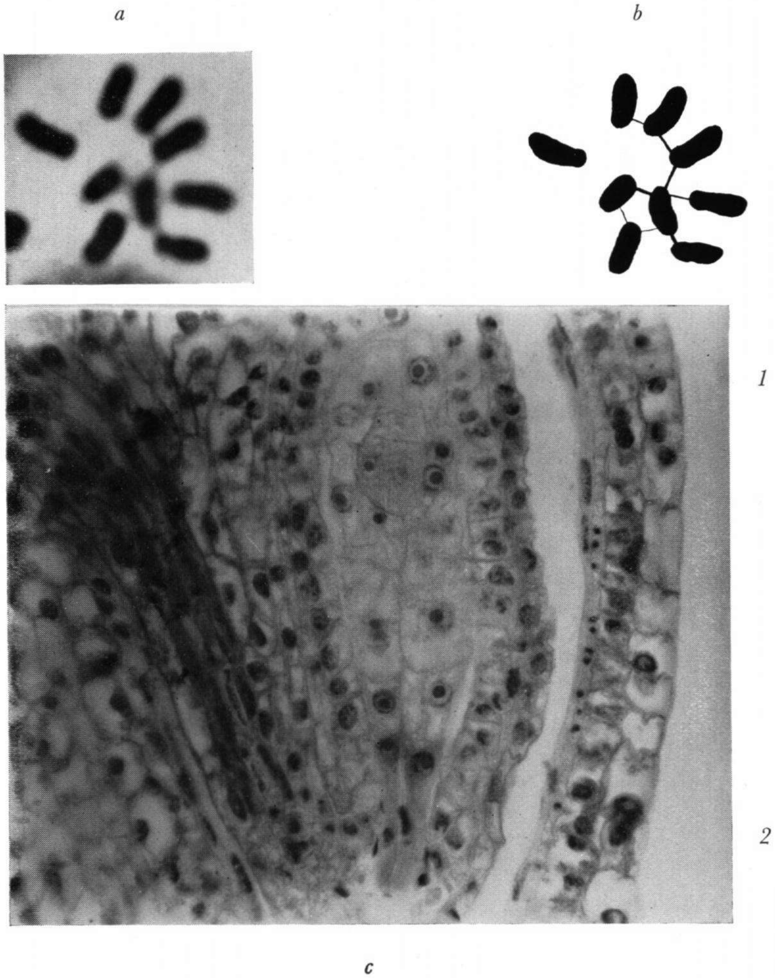

f

PLATE 5



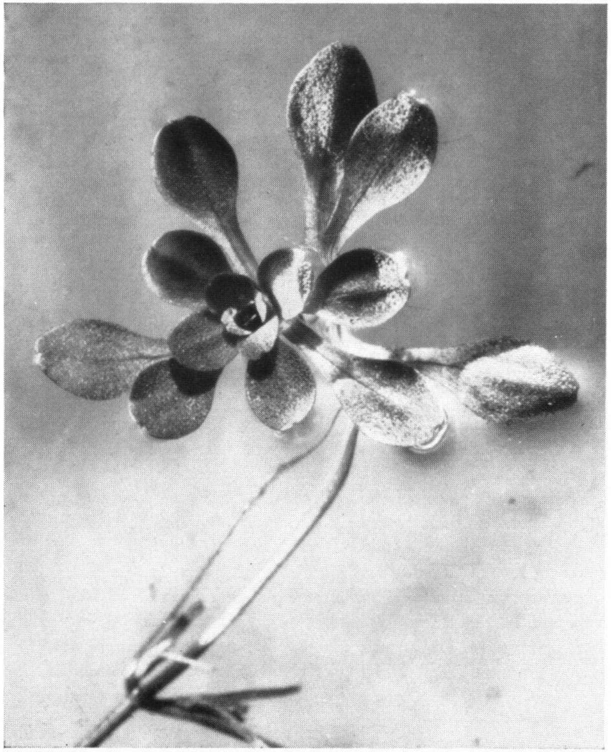
a. C. palustris. Longitudinal section of the ovule with T-shaped tetrad.
b. C. palustris. The same. Aposporous somatic cell near the base of the tetrad.
c. Explanatory diagram of *b*. 17 chromosomes can be counted.
a and *b* stained with crystal violet.

PLATE 6

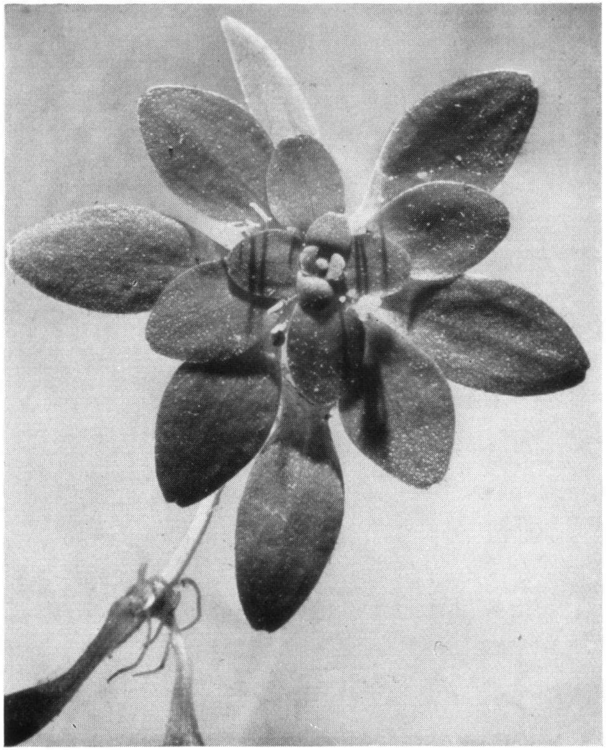


a. C. palustris. Part of mitotic metaphase, showing the "threads" between the chromosomes. Perm. Feulgen squash.
b. Explanatory diagram of *a*.
c. C. palustris. Longitudinal section of the ovule, stained with crystal violet.
1. young embryo surrounded by cellular endosperm.
2. chalazal haustorium cells.

PLATE 7


a

a. C. hamulata. Floating rosette of flowering plant. × 3½.


b

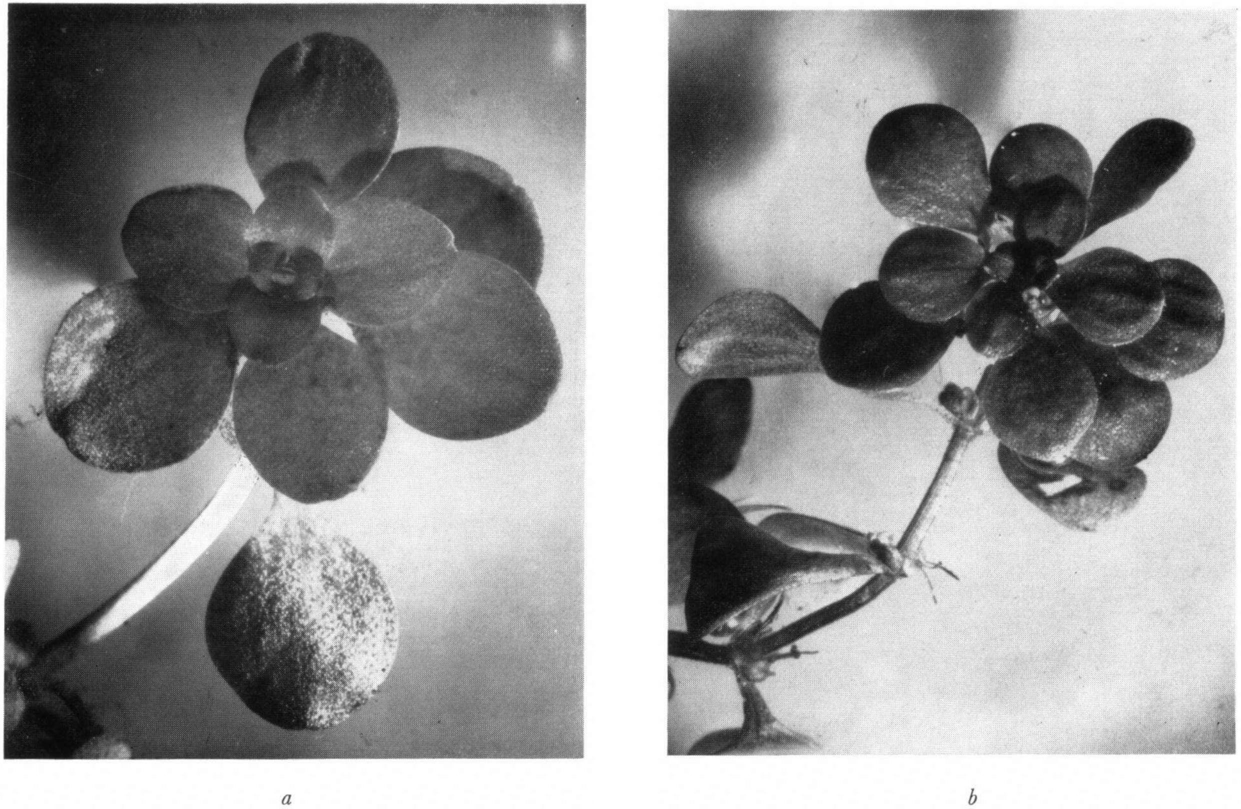
b. C. platycarpa. Floating rosette of flowering plant. × 3½.

PLATE 8

a

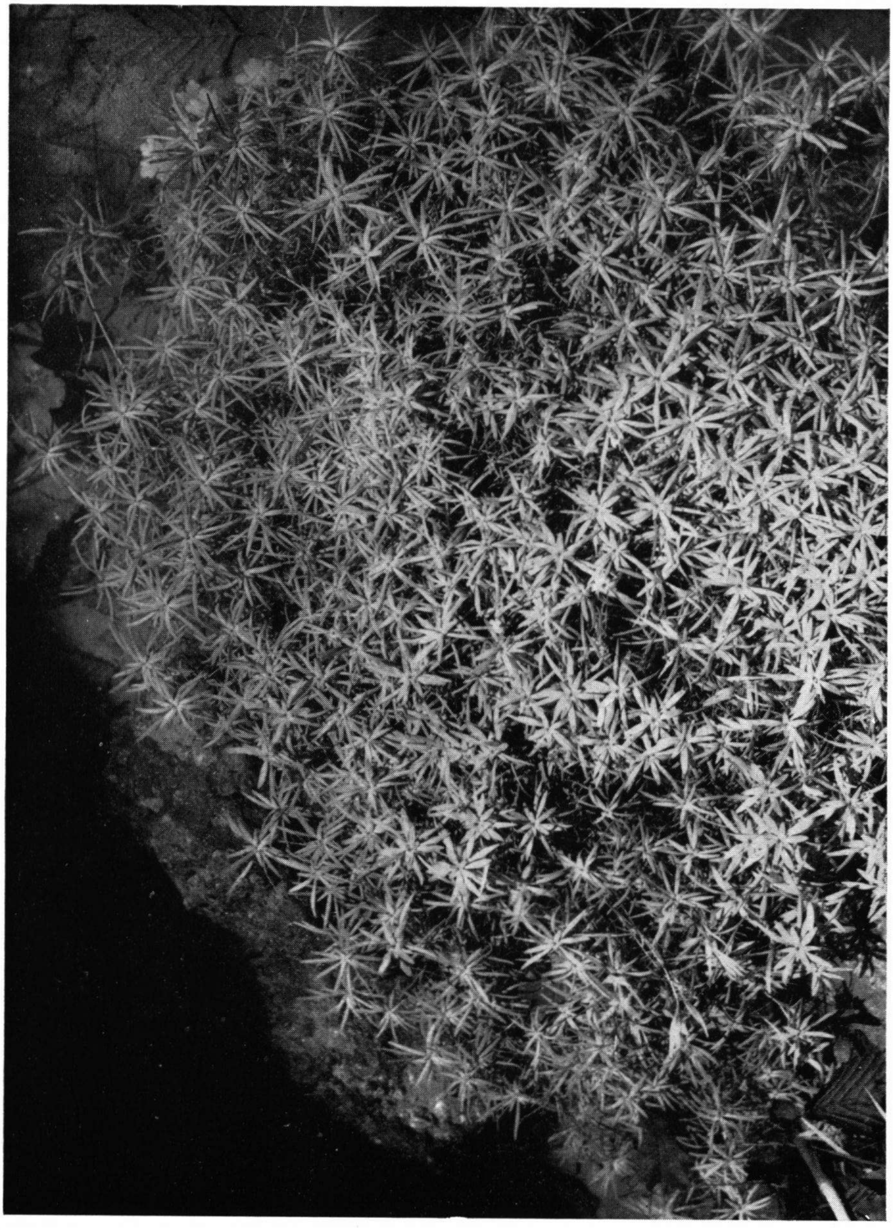
b

a. C. obtusangula from the Isle of Texel (Netherlands). Floating rosette of flowering plant. × 3½.
b. C. obtusangula from the province of Zeeland (Netherlands). × 3½.



a. C. stagnalis. Floating rosette of flowering plant. × 3½. *b.* C. palustris. Floating rosette of flowering plant. × $3^{1}/_{2}$.

PLATE 10

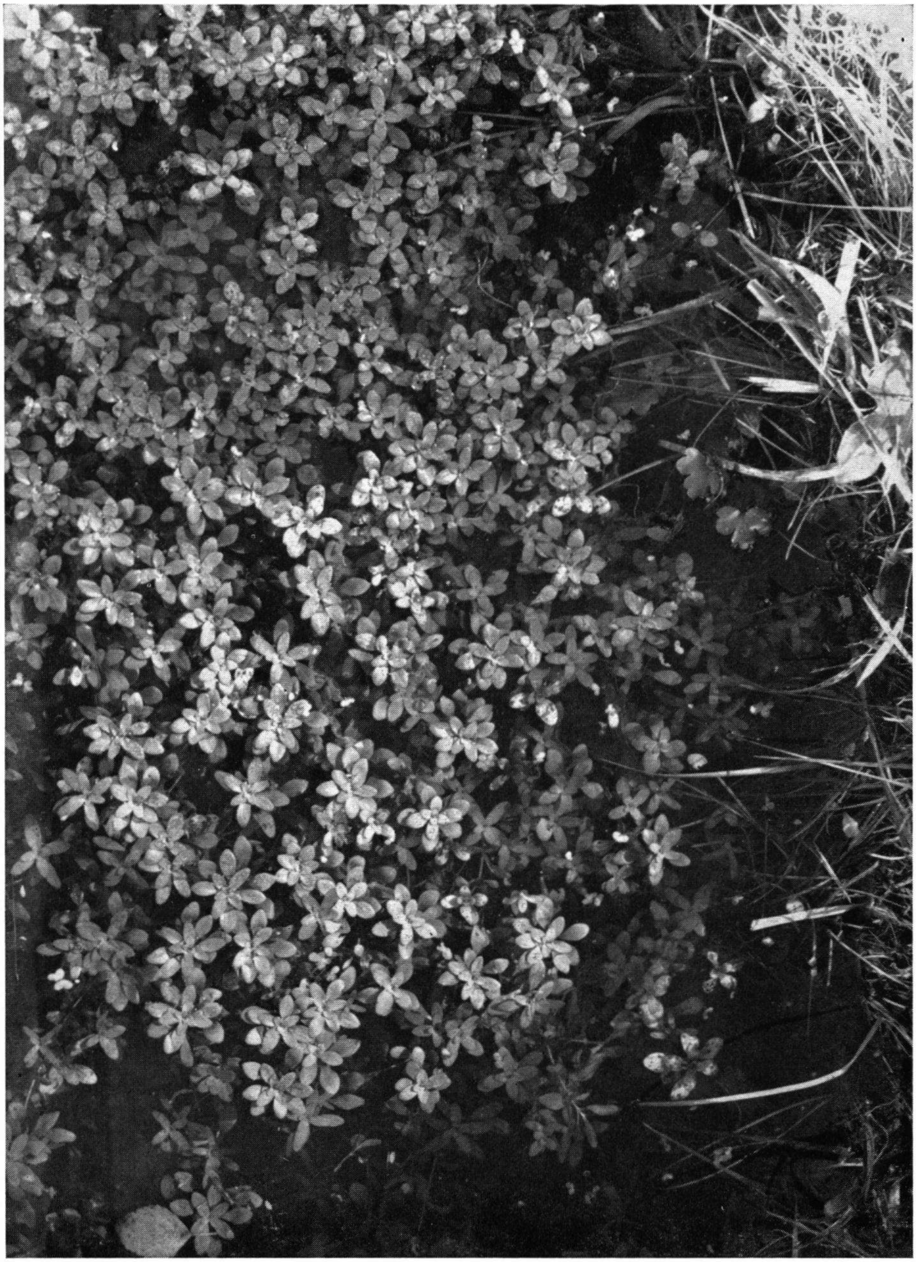


C. obtusangula. Waterform in winter. ½ × nat. size.

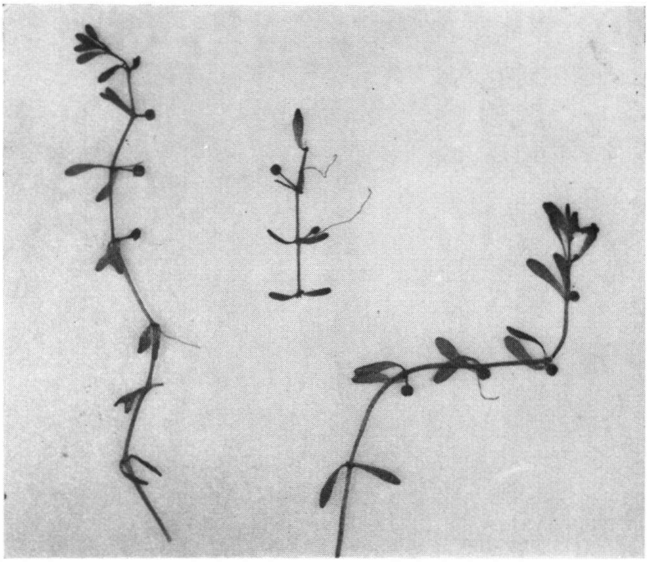
PLATE 11

C. obtusangula. Waterform in autumn. ¾ × nat. size. In the middle: summerrosette with rhomboid leaves, other branches with linear winterleaves.

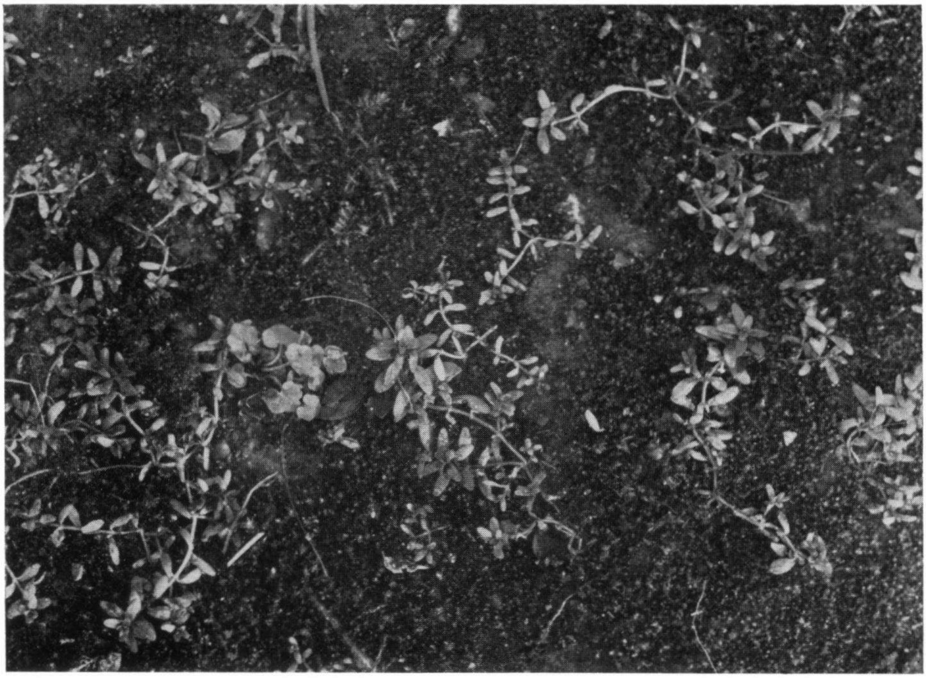
PLATE 12



C. platycarpa. Waterform in early summer. Floating rosettes with elliptical leaves. $^2/_3$ × nat. size.



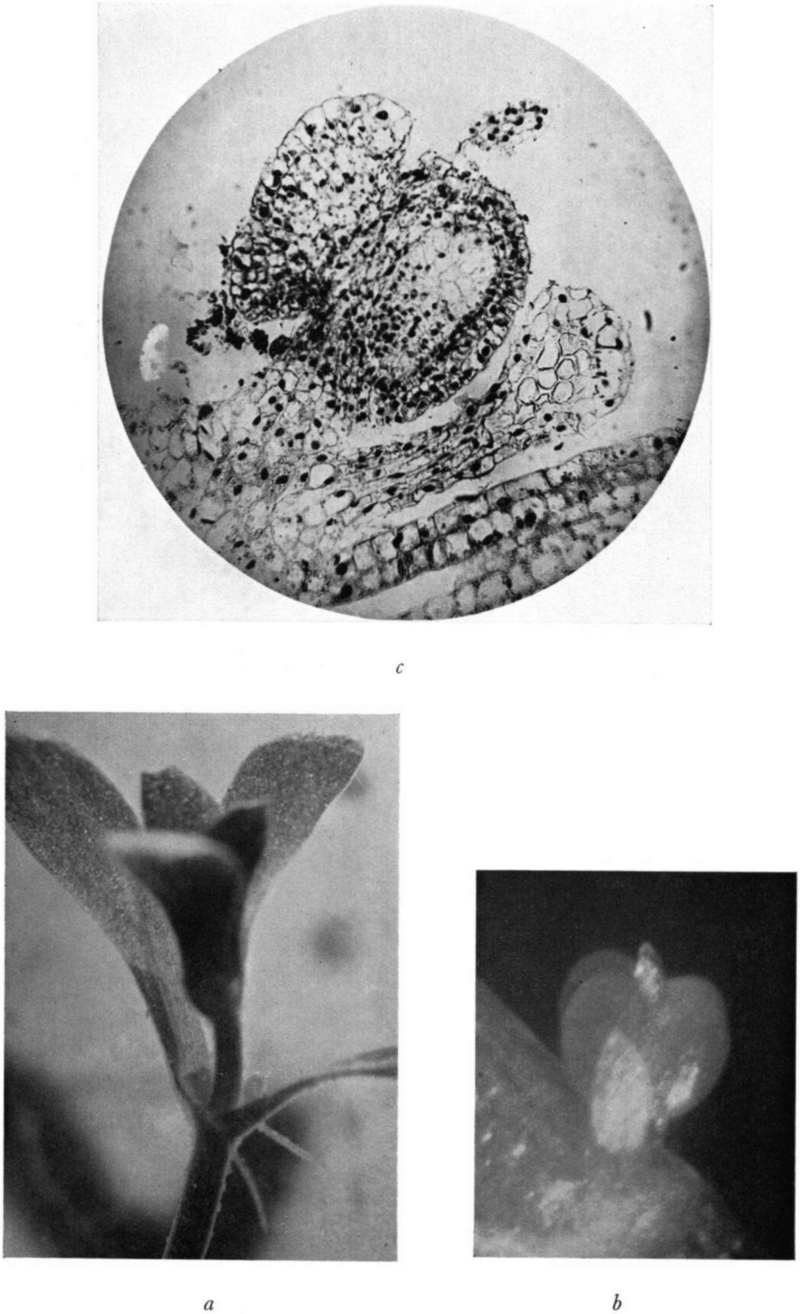
a



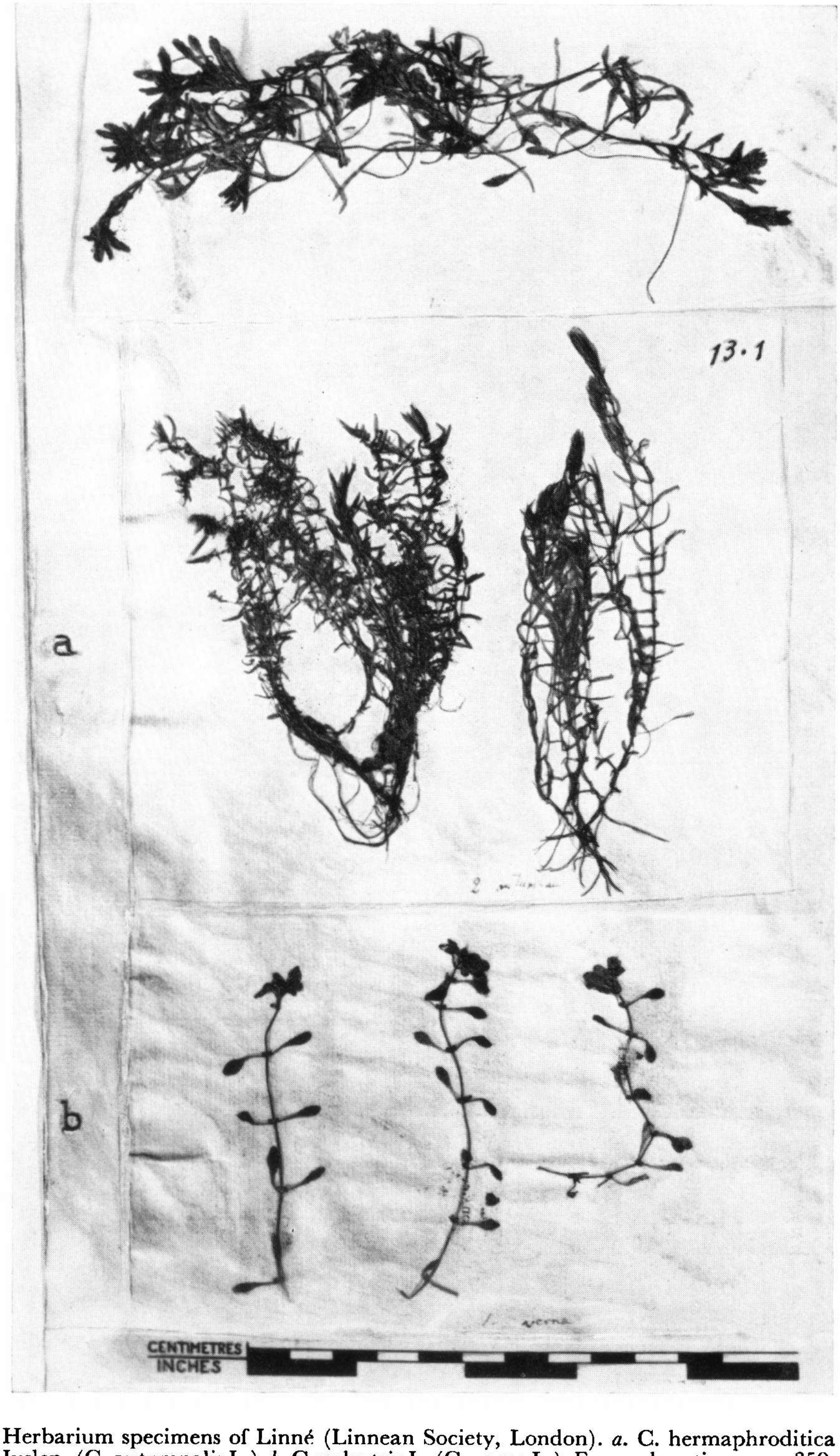
b

a. C. hamulata. Landform with stalked and sessile fruits. Nat. size
b. C. platycarpa. Landform. Nat. size.

PLATE 14

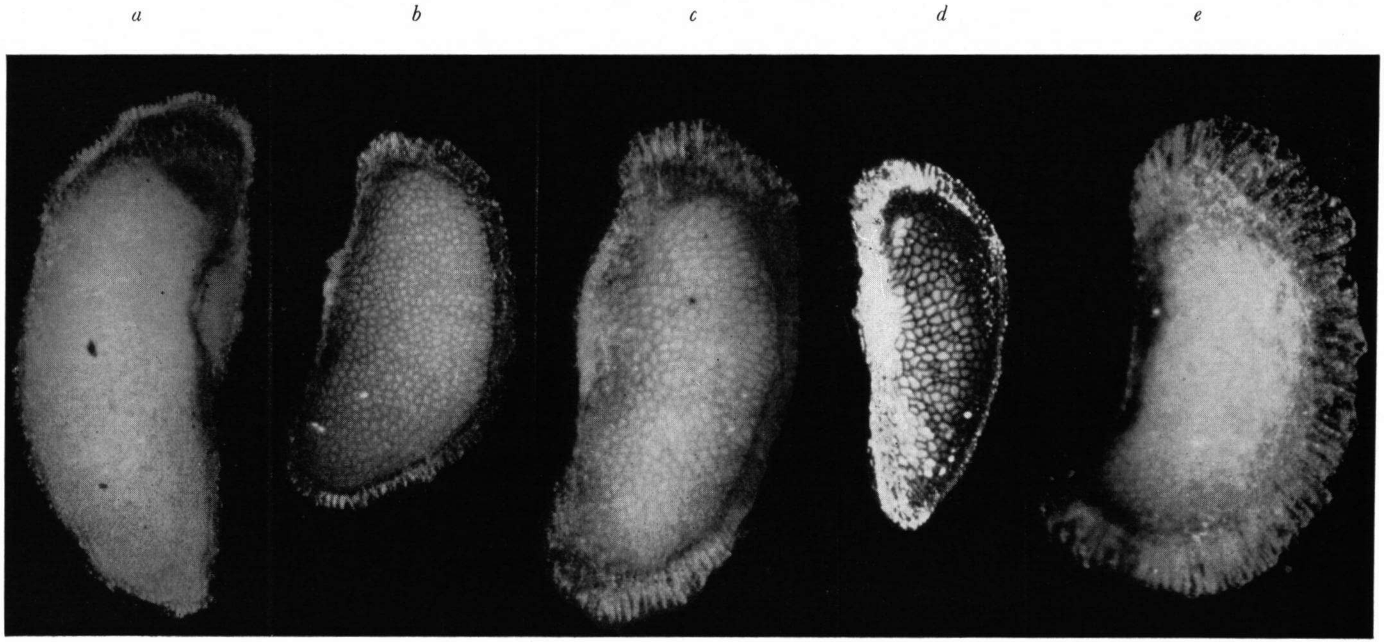


a. C. hamulata. Waterform. In the left leafaxil the female flower with reflexed stigmata, in the other leafaxil the young anther. × 7½.
b. C. palustris. Landform. Female flower with reduced stigmata. × 20.
c. C. palustris. Longitudinal section of a leafaxil with two flowers. × 45. On the left: pistil with partly reduced stigmata. On the right: reduced stamen with only a few pollengrains. Stained with crystal violet.



Herbarium specimens of Linné (Linnean Society, London). *a.* C. hermaphroditica Juslen. (C. autumnalis L.). *b.* C. palustris L. (C. verna L.). For explanation see p. 359.

PLATE 16



Seeds. × 50. *a.* C. obtusangula, *b.* C. hamulata, *c.* C. platycarpa, *d.* C. palustris, *e.* C. stagnalis.