TYGE CHRISTENSEN

VAUCHERIA COLLECTIONS FROM VAUCHER'S REGION

Det Kongelige Danske Videnskabernes Selskab
Biologiske Skrifter **16**, 4

Kommissionær: Munksgaard
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Synopsis

Modern taxonomy in the algal genus *Vaucheria* goes back to the basic but somewhat controversial work published by VAUCHER in 1803. This author distinguishes eleven species, ten of which are typified by illustrations and descriptions of plants from the Geneva region. The present paper gives an account of recent *Vaucheria* collections from the same region. The information gathered is intended to serve as a clue to the taxonomy of VAUCHER, at the same time adding to general knowledge of the species.

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Aims of Investigation

The present paper has two purposes. One is to improve knowledge of the Central European species of *Vaucheria* by studying their morphology and their occurrence in nature within a restricted area. The other is to solve some problems as to the identity of species established by VAUCHER (1803), by choosing for such study the region round Geneva where VAUCHER's observations were made.

For these two purposes the algae have been dealt with mainly as they appear when collected in nature. As some species may occur in running water, in stagnant water as well as on soil, this approach gives a good deal of variation even in a material that is genetically homogeneous or nearly so. More details of such variation mean a more precise concept of the species in question and knowledge of how the plants may appear in nature in this region is a prerequisite for a true understanding of VAUCHER's descriptions. On the other hand, the phenotypical variation may obscure smaller genotypical differences. Such differences are to be studied by growing related plants under equal culture conditions. For that purpose, however, strains from other parts of the world should be included along with plants from the Geneva region, which leads beyond the scope of the work undertaken here.

Material and Methods

Collections were made on 19–20 June 1954, 17–22 April 1957, 11 Sept. 1963 (only a few samples), 26 Oct. 1963, 2 April 1965 and 14–15 Feb. 1967. All the samples are from the area shown in Fig. 1.

In dealing with the material each species in each sample has been given a number of its own, and each drawing has been designated by a letter added to this number. These numbers and letters have been used in labelling the illustrations instead of an ordinary system of consecutive letters, because they enable the reader to see immediately whether two drawings of a given species show plants from the same collection or from different collections. "cr.c." after this designation indicates that the drawing in question shows material from a crude culture.

A magnification of 100 × has been used throughout except in Fig. 17. This makes it possible to read all dimensions from the figures by means of a centimeter rule, rendering superfluous the large number of measurements which would otherwise be

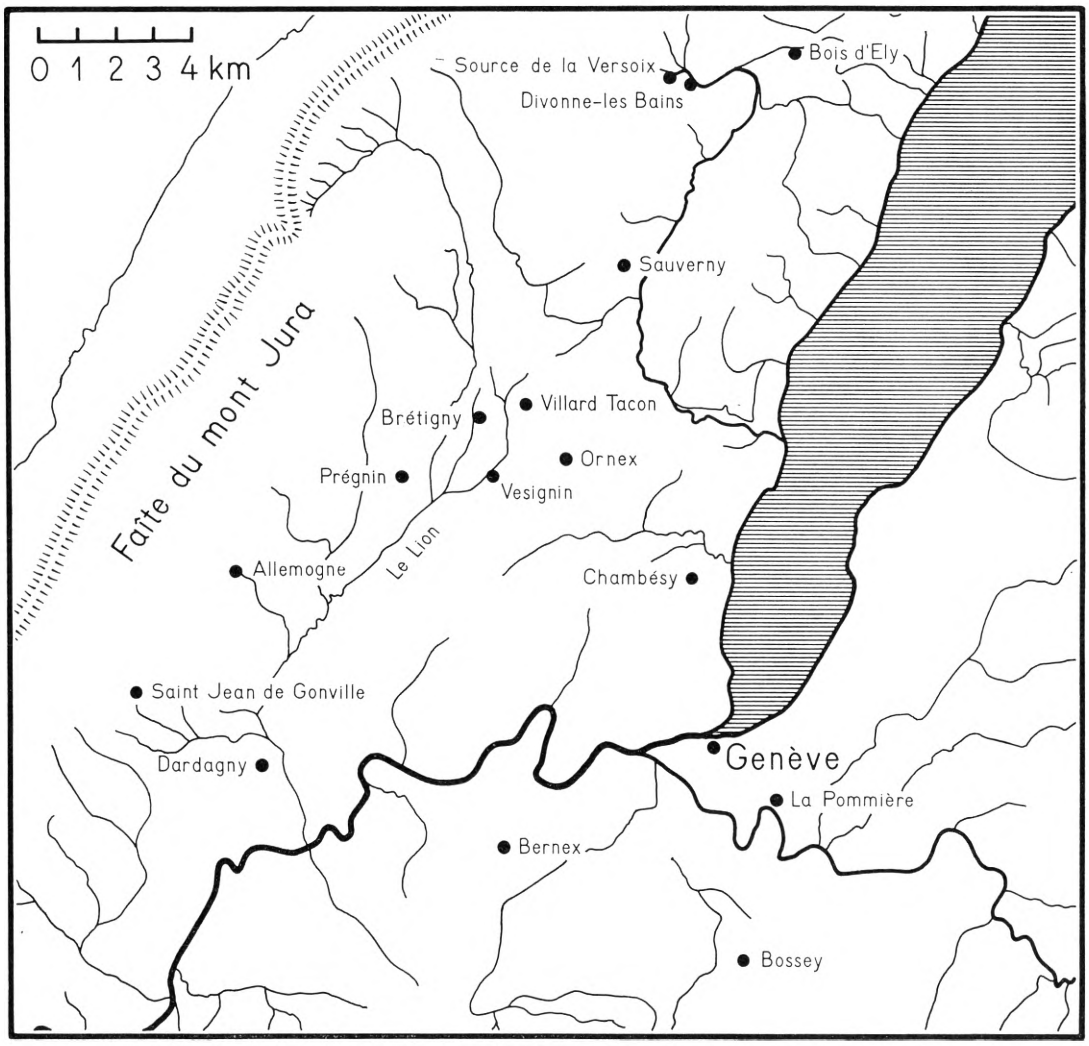

Fig. 1. Map showing the area of collecting and the places mentioned in the text.

given in the text. In all cases drawings were made from material kept in glycerol, which means that the dimensions are slightly smaller than in living plants.

The illustrations are mainly line drawings made with a uniform thickness of lines. In the case of thick-walled oospores, however, the thickness has mostly been especially accounted for, and the same applies to various other cases of remarkably thick-walled structures. Such walls often swell in glycerol and, consequently, may have been rendered thicker than they are in living material. Strongly gelatinized oogonial walls have been omitted, the outline of the oospore being shown instead. Shading in Fig. 17 is arbitrary and has also been applied to parts that were dead and empty at the time of collection.

Comments on the Individual Species

The material falls into eleven distinct taxonomic entities, referred to in the following by the letters *A* to *K*. Their sequence has been chosen to allow for the most convenient system of cross references, with no regard to natural affinities.

A. (Figs. 3–5). *Vaucheria canalicularis* (L.) T. CHRISTENSEN 1968, *Conferva canalicularis* L. 1753, *Vaucheria disperma* DC. 1801 c, *Ectosperma ovata* VAUCH. 1803, *Ectosperma cespitosa* VAUCH. 1803, *Vaucheria cespitosa* (Vauch.) DC. in LAM. et DC. 1805, *Vaucheria geminata* var. *caespitosa* STOCKM. 1890, *Vaucheria geminata* sensu GÖTZ 1897, non vel partim modo *Vaucheria geminata* (Vauch.) DC. in LAM. et DC. 1805, *Vaucheria woroniniana* HEERING 1907.

This is the species first studied by VAUCHER in its sexual condition, and undoubtedly also that first studied with aplanospores. VAUCHER found plants with aplanospores in the autumn of 1799, and in the course of the following winter carried out a veritable culture experiment with them, collecting the spores in December, observing their germination in February, and in April finding that the new-formed filaments bore spores similar to those collected in nature. A report on these observations was first presented at a meeting in Geneva on 17 April 1800, and later printed in Paris (VAUCHER, 1801). The alga with aplanospores was referred preliminarily to *Conferva fontinalis* L. taken as a collective species. In his final account VAUCHER (1803) named it *Ectosperma ovata*.

Before presenting his observations on the plants with asexual spores, VAUCHER also found filaments with sexual organs. He saw both antheridia and oogonia, and correctly interpreted them as male and female organs. Unfortunately he also considered the aplanospores to be the result of a fertilisation process, taking some sporangium initials for the male organs. Besides, his sexual plants were found in the cascades at the source of the Versoix River (Fig. 2), while the asexually reproducing material had been collected in muddy ditches. So VAUCHER was lead to regard his two finds as representing two different species. An illustration and a brief description of the sexual plant were included in his first report (VAUCHER, 1801).

In the summer of 1800 VAUCHER made some germination experiments with spores from the Versoix River source, and afterwards wrote a report dealing exclusively with this plant. This report, dated 8 Aug. (VAUCHER, manuscript 1800) and a plate in water colours were sent to "l'Institut" in Paris. They were presented on 8 Sept., 1800 (cf. Institut de France, Académie des Sciences, 1912) at a meeting of the "Classe des Sciences Physiques et Mathématiques", which for some years after the revolution replaced the Academy of Sciences, and they are still kept in the archives of the Academy.

The second report by VAUCHER was never published as such, but VAUCHER's former pupil A. P. DE CANDOLLE, then a student in Paris, wrote a brief summary of it for a monthly abstract journal (CANDOLLE, 1801 b). On the same occasion DE CAN-

DOLLE epitomized VAUCHER's first report (CANDOLLE, 1801 a), the summary being accompanied by a reproduction of some of the illustrations made for this report, including that of the plant from the Versoix River source.

Shortly afterwards DE CANDOLLE published a paper of his own, suggesting a subdivision of the genus *Conferva* and introducing among others the generic name *Vaucheria*. One of the species referred to this new genus was VAUCHER's plant from the Versoix River source, now named *Vaucheria disperma* by DE CANDOLLE. As had been the case with VAUCHER's first report, the contents of DE CANDOLLE's paper were first summarized in the abstract journal (CANDOLLE, 1801 c), later published in full (CANDOLLE, 1802). The short Latin diagnosis is given in both publications. For a detailed description and an illustration of the species reference is made in the first case to the summaries by DE CANDOLLE (1801 a and b), in the latter to the paper by VAUCHER (1801), published in between.

VAUCHER, in his final comprehensive account (1803) modestly refused to accept the generic name *Vaucheria*, and instead called the genus by the new name *Ectosperma*. For the plant from the Versoix River source he introduced the epithet *cespitosa*. The illustrations and part of the text are taken from his unpublished second report (VAUCHER, manuscript 1800). Besides, there is a reference to the description in his first report (1801), whereas no mention is made of the specific name suggested by DE CANDOLLE (1801 c).

In the third edition of LAMARCK's Flore Française (1805), DE CANDOLLE accepted the specific name preferred by VAUCHER, but combined it with the generic name *Vaucheria*. The epithet *disperma* was added as a synonym.

WALZ in his monograph (1866) discarded most of VAUCHER's species, among these *E. cespitosa* and *V. geminata*, but uncautiously used some of the epithets for species independently described by himself. Thus the epithet *geminata* was applied to a "new species" which was, at least in part, *Vaucheria cespitosa* (Vauch.) DC. This started some confusion which, through a sequence of errors in reading and observation, lead to a merging of *V. cespitosa* (Vauch.) DC. into *V. geminata* (Vauch.) DC., along with the synonym *V. disperma* only remembered by few authors. STOCKMAYER (1890) pointed out some important differences between the two entities but accepted them as varieties of the same species because of a wrong interpretation of the galls correctly interpreted by VAUCHER. GÖTZ (1897) realized that there were two independent species but applied the epithet *geminata* to the wrong entity, and finally HEERING (1907), correcting this, introduced the new epithet *woroniniana* for the species erroneously called *geminata* by GÖTZ.

The specific identity between *Vaucheria disperma/cespitosa* on one side and *A*, *Vaucheria canalicularis* on the other appears both from VAUCHER's description and from his observations on the ecology. The arrangement of the oogonia on the fruiting branch of *V. disperma* is that of either *A* or perhaps *C* and—although VAUCHER's figure is not very detailed—can hardly fit with any other species. In the 1803 illustration all sets of fruiting organs are shown in a terminal position on long shoots. This

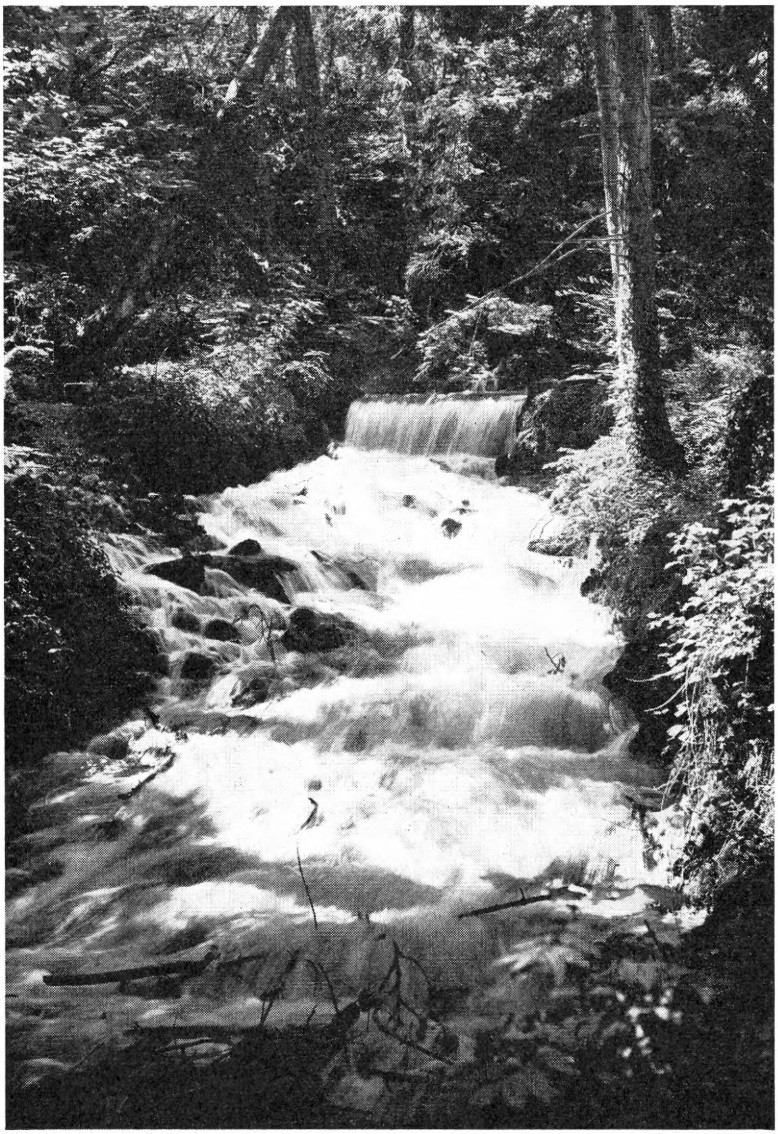

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Fig. 2. Source of the Versoix River springing from several outflows at the bottom of a wooded slope.

is common in both *A* and *C* when growing in dense tufts, while in all others terminal fruiting is something exceptional. The tufted growth described by VAUCHER and referred to by the specific name *cespitosa* is a regular phenomenon in *A* when the plant grows at the edge of swiftly running water (it was also referred to by the name given to it by DILLENIUS, 1741). Something similar may be found in *C* though more rarely.

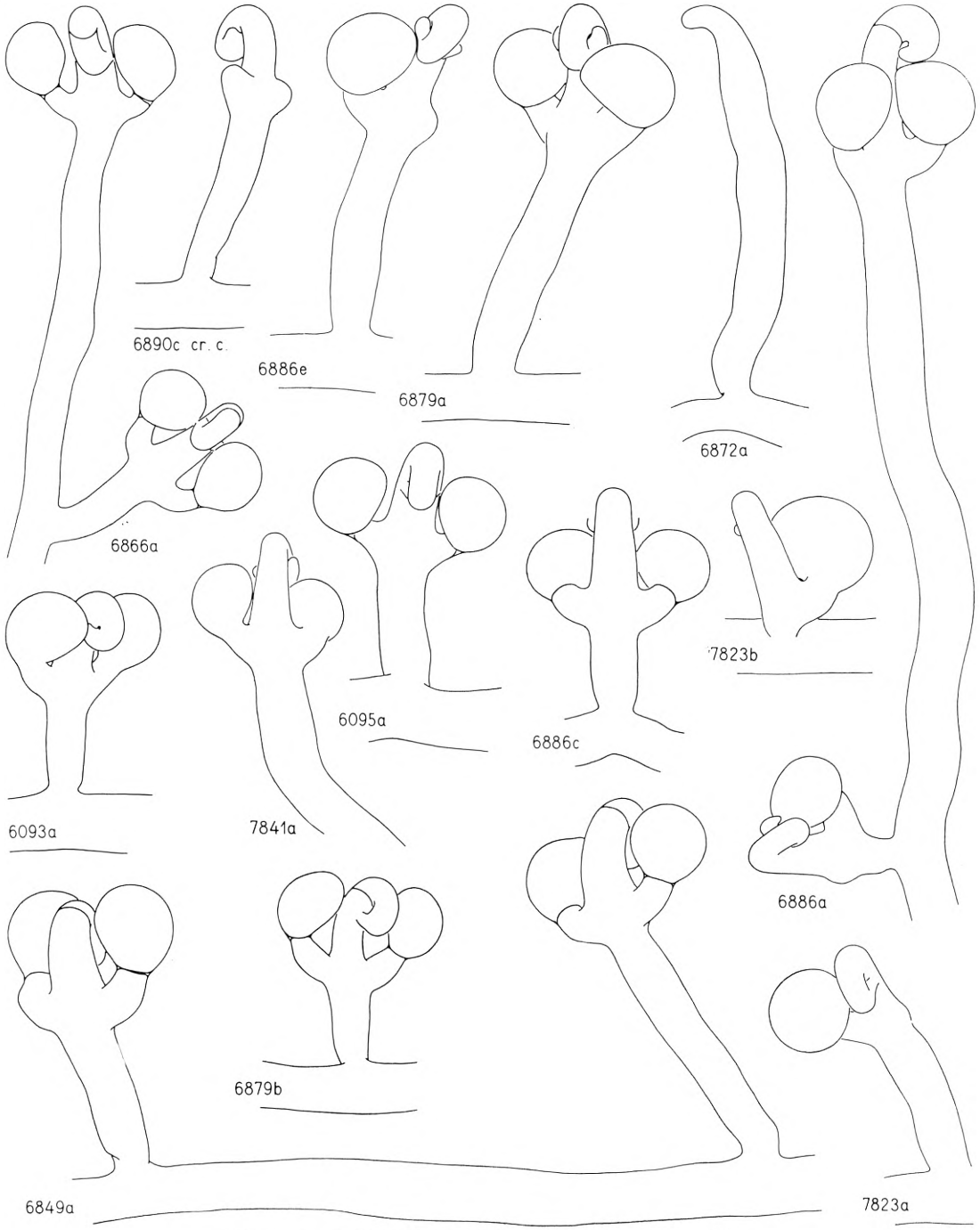


Fig. 3. *A*; *Vaucheria canalicularis*, sexual organs. × 100.

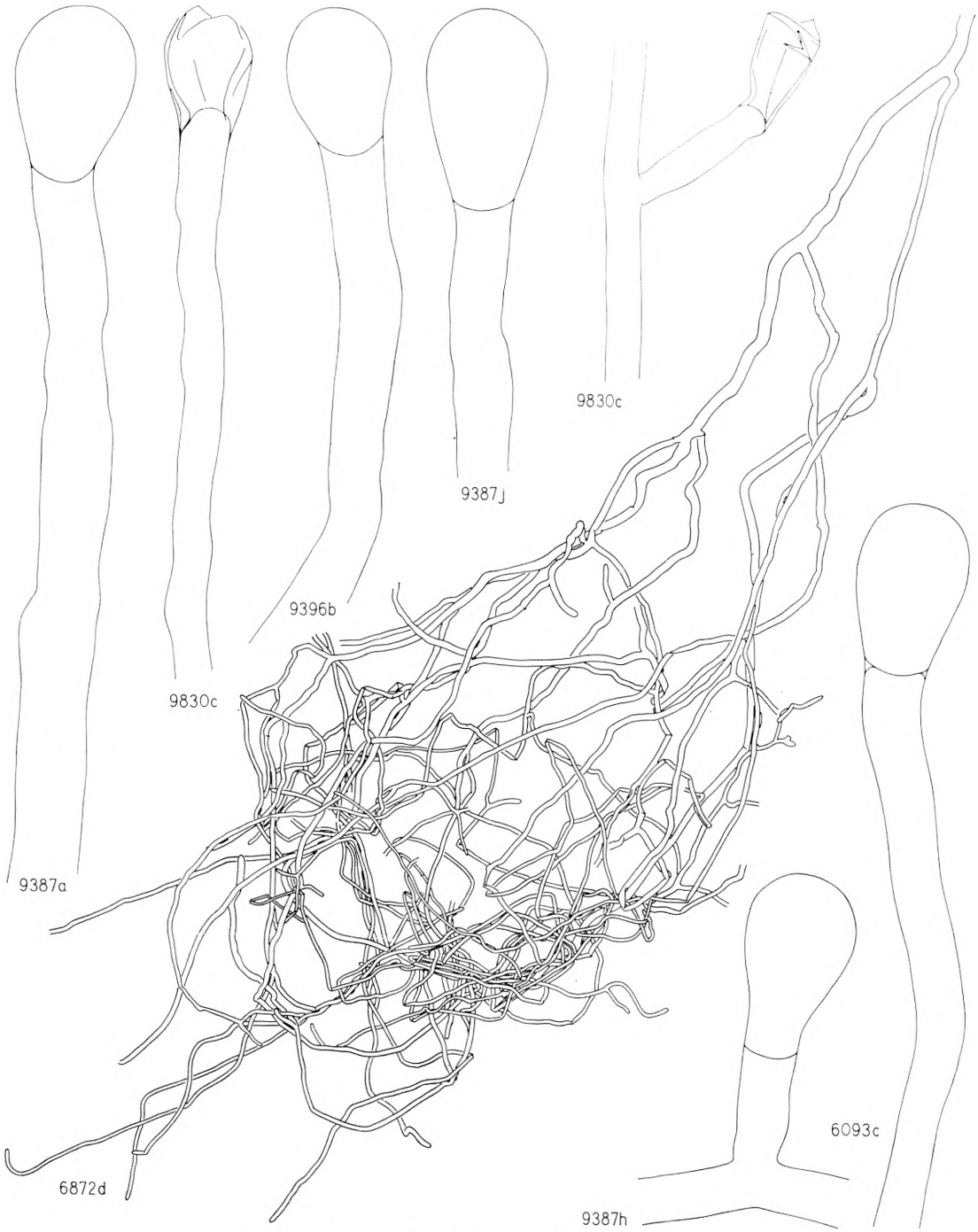


Fig. 4. *A*; *Vaucheria canalicularis*, rhizoids and aplanosporangia. × 100.

However, since *C* is covered by VAUCHER's *Ectosperma cruciata*, said to be much the thinnest of the species with two oogonia per antheridium, *A* must be the plant covered by his *cespitosa*, previously named *Vaucheria disperma* by DE CANDOLLE. As to the ecology, VAUCHER says that *Ectosperma cespitosa* is abundant in all the sources at the foot of the Jura Mountains and that it is the only species he has found in them. Today *A* is dominant in the same places. *C*, *E* and *J* have also been found in such places by the present author, but they do not occur with such regularity nor in such abundance as *A*, and their appearance in nature is different from that described by VAUCHER for *Ectosperma cespitosa*. VAUCHER found that *E. cespitosa* abounded in the source of the Versoix River and first studied it here. Today, in most seasons *A* is very abundant a little below the source, where the stream receives more light. The source itself is perhaps more shaded than in the days of VAUCHER (cf. Fig. 2), but *A* has been found there at all visits though less plentiful, and no other species has been noticed except for a little of *E*.

Thus there is ample evidence that *Vaucheria disperma* is identical with *A*. It may be added that this species is very common and very conspicuous in the aquatic and semiaquatic habitats of the Geneva region. So it must inevitably be among the species dealt with by VAUCHER and it seems natural that this was the species first observed by him as to sexual as well as asexual reproductive organs before he turned his eye to other species.

Nearly half the author's collections are from ditches. VAUCHER collected his material of asexually reproducing plants in ditches (the author has it from the Versoix River source as well) but does not mention the sexual *E. cespitosa* from such places. It seems improbable that he never found sexual stages in these environments. More likely he did not realize that such sexual plants represented the same species as his finds from the sources. Instead, he may have referred them to his *E. geminata*, cf. p. 12.

In the author's material a large majority of the samples with *V. canalicularis* also contain other species. As appears from Table 1 (p. 29) the forms most commonly found together with it are *V. cruciata*, *V. frigida* and *V. bursata*. Without exception, the stations are associated with running water. A little less than a third of the samples are from swift waters, where the plant is mostly found as densely tufted masses at the water's edge. A smaller fraction are from slow water courses or stagnant waters such as ponds with brooks running into them and ditches with little water left. In such places the species forms loose masses of relatively long filaments when growing submerged, and dense mats where there is very little water left, as on the bottom of ditches that are drying out. More than a third of the samples come from shady places at the border of streams and ditches. Unlike the lawn-like growth found in very shallow sheets of water on the bottom of ditches exposed to full day-light, the plants growing on soil above the water normally form an open tangle of creeping filaments. Finally three samples are from level ground with a terrestrial phanerogam vegetation but situated less than a meter from a freshwater course.

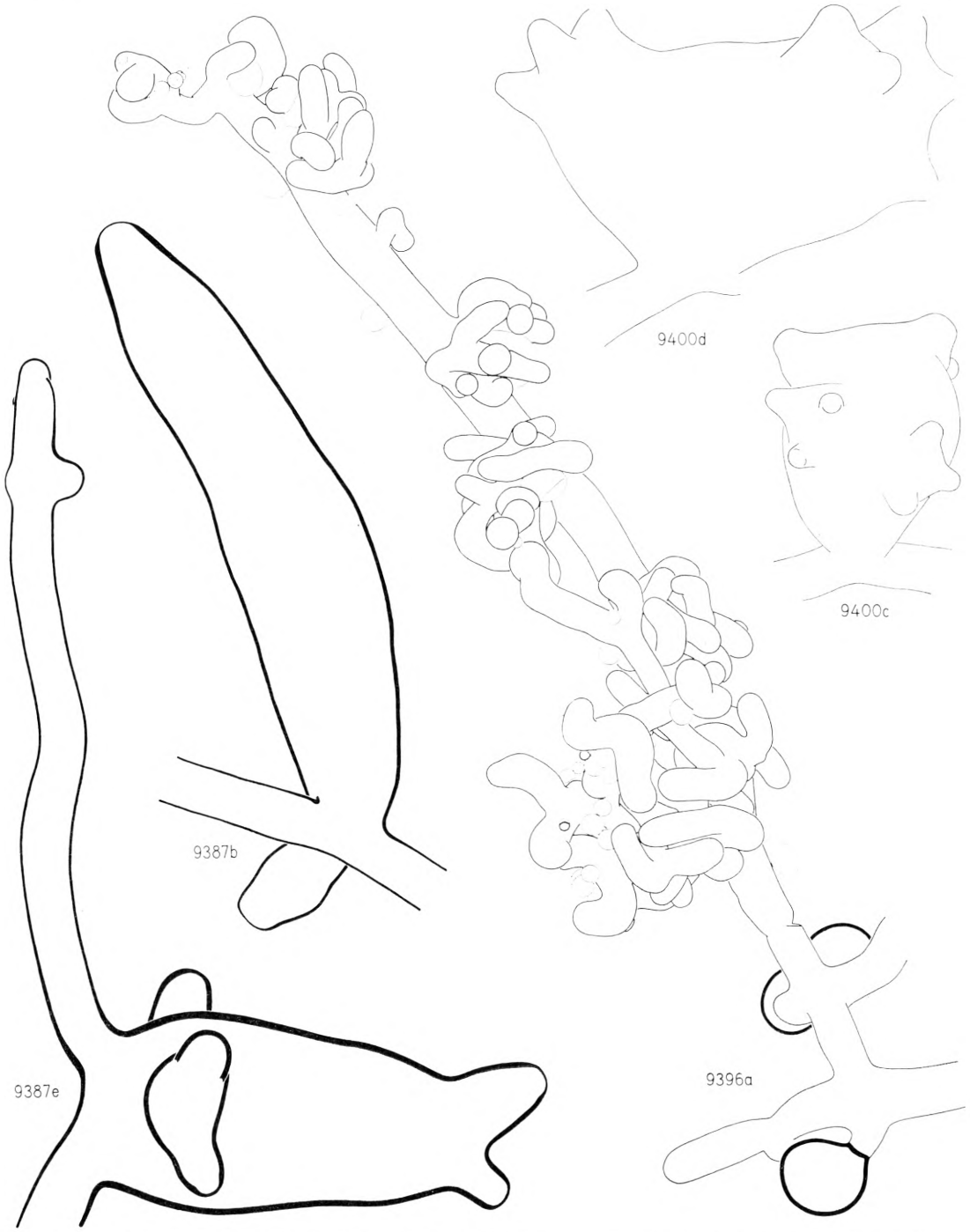


Fig. 5. *A*; *Vaucheria canalicularis*, deformations caused by parasites. Smaller fungal sporangia not shown. × 100.

In 36 of the 51 samples sexual organs are found. 6 collections have both oospores and aplanospores, and 6 have only aplanospores. Most of the aplanospore-forming samples are from October, while the percentage of sexually reproducing plants is about the same at all seasons of collecting, except that most samples from February are sterile.

Gall formation caused by the rotatorian *Proales wernecki* (Ehrb.) occurs in two samples, both collected in October and both with sexual organs and aplanosporangia as well. One of them was taken in the Versoix River at Divonne-les Bains. In this, most of the galls are relatively narrow with two openings at the top and sometimes one or more at the base (Fig. 5, 9387). In the other sample *V. canalicularis* is mingled with *V. frigida* and *V. bursata*, collected amongst moss on a stone in the brook that separates Switzerland and France near the road between Dardagny and St. Jean de Gonville. In this, the breadth of most galls is greater than the length and the more elongate types are vase-shaped (Fig. 5, 9400). The number of preformed openings is considerable, usually between 5 and 10 with 16 as the maximum number observed.

In three samples there are growth disturbances connected with attacks by the phycomycete *Zygorhizidium vaucheriae* Rieth. None of the samples were submerged at the time of collection. One was taken in April on the muddy bank of a brook in the wood northnorthwest of Bernex, one in June on the steep side of the lode carrying water from the former Marsh of Bossey, and one (Fig. 5, 9396 a) in October at the source of Allemogne, away from the large basin in a corner where just a little ground water was oozing out. The Bernex sample contains more *V. cruciata* than *V. canalicularis*, but only the latter species is infected by the fungus. In all cases the short contorted laterals are rather scattered compared with the situation found in attacked *V. cruciata*. The morphology of the fungus agrees well with the description given by Rieth (1967).

B. (Fig. 6). *Vaucheria geminata* (Vauch.) DC. in Lam. et DC. 1805, *Ectosperma geminata* Vauch. 1803, non *Vaucheria geminata* sensu Götz 1897.

Ectosperma geminata is said by Vaucher to resemble *E. cespitosa*. The distinctive characters mentioned are that the oogonia are stalked and borne on special fruiting branches instead of forming terminal pairs on the main filaments, that the oospores are concave on one side, not rounded all over, and that the species forms dull green masses in ditches with stagnant water, not dark green tufts in running water.

The different shape of the oospores was probably often difficult to see in the primitive microscope at Vaucher's disposal—it is not apparent from the illustrations, which, according to the introduction, were made by his wife. The other characters would serve to separate *B* together with stagnant water forms of *A* from swift water forms of *A*. Very probably such separation covers Vaucher's species concept, which was apparently guided more by field characters than seems appropriate today. Tradition has attached Vaucher's specific name with something like *B*. Though the identity is not certain the author sees no reason to change current usage of the name since,

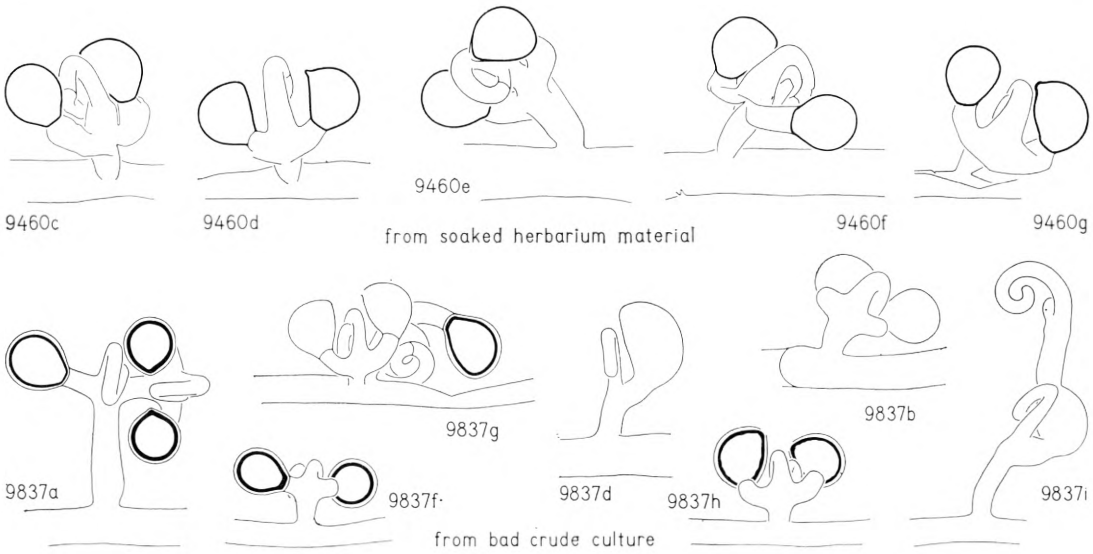


Fig. 6. *B*; *Vaucheria geminata*. × 100.

in any case, *B* may fall under VAUCHER's concept of *E. geminata*, while other names are available for *A*.

The only good material of *B* at the author's disposal is a herbarium specimen kept at the Conservatoire botanique de Genève. It was collected on 24 Feb., 1867 in "fossés pleins d'eau" at la Pommière, a place now occupied by gardens and houses. In addition, a few similar looking filaments have been found in an old crude culture. The culture was in a rather bad condition and most fruiting organs of this species were aborted. Illustrations of this plant, therefore, are given with considerable reservation. The sample in question was collected on 14 Feb. 1967 in a meadow south of Brétigny, growing in grass close to an ice-covered pool in a place obviously much trodden by cattle in the summer.

C. (Fig. 7). *Vaucheria cruciata* (VAUCH.) DC. in LAM. et DC. 1805, *Ectosperma cruciata* VAUCH. 1803, *Vaucheria debaryana* WOR. 1880.

According to VAUCHER, this species grows in the same places as *V. geminata*. In its general appearance, too, he finds it very similar to this species, and therefore will not exclude the possibility that it is only a variety of it. As distinctive features he mentions that the filaments of *V. cruciata* are much thinner, that all dimensions of its fruiting organs are about half those found in *V. geminata* and that the antheridium is shaped like a cross. Later authors have failed to refind the peculiar type of antheridium indicated by VAUCHER, and therefore have mostly regarded *V. cruciata* as a species inquirenda, but the agreement between *C* and *V. cruciata* in size and general appearance as well as in habitat make their identity obvious. VAUCHER's description of the antheridium certainly does not apply, but the structures in question are delicate and

give little contrast, so VAUCHER cannot have seen them very clearly through his primitive microscope. He also describes the antheridia of the Corniculatae as being straight at the beginning and coiled after fertilization (1803, p. 17), and draws the emptied antheridium of *V. canalicularis* like those of the Corniculatae. When seeing *V. cruciata* best he has apparently been able to distinguish the striking feature of spouts issuing at right angles to the antheridium branch, and then perhaps has conjectured the terminal part of the antheridium to be of the standard type also erroneously attributed to *V. canalicularis*, only thinking it was hard to see because of the coiling.

The species is commonly associated with *V. canalicularis*, *V. bursata* and *V. frigida*, each of which occurs in about half the samples containing *V. cruciata*, cf. Table 1. In one sample only it is unaccompanied by other species of *Vaucheria*. This sample was taken in the rapids of a brook otherwise devoid of larger algae, and consisted of small cushion-like masses so heavily encrusted with lime that they felt hard and stone-like when collected. It is remarkable in consistently having only one oogonium on each fruiting branch. Otherwise two is the normal number; mingled with two-spored branches one-spored are of frequent occurrence, while branches with three are pretty rare.

More than half of the samples were taken on soil near running water; a smaller number were actually in the water, and a few were found on more or less level ground in places which are probably flooded by water now and then.

The majority of finds are from April, but the species has also been found in February, June and October. In February the plant was mostly sterile, otherwise nearly all samples are fruiting.

Growth disturbances caused by *Zygorhizidium* are found in one sample, taken in April in swiftly running water in a roadside ditch between Sauverny and the frontier station. Mostly, the contorted laterals form dense clusters separated by relatively long spells of normal looking filament. The primary sporangium found in the centre of such a cluster often reaches a considerable size, like that pictured by RIETH (1967) in his fig. 1g and others. The infected filaments are too dirty to allow a closer study of smaller sporangia sitting on their surface. The zygotes, however, stand out clearly and show a coating of veritable spines, longer and more pointed than those pictured by RIETH and those seen by the author in the parasite of *V. canalicularis*.

D. (Fig. 8). *Vaucheria terrestris* (VAUCH.) DC. in LAM. et DC. 1805, *Ectosperma terrestris* VAUCH. 1803, non *Vaucheria terrestris* sensu GÖTZ 1897.

This species is said by VAUCHER to occur on moist soils during autumn and winter. This applies to *D*, and there is complete agreement between *D* and the description and figure of *E. terrestris* given by VAUCHER, so identity is quite obvious. From the author's observations the species appears rather uniform in morphology as well as ecology. At the same time, however, it is very closely allied to *E* as well as *F*. The features distinguishing it from these allies are pointed out in dealing with the species in question.

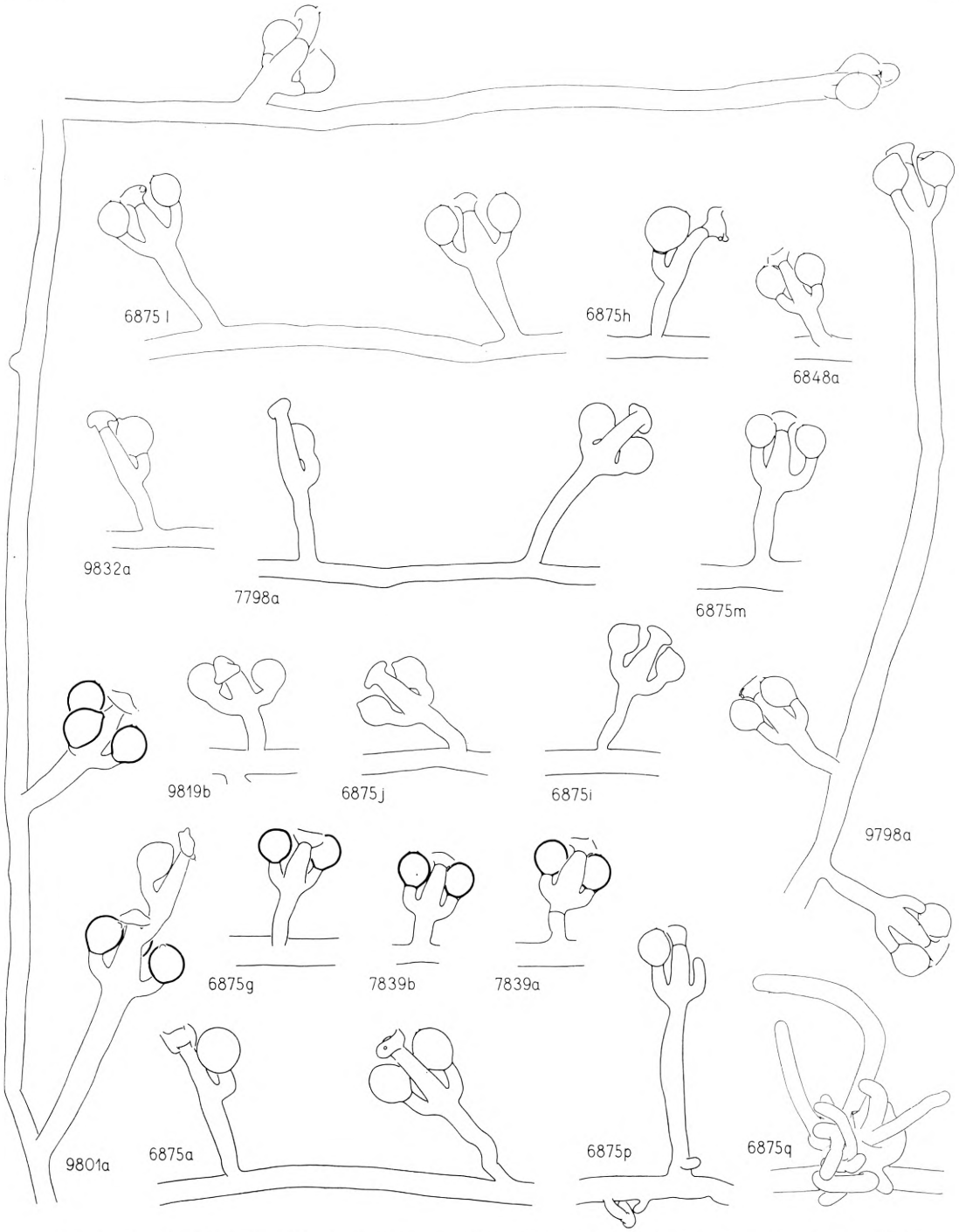


Fig. 7. *C*; *Vaucheria cruciata*. Lower corner right: deformations caused by *Zygorhizidium*. × 100.

Nearly all that has been collected of *V. terrestris* was taken in October, growing on soil in fields or gardens, mostly mingled with *F.* A single find was made in February. Three finds from April may belong in the same species but may also be small representatives of *E,* and therefore have been registered as unidentified.

All samples obtained were fruiting at the time of collection.

E. (Fig. 9). *Vaucheria frigida* (Roth) C. Ag. 1824, *Conferva frigida* Roth 1797, non *Conferva frigida* sensu Dillwyn 1802, *Ectosperma hamata* Vauch. 1803, *Vaucheria hamata* (Vauch.) DC. in Lam. et DC. 1805, *Ectosperma multicornis* Vaucher 1803, *Vaucheria terrestris* sensu Götz 1897, non *Vaucheria terrestris* (Vauch.) DC. in Lam. et DC. 1805. — Uncertainty as to the proper application of Art. 13 of the Code of Nomenclature makes it doubtful whether the name *frigida* or the later name *hamata* should be used (cf. Christensen, 1968). Pending a clarification of this matter the author prefers to use the epithet *frigida* to avoid confusion of *V. hamata* (Vauch.) DC. with *V. hamata* sensu Götz.

Ectosperma hamata, according to Vaucher, has oospores more rounded than those of *V. terrestris* but less so than the aplanospores of *V. canalicularis.* Otherwise, it resembles *V. terrestris* rather a lot in morphology but differs ecologically by growing and fruiting submerged on the bottom of ditches and by being characteristic of early spring. It is said to be rather common in the Geneva region. As *V. frigida* looks like a bigger *terrestris,* is common in Vaucher's region, and sometimes submerged, the identity of Vaucher's plant seems beyond discussion. It may be added that *V. frigida* has been found in the only locality mentioned by Vaucher for *E. hamata,* namely the ditches in the Marsh of Bossey. Only this gives very little extra support, as the marsh has been drained and the ditches replaced by one deep lode, in which the plant is now to be found.

Proliferation of the fruiting branches often occurs. It is obvious, and generally agreed on, that Vaucher's *Ectosperma multicornis,* characterized by having several antheridia on each fruiting branch, is nothing but a proliferating state of a plant that otherwise has only one. The species shown in Vaucher's illustration must be *V. frigida.*

V. frigida has larger dimensions than *V. terrestris* in all respects, thicker tubes, thicker fruiting branches, less densely coiled antheridia and larger oospores. As a vague but rather general character it can be added that fruiting branches of *V. terrestris* often exhibit an elegant straightness in their lines, whereas those of *V. frigida* show a somewhat elephant-like plumpness, often with small irregular bends.

Even kept apart from *V. terrestris, V. frigida* is not absolutely uniform. In addition to plants that agree entirely with the Dillenian type material there are some, like 6898 and 7805 (Fig. 9), with thinner filaments and less elongate oogonia, and others that combine narrower filaments with greater distance between antheridium and oogonium and a more pointed oogonial beak. These aberrant forms seem to differ little from the rest as to their occurrence in nature, and are comprised with them in the following. One find very close to *V. terrestris* has been registered as unidentified,

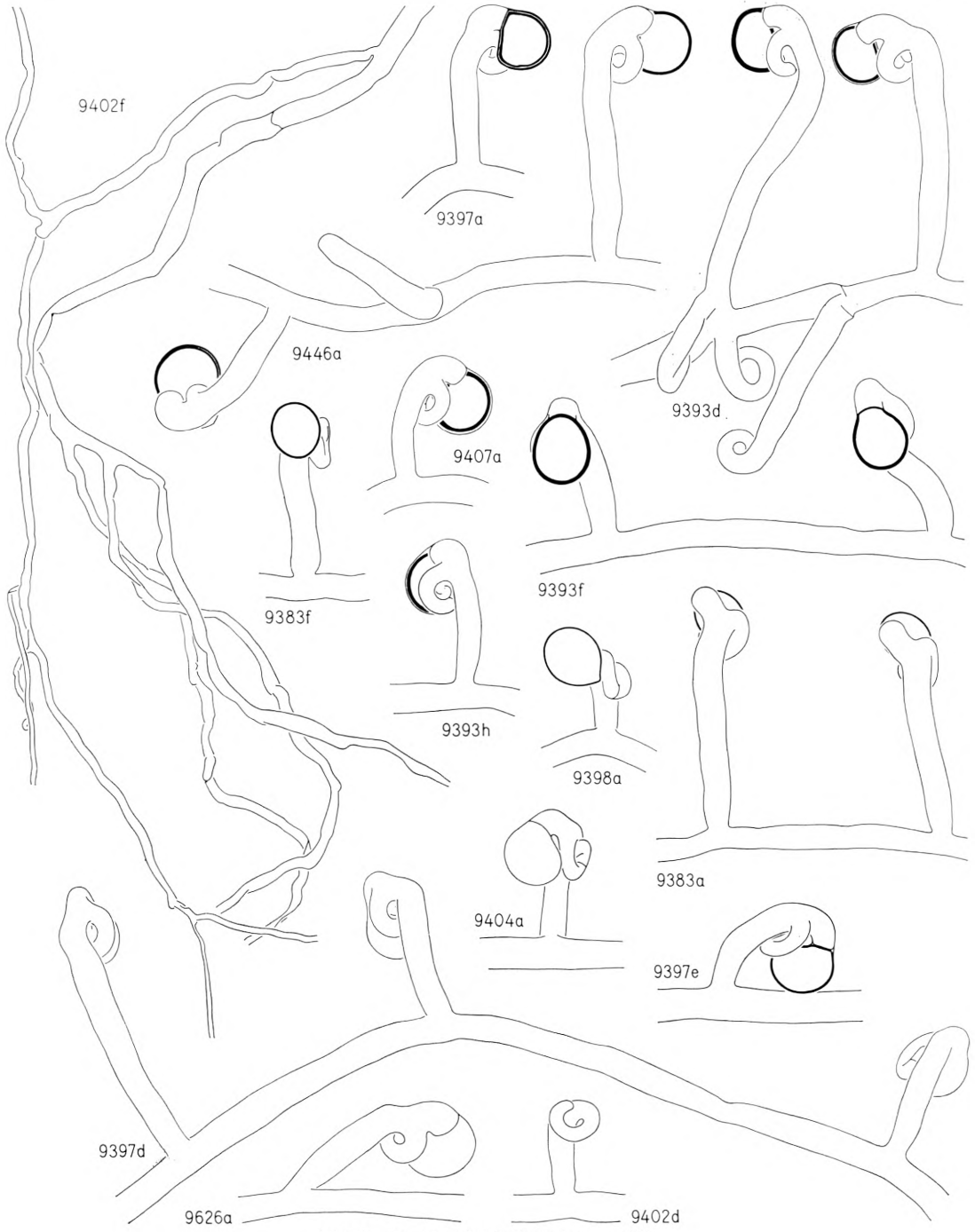


Fig. 8. *D*; *Vaucheria terrestris*. × 100.

as were three finds of probable *V. terrestris* too similar to *V. frigida*. The necessity of such unsatisfactory procedure is an indication that *V. terrestris* and *V. frigida* are taxonomically very close to one another.

For VAUCHER it was natural to keep the two plants apart because he found them totally different as to their appearance in nature. While his *Ectosperma terrestris* was a representative of the Linnaean genus *Byssus*, forming a thin felty cover on soil, his *E. hamata* was a typical Linnaean *Conferva*, consisting of longer and straighter filaments that grew in the water. Therefore he had to explain why he placed the two in one genus, rather than why he did not put them into the same species. Today the ecological difference between them appears less well defined. *V. frigida* is amphibious. It may flourish and fruit under water but more frequently grows at the water's edge or just above the water. The prevailing habitat in the Geneva landscape of today is on soil along water-courses, where trees and shrubs provide a suitable combination of moisture, light and temperature, particularly in the spring. From this way of life there does not seem to be a great distance to that of *V. terrestris*, which thrives on arable land in late autumn and winter, when air and soil are moist and sunshine not too bright. Actually, the two are so close that it would be tempting to lump them into one, had it not been for the fact that *V. terrestris* is also very closely allied to the following species. Instead, a future splitting of *V. frigida* on the varietal level may perhaps clarify things.

Most of the author's material is from April and this, like that from June and October, is fruiting nearly throughout. In the material from February only two out of seven samples are fruiting.

F. (Fig. 10). *Vaucheria prona* T. CHRISTENSEN 1970, *Vaucheria hamata* sensu GÖTZ 1897, non *Vaucheria hamata* (VAUCH.) DC. in LAM. et DC. 1805.

This species looks like *V. terrestris* in most respects, differing mainly in the situation and number of the oogonia. In *V. terrestris* the stalk of the single oogonium starts as a bulge from the back of the antheridium stalk at the transition between the straight and the curved part. It grows out in a direction mostly little different from that of the straight part and then, itself, turns in the same direction as the curved part, lying above the latter. *V. prona* normally forms two oogonia per antheridium, and then is immediately recognizable by this character alone. Sometimes it forms only one, as is the case with all two-spored species, and such fruiting branches may resemble those of *V. terrestris* rather a lot. No matter if there are one or two per antheridium, however, the oogonia are initiated from the sides, not the backs, of the antheridium stalks. If only one oogonium is formed its stalk still does not ride on top of the antheridium stalk but projects side by side with it, both reaching about the same height above the vegetative filament. BLUM (1953), on the basis of herbarium studies, came to the conclusion that the two were identical. Undoubtedly they are very closely allied, but in the present author's material seemingly intermediate samples have turned out to be mixtures.

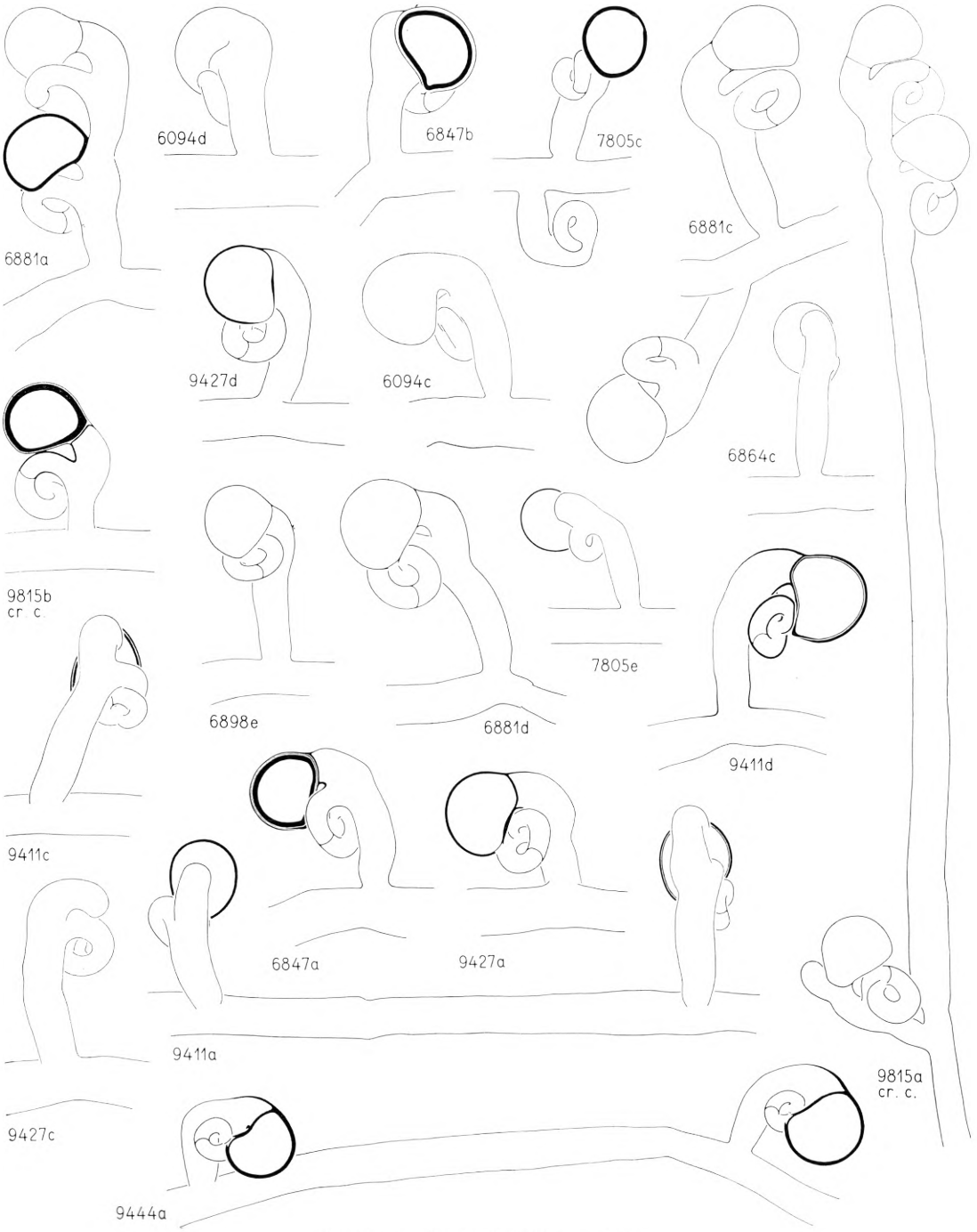


Fig. 9. *E*; *Vaucheria frigida*. × 100.

As to ecology and appearance in nature the two species are very similar, except that *V. prona* appears to have a wider ecological range than *V. terrestris*. Their similarity when viewed by the naked eye must be the reason why VAUCHER did not realize the existence of a two-spored terrestrial species though it is quite common in his region. He normally distinguished species in the field, and his algal studies were made over a remarkably short period. So, after studying one or a couple of samples of *V. terrestris* —which he may well have had in his own garden—he probably preferred to go ahead looking for new forms rather than to bring home more samples of what he thought he knew and had enough drawings of.

Twenty of the author's 32 samples were taken in October, and a much larger proportion would have come from this season if the species had been collected wherever it could. Nearly all these twenty samples grew in fields or gardens, under maize, vine, beets, cabbage or weeds, or between grass or stubble in places not exposed to full sunlight. About half of them also contained *V. terrestris*, while only two contained other species of *Vaucheria*. Among the samples taken at other seasons—four in February, seven in April and one in June—only two came from fields or gardens. More were taken in woods or along hedges, and most in amphibious or even aquatic environments. While all the October samples had well developed fruiting organs, these were missing or badly developed in more than half of those from other times of the year.

G. (Fig. 11). *Vaucheria pseudogeminata* P. DANG. 1939, *Vaucheria hamata* sensu WALZ 1866?, non *V. hamata* (VAUCH.) DC. in LAM. et DC. 1805.

The material agrees very well with the description given by DANGEARD. VAUCHER obviously did not find this species, which is quite understandable since it is not very common, and since it is relatively small and normally grows mingled with larger species.

There are five samples in all. Three of them were taken in April. One grew by a woodland track, one along a path following a brook through a small wood, both mingled with *V. prona* as well as *V. cruciata*, the latter also with *V. frigida* and *V. canalicularis*. The third April sample came from the side of a ditch, mingled with *V. cruciata*, *V. canalicularis* and *V. bursata*. A sample from June also grew on the side of a ditch, mingled with *V. canalicularis*. The fifth sample was taken in October on a field between stubble and young lucerne, mingled with *V. terrestris* and *V. prona*. All samples were fruiting at the time of collecting.

H. (Figs. 12–13). *Vaucheria racemosa* (VAUCH.) DC. in LAM. et DC. 1805, *Ectosperma racemosa* VAUCH. 1803, non *Vaucheria racemosa* sensu GÖTZ 1897, *Vaucheria walzii* ROTHERT 1896a, *Vaucheria uncinata* sensu GÖTZ 1897, non *Vaucheria uncinata* KÜTZ. 1856.

GÖTZ (1897) designated this plant as *V. uncinata*, at the same time applying the name *V. racemosa* to *V. geminata* (Vauch.) DC. jointly with a plant probably referable to *V. verticillata* MENEGH. The true *V. uncinata*, however, is a very different plant, as pointed out by BLUM (1953), and has only one or two, rarely three oogonia on each fruiting branch. *V. verticillata* mostly has four, all arranged in a whirl around the

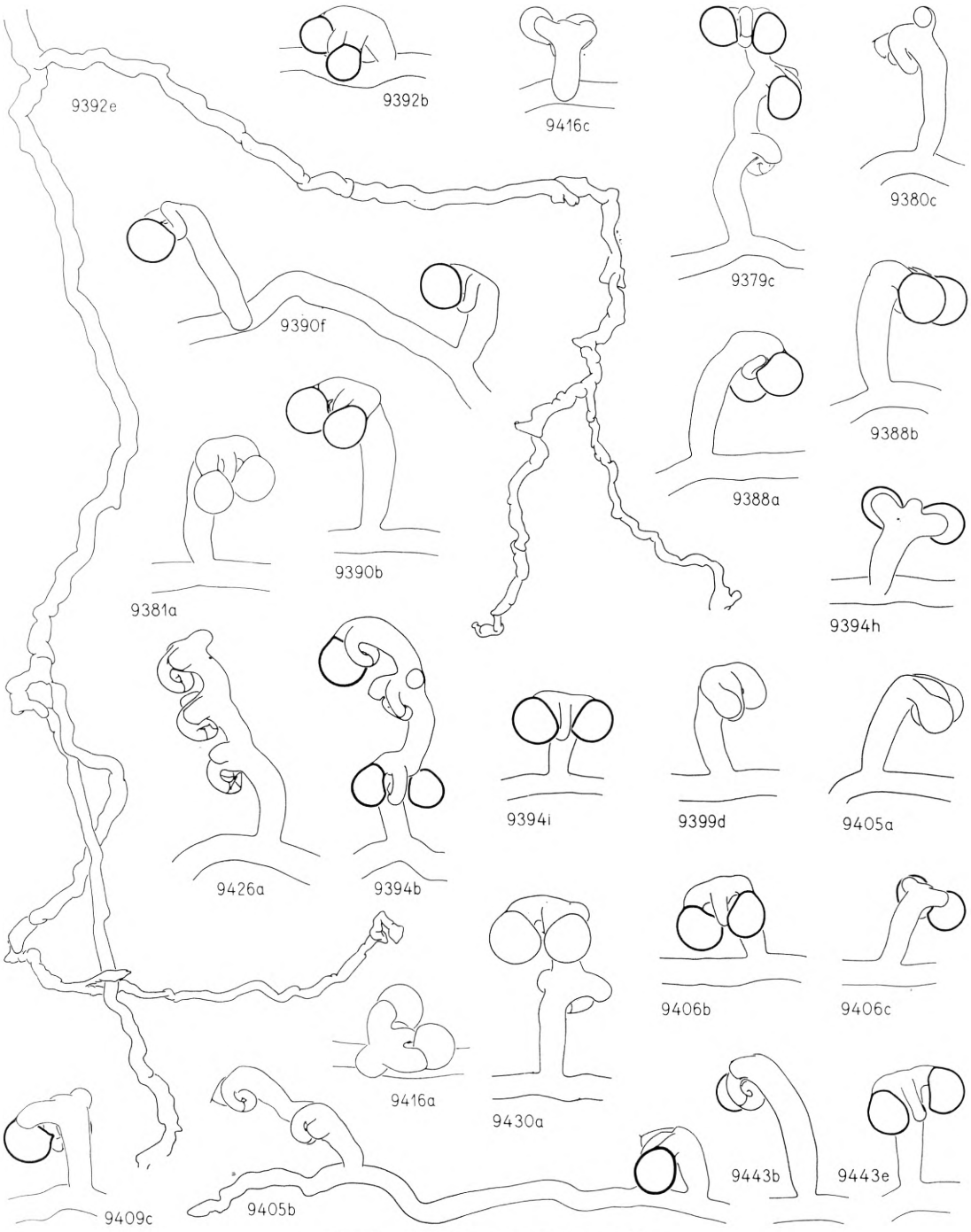


Fig. 10. *F*; *Vaucheria prona*. × 100.

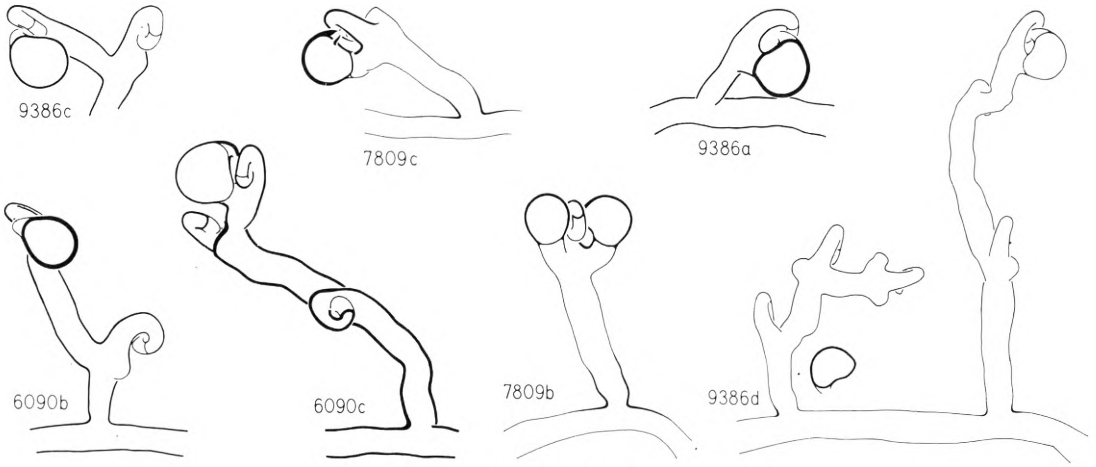


Fig. 11. *G*; *Vaucheria pseudogeminata*. × 100.

branch and pointing upwards. A well developed fruiting branch of *H* also bears four, but situated one above the other on either side of the branch, and all directed sideways towards the coiled antheridium. It is seen from VAUCHER's illustration of *V. racemosa* that his epithet can cover neither *V. uncinata* nor *V. verticillata* but only *H.* This agrees with the fact that *H* but not the two others has been found in VAUCHER's region by the author, and that *H* is the favourite host of *Proales wernecki*, which was also found by VAUCHER in *V. racemosa*.

VAUCHER says the species is found in nearly all the ditches, especially in the spring. The author has only found it in three places. He may not have hit the best season, but probably the species has also become rarer because the ditches are cleared more thoroughly than in those times. From elsewhere it is the author's impression that *V. racemosa* is favoured by more or less stagnant water over a muddy bottom with decaying leaves. One of the three stations was just that type, a relatively shallow pond at Chambésy with a brook passing through, and surrounded by large trees. Here the plant was found with both aplanosporangia and sexual organs in April 1957, mingled with *V. bursata, V. cruciata* and *V. frigida*. On a visit in October 1963 nothing was found of the species. On a last visit in April 1965 the pond was being drained, but a culture strain was secured from a mud sample. Another find was made on mud at a brook fringed with trees at Bois d'Ely. This sample, which was taken in June, contained only a little of *V. racemosa* with old and badly developed fruiting organs, accompanied by the same three species as found in the previous locality. The third station, probably a more accidental one, was a stone basin under the spout of the village well of Ornex. Here the plant was found with aplanosporangia in February, growing in large masses unmingled with other species.

Proales galls were found in a crude culture reared from the last sample taken at Chambésy. They are vase-shaped like those studied in the same species by ROTHERT (1896b), and have 3–9 openings, cf. Fig. 13.

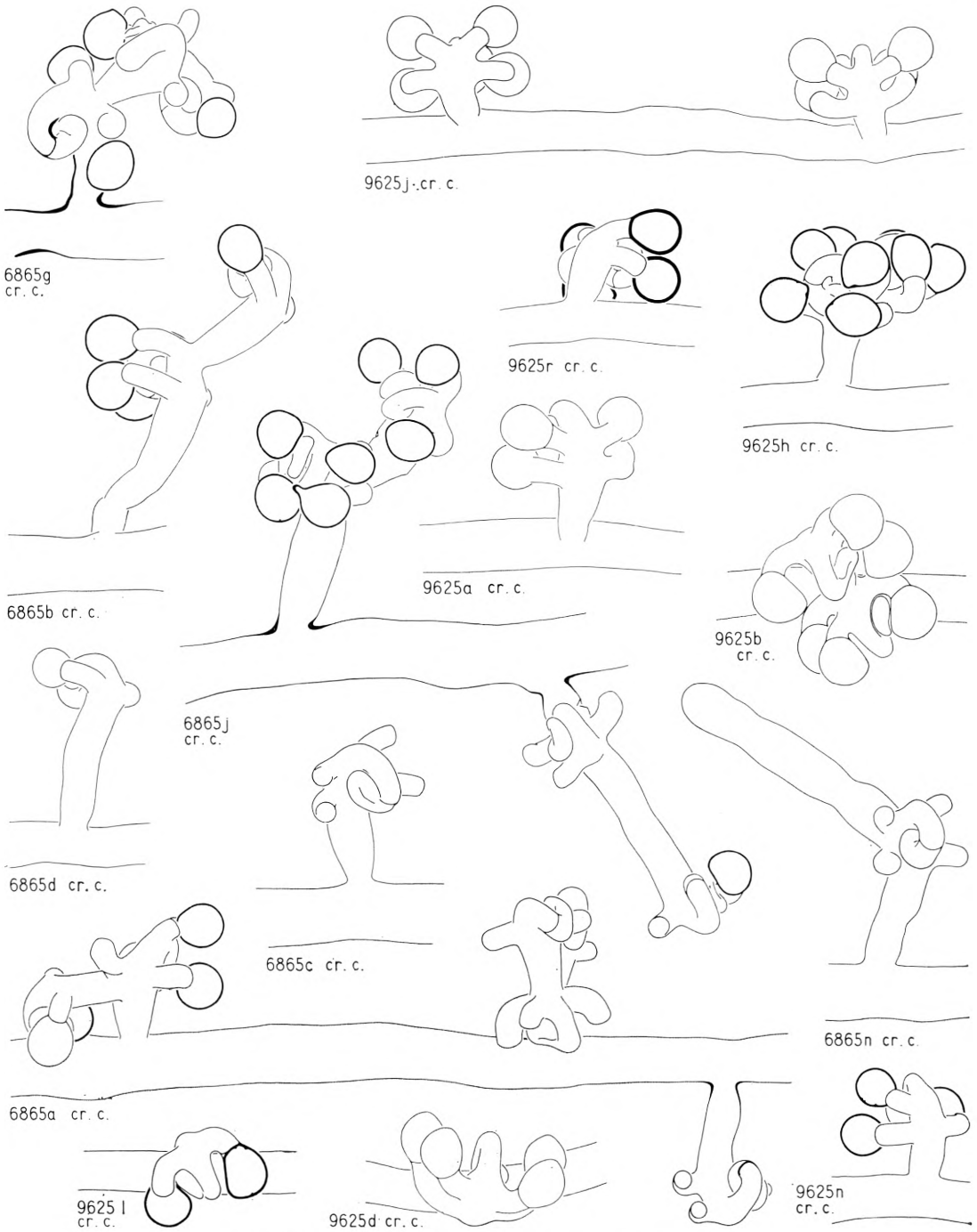


Fig. 12. *H*; *Vaucheria racemosa*, sexual organs. × 100.

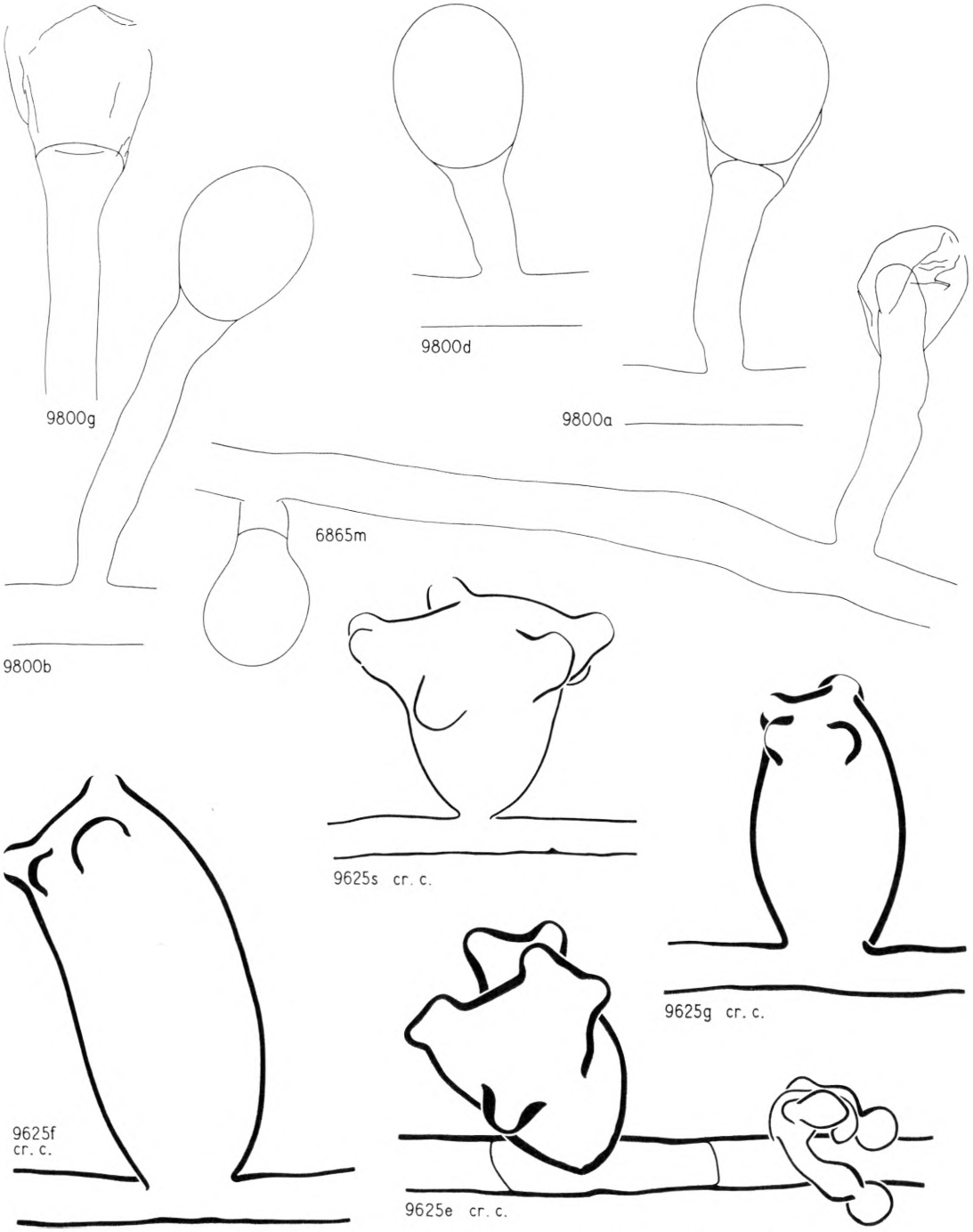


Fig. 13. *H*; *Vaucheria racemosa*, aplanosporangia and galls. × 100.

The plant described by VAUCHER under the name *Ectosperma appendiculata* can hardly be anything but *Vaucheria racemosa* with aplanospores if its appendages are *Proales* galls. If so, this material must either have had unusually small dimensions or must have been rendered at a lower magnification than the rest, contrary to VAUCHER's general statement that all the illustrations were made at the same enlargement. However, *Ectosperma appendiculata* was studied only once, being brought from Lons-le Saunier 70 km away from Geneva. Moreover, the material studied was obviously in a rather bad state. After studying good material of *Proales* galls from the Geneva region as illustrated in the paper finished in April 1800 and printed in 1801, VAUCHER may possibly have assumed that this inferior material was in closer agreement with that first studied than was actually the case. If the appendages shown in the Lons-le Saunier material are not excrescences from the alga, the latter may also be a brackish-water plant, a possibility that was adduced by VAUCHER himself because his find was made at the salt works exploiting the brine source of the town. The particular station does not exist any more, the brine being pumped up from roofed wells and evaporated indoor. A search for topotype specimens in the Geneva, Lyons and Paris herbaria has been fruitless. So the identity of *Ectosperma appendiculata* remains doubtful.

I. (Fig. 14). *Vaucheria dillwynii* (WEB. et MOHR) C. AG. 1812, *Conferva dillwynii* WEB. et MOHR 1803, *Vaucheria pachyderma* WALZ 1866.

This species ranks as number seven out of eleven with regard to frequency in the author's material. So it is rather surprising that VAUCHER does not report it at all. One may assume that he referred all plants with sessile oogonia to his *Ectosperma sessilis*, or that today's landscape has more suitable places for *V. dillwynii* than that known by VAUCHER.

The plant may form rhizoids, rather evenly tapering like those figured from *V. canalicularis* (Fig. 4). Eight of the thirteen samples were taken on the bank of a watercourse, six consisting of creeping filaments like similar growths of *V. frigida*, two more cushion-like, probably started under water. A change with regard to the trees and shrubs now fringing nearly every watercourse of the region may well have increased the possibilities of amphibious growth in such places since the time of VAUCHER, hereby favouring both *V. dillwynii* and *V. frigida*. Two samples were taken under water, both growing on the bottom of ditches with a strong current. Finally, there are three samples from soil not along watercourses. In the latter the species is

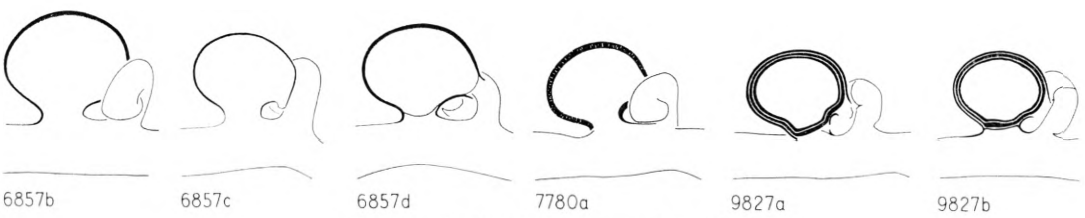


Fig. 14. *I*; *Vaucheria dillwynii*. × 100.

mingled with *V. prona*, in one of them also with amphibious species. All other samples are mixtures with one or more amphibious species, *V. cruciata*, *frigida*, *canalicularis* and *bursata*, cf. Table 1. There are seven April samples, mostly fruiting, five February samples, mostly sterile, and one October sample, which is fruiting.

J. (Fig. 15). *Vaucheria bursata* (O. F. Müll.) C. Ag. 1812, *Conferva bursata* O. F. Müll. 1779, *Ectosperma sessilis* Vauch. 1803, *Vaucheria sessilis* (Vauch.) DC. in Lam. et DC. 1805, *Vaucheria repens* Hass. 1843, *Vaucheria orthocarpa* Reinsch 1887.

This species varies a good deal with regard to the direction of the oogonium beak, the width of the filaments, and the tendency to form only one oogonium at an antheridium. Like Rieth (1963), the author finds it impossible to subdivide the variation complex on the basis of these characters today. The variation in width exceeds what is found in most species, but the width also varies with culture conditions. Besides, measurements of preserved material have to be used with much caution because very often the filaments are oval in transverse section. Therefore, the author prefers to deal with *V. bursata* as a single entity, at least until proper cultural studies have been carried out.

About half the samples at hand are from swiftly running water, where the species may form large soft cushions constantly submerged or more compact tufts at the water's edge, somewhat similar to those formed by *V. canalicularis* but usually flatter and more even. Slightly fewer samples consist of creeping filaments grown on soil at a watercourse, while only a few come from stagnant water. There are twenty samples taken in middle April, June or October, nineteen of them fruiting, while seventeen samples from February or early April are all sterile. Zoosporangia are formed abundantly when a crude culture is started but have not been observed in nature.

A sample collected in February as dense cushions just under water in the Lion River between Prégnin and Vesignin had *Proales* galls seven days later. The galls are spindle-shaped. Usually they have a single terminal opening, but there may also be two close to one another. In addition, there are mostly one or two short outgrowths from the filament close to the base of the main gall body, pointing in the opposite direction and each forming a single terminal opening (Fig. 15).

K. (Fig. 16). *Vaucheria fontinalis* (L.) T. Christensen 1968, *Conferva fontinalis* L. 1753, *Ectosperma clavata* Vauch. 1803 pro parte saltem, *Vaucheria ornithocephala* C. Ag. 1817, *Vaucheria polysperma* Hass. 1843.

Vaucher did not find this species in the fruiting state, but his description of *Ectosperma clavata* covers its appearance when reproducing asexually. As to the zoosporangia there is little difference between *V. bursata* and *V. fontinalis*, and the illustration given by Vaucher in 1803 may show either. In his first account he pictured three species with club-shaped terminal structures assumed to be antheridia, one of them referred to *Conferva fontinalis* L. (Vaucher, 1801, p. 354, fig. 13). Later he

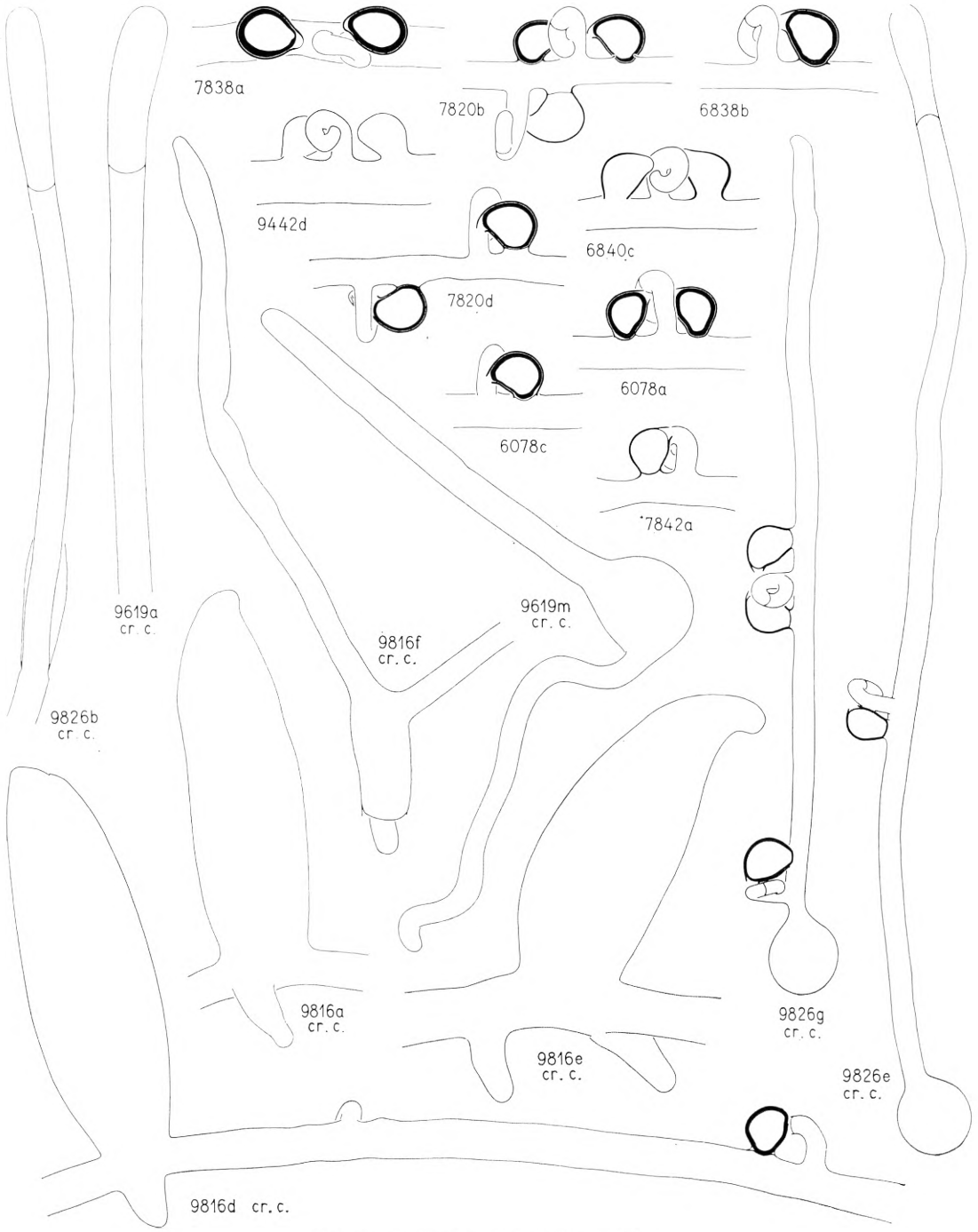


Fig. 15. *J*; *Vaucheria bursata*. × 100.

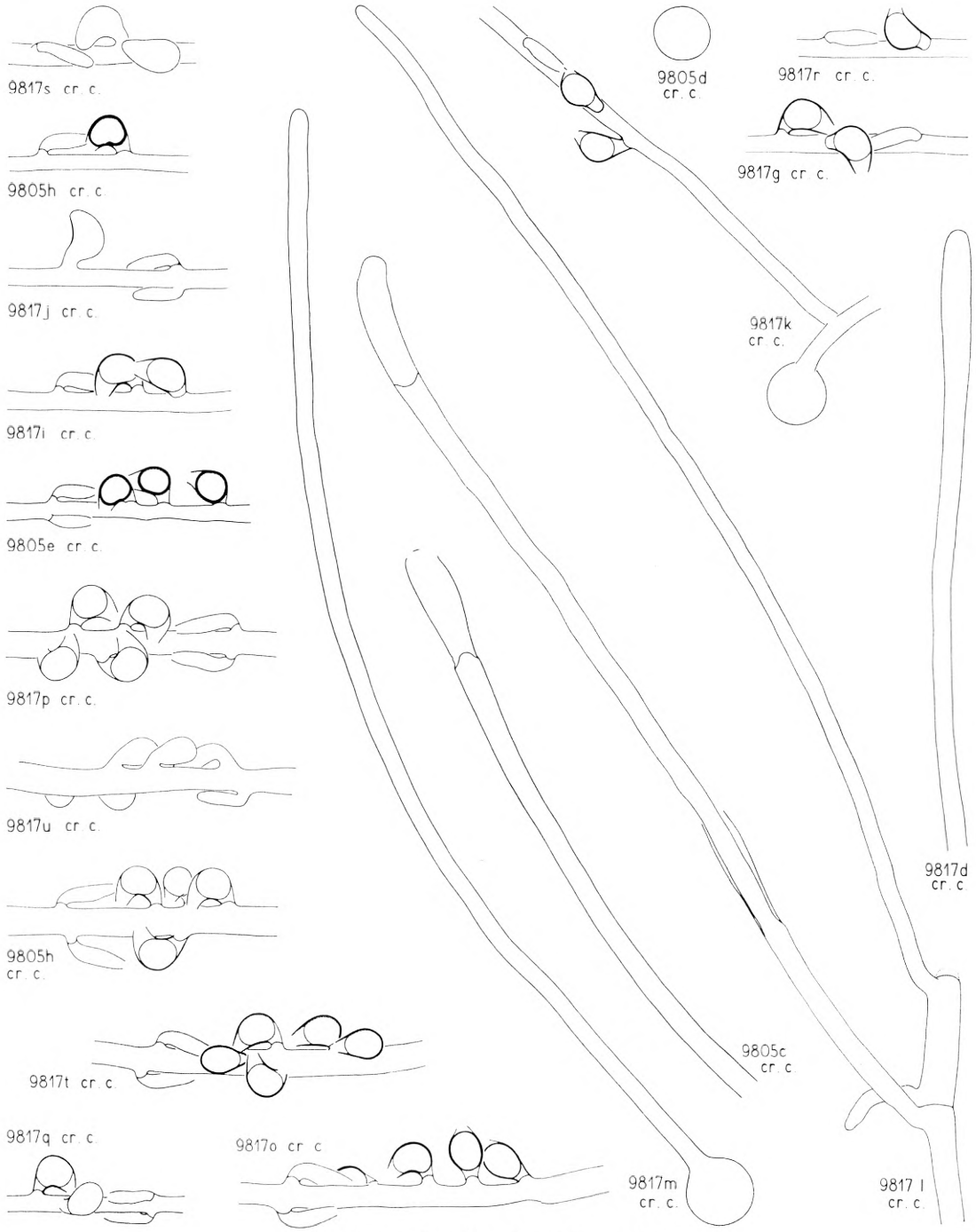


Fig. 16. *K*; *Vaucheria fontinalis*. × 100.

TABLE 1. Frequency of each species in unmingled samples, and mingled with each of the others.

Species	Number of samples in all	Number of samples with no other Vaucheria species	Number of samples containing also											
			V. canalicularis	V. geminata	V. cruciata	V. terrestris	V. frigida	V. prona	V. pseudogeminata	V. racemosa	V. dillwynii	V. bursata	V. fontinalis	unidentified
V. canalicularis . . .	51	13		0	21	0	21	8	3	1	6	15	0	0
V. geminata	1	0	0		1	0	1	1	0	0	1	1	0	0
V. cruciata	41	1	21	1		0	20	8	3	2	10	20	2	1
V. terrestris	14	3	0	0	0		0	11	1	0	0	0	0	0
V. frigida	41	7	21	1	20	0		7	1	2	9	17	0	0
V. prona	32	8	8	1	8	11	7		3	0	4	3	0	1
V. pseudogeminata	5	0	3	0	3	1	1	3		0	0	1	0	0
V. racemosa	4	1	1	0	2	0	2	0	0		0	3	0	0
V. dillwynii	13	0	6	1	10	0	9	4	0	0		6	0	0
V. bursata	37	5	15	1	20	0	17	3	1	3	6		3	0
V. fontinalis	3	0	0	0	2	0	0	0	0	0	0	3		0

obviously came to the conclusion that there were only two such species, *Ectosperma ovata* with known spores and a second species in which the spores were still unknown. His written description of this second species, now named *Ectosperma clavata* (1803) must be based on *V. fontinalis*, as the filaments are said to be much thinner than those of other species.

The author has three samples of *V. fontinalis* from the area, all taken in February and all collected in the Lion River, one west of Villard Tacon, one at Vesignin and one 1.5 km further down. The plant grew submerged, forming loose tufts on large stones where there was a swift current and some shade from trees around. In two of the localities large cushions were found mainly consisting of *V. fontinalis*, but in all samples *V. bursata* was also present, and in two of them *V. cruciata* as well. The plant was sterile at the time of collecting.

Frequency and Ecological Similarity of the Species

Table 1, in its first column of figures, gives the number of finds of each individual species. These figures, when compared with one another, give an estimate of the relative frequency of the species. From the following columns it can be seen how often any given species has been found unmingled with other species, and how often mingled with each of the others. The figures for common occurrence of two particular species should be compared with the total number of finds for each of them to give an impression of their ecological similarity.

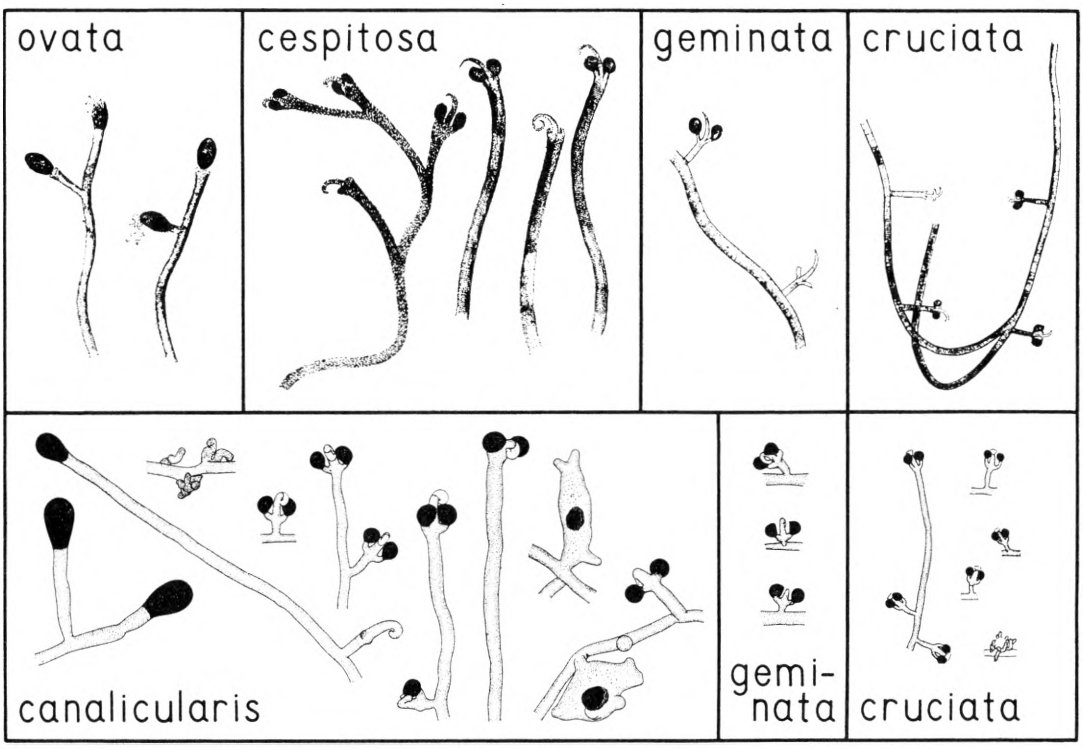
The proportions found are very far from giving precise indications. In the autumn, species that are common on soil can be collected nearly anywhere, and in the spring the same applies to species that are common in ditches. In such cases, therefore, the number of finds is rather an indication of the author's perseverance collecting the same plant under the same conditions over and over again. On the other hand, interesting localities have been looked for more eagerly than average localities and have often been visited more than once, thus giving too large figures for the rarer species. In spite of these deficiencies, however, the figures conclude with tolerable certainty that some of the species are common in the area and that some are mutually rather similar in their ecology. The species that have low figures throughout are likely to be rare or restricted with regard to season or habitat.

Acknowledgements

The author's first collections in the Geneva region were undertaken in connexion with a trip paid for by the University of Copenhagen. Large numbers of drawings for comparative purposes were obtained by microprojection, using an arc lamp provided by The Danish State Research Foundation. Professor R. Heim, Member of the Paris Academy of Sciences, kindly provided a copy of Vaucher's manuscript from August 1800 kept by the Academy. Dr. C. E. B. Bonner and Dr. R. Weibel of the Geneva herbarium, Dr. P. Bourrelly of the Paris herbarium and Mme A. Gilles of the Lyons herbarium have all been very helpful during visits to their institutions. Mrs. Cynthia Gyldenholm has carefully checked the English text. The author wishes to express his sincere thanks to all these persons and institutions for their help.

Fig. 17 pp. 32–33.

Comparative survey of the species taxonomy of VAUCHER and that arrived at by the present author. Names and illustrations in the upper rows are from VAUCHER (1803) except for the first figure of *Ectosperma cespitosa*, which is from VAUCHER (1801). The illustrations in the lower rows are by the author.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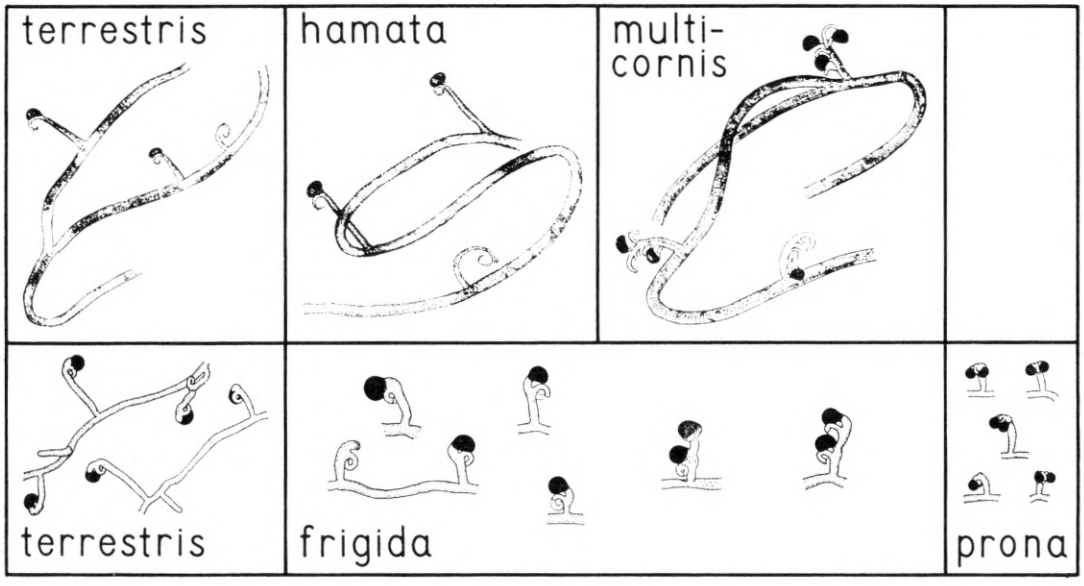
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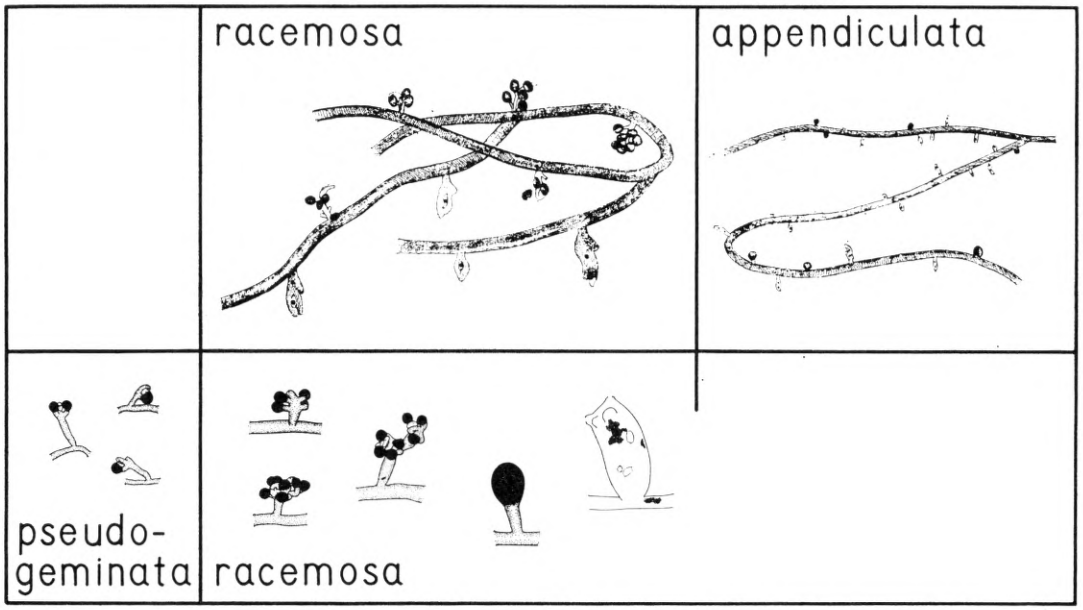
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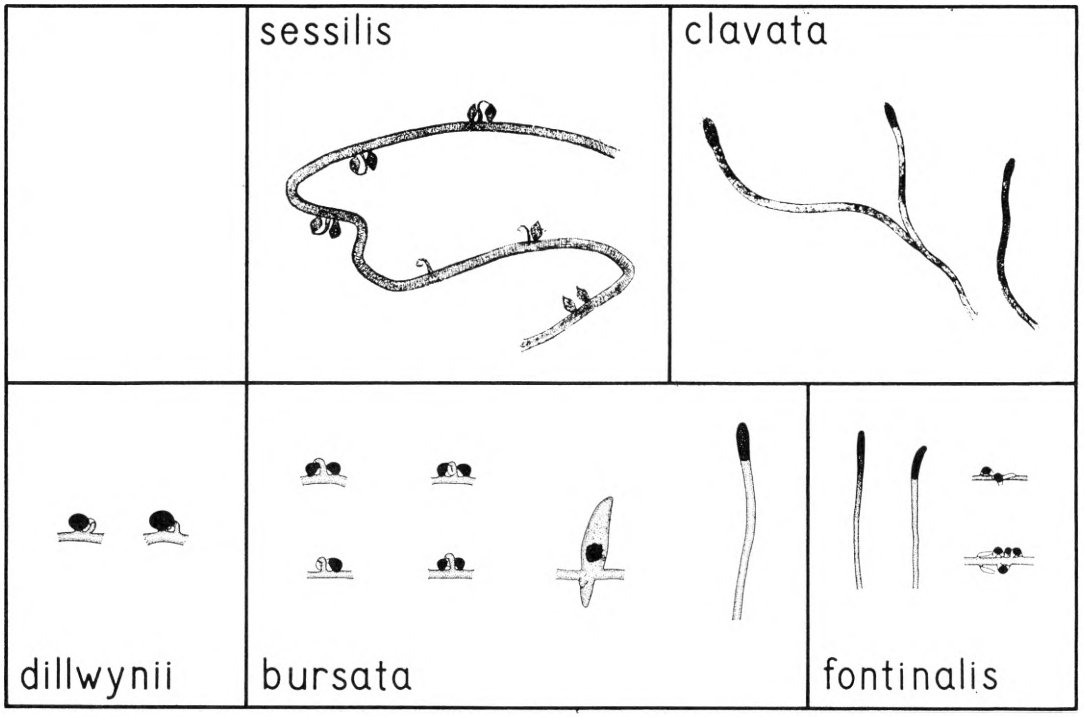
sessilis
clavata
dillwynii
bursata
fontinalis

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