

TAXONOMIC STUDIES ON VAUCHERIA (VAUCHERIACEAE, CHRYSOPHYTA)
IN SOUTH-EASTERN AUSTRALIA

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CHAPTER FIVE

A MONOGRAPH OF VAUCHERIA (VAUCHERIACEAE, CHRYSOPHYTA)

IN SOUTH-EASTERN AUSTRALIA

INTRODUCTION

There has been no previous monograph of Vaucheria (Vaucheriaceae, Chrysophyta) for Australia and most earlier records of occurrence are not verifiable due to the absence of voucher material and/or inadequate published descriptions. Vaucheria glomerata Blum & Womersley (1955) is the only species recorded from saline habitats in south-eastern Australia. V. velutina C. Agardh, normally found in brackish or marine areas (Blum 1972), was listed by Watts (1887) as a freshwater alga from Victoria. Four other species, from freshwater sites, have also been reported from south-eastern Australia: V. incurva Christensen (1986b), V. bursata (O.F. Müller) C. Agardh [Hardy 1906, as V. sessilis (Vaucher) de Candolle], V. geminata (Vaucher) de Candolle [Phillipson 1935, as V. hamata (Vaucher) Lyngbye] and V. clavata (Watts 1887). Vaucheria bursata and V. geminata, but not V. incurva, were found during the current study, while the identity of Watt's (1887) record of V. clavata could not be verified. Watts (1887) gave no author or reference for V. clavata, but the collection was identified by Kützing (D. Sinkora, per. comm.). Kützing (1856, p.23, pl. 66 fig. 1) described and illustrated V. clavata C. Agardh, to which Kützing referred all species with zoosporangia (see also Christensen 1969). As all material collected by Watts and deposited at MEL is sterile, this record could refer to any of a number of currently recognised species.

Outside the study area, three additional species have been recorded from Australia: V. caloundrensis Cribb (1960), V. mayyanadensis Erady, associated with mangroves in Queensland (Cribb 1979); V. dichotoma (Linnaeus) Martius, from coastal New South Wales (May 1938); and V. fastigiata C. Agardh^(Sonder 1880) [now the basionym for Chlorodesmis fastigiata (C. Agardh) Ducker 1969]. Further records of V. geminata, from New South Wales (Playfair 1917) and Queensland (Bailey 1893, Möbius 1892), and V. bursata, from Queensland (Möbius 1895, as V. sessilis), have also been made. Sonder (1881) recorded V. clavata C. Agardh from Queensland, but as with Watt's (1887) record of this taxon, its identity cannot be confirmed.

The Vaucheria flora of New Zealand has been more extensively studied (see Sarma 1973, 1974 and Cassie 1984), and includes six taxa not found in south-eastern Australia: V. jaoi Ley (Cassie 1984, Sarma 1973, Sarma & Chapman 1975b), V. pseudosessilis Chapman (1956), V. sessilis f. hookeri (Kützinger) Nordstedt (Nordstedt 1888, Cassie 1984, Chapman et al 1957, Sarma 1973), V. synandra Woronin (Chapman, 1956), V. terrestris f. megacarpa Nordstedt (1888) and V. undulata Jao (Cassie 1984, Sarma & Chapman 1975b, Sarma 1974).

The aim of this study has been to monograph the genus Vaucheria in south-eastern Australia. Proceeding this, is an evaluation of taxonomic characters used in the delineation of sections, and an assessment of sectional concepts in the genus. This is followed by a description of Vaucheria and a key to the sections represented in south-eastern Australia, and accounts of the 24 species found.

MATERIALS AND METHODS

LABORATORY PROCEDURES: Herbarium practice and light and scanning electron microscopy preparation have been outlined in Chapter 3 (p.26).

Living material was maintained in crude culture (portion of field material kept moist in a petri dish), in one of the ASP-V variations described in Chapter 2 (see p.11 and Table 2.2) solidified with 1% agar, ES (Stein 1973, p.43) & 20 μg Iodine & 0.01% Oxoid Liver Broth, or soil/water media (Stein 1973, p.22). All cultures (except those studied in Chapters 2 & 3) were grown in a 14:10 light:dark photoperiod, photon flux density 10-50 $\mu\text{mol}/\text{m}^2/\text{s}$, and temperature 15-20°C. Herbaria abbreviations are from Holmgren et al (1981).

HABITAT: Collections were made from moist soil, streams, freshwater and saline lakes, salt marshes and intertidal mudflats. Most species can tolerate at least short periods of exposure to the atmosphere - in particular those growing on riverbanks and in tidal marshes - and some can withstand high fluctuations in salinity.

The degree of submergence has been described in this study using one of the following terms: TERRESTRIAL, for fully emergent plants distant from a permanent water-body; SEMI-TERRESTRIAL, for plants occasionally submerged, e.g. riverbank; SEMI-AQUATIC, for plants partly exposed to the atmosphere, on fully saturated substrate, e.g. intertidal; and AQUATIC, for plants nearly always submerged, e.g. in river or lake below lowest water level.

The salinity of the water or substrate has been described in this study as either: FRESHWATER, when the salinity was probably < 1 o/oo; or SALINE, when it was brackish, at ocean salinity (35 o/oo, Womersley

1981a), or hypersaline.

All parameters are qualitative; the degree of submergence was based on observations at the time of collection, and the salinity estimated from surrounding vegetation and the locality of the site.

STUDY AREA: The study area (Fig. 5.1) covers the south-eastern portion of mainland Australia - bounded to the north by the Murray River (part of the state border between Victoria and New South Wales) and to the west by Spencer's Gulf, South Australia - and is approximately 300,000 km² in area.

The western boundary is the approximate limit of the salt-marsh areas in the eastern half of Australia. There is some mangrove development on the western side of Spencer's gulf and isolated salt-marshes further westward (Specht 1972) but the gulf provided a convenient geographical boundary. Permanent inland lakes and rivers are nearly absent west of this boundary and the only likely habitats for Vaucheria would be the coastal areas. The climate, and structure of the water-bodies, gradually change over the north-south gradient and the Murray River provided a suitable geographical boundary in this direction. In the east, the New South Wales-Victoria state border was used from the source of the Murray River to the coast, and in the west, a line from the New South Wales-Victoria-South Australia border intersection (on the Murray River) to the top of Spencer's Gulf. North of this boundary, the rainfall increases and becomes more dominant in the east in summer, and is reduced in all seasons in the west.

This study area is more restricted than that illustrated as south-eastern Australia by Entwistle & Kraft (1984) but closer to the area defined by Costermans (1981). It has a warm temperate rainy climate,

with a warm (dry in the north-west) summer and a mild (wet in the north-west) winter (Tierney 1969). Rainfall is 200-1100 mm/yr and the temperature range is -3° to 33°C (monthly average minimum and maximum). The elevation of the land ranges from sea level to 1984 m in the study area, with the highest collection site at 1560 m.

VAUCHERIA AND ITS SECTIONAL CLASSIFICATION

Generic Classification

The genus Vaucheria is usually included in the family Vaucheriaceae, order Vaucheriales, class Xanthophyceae (or Tribophyceae) and division Chrysophyta (Bold & Wynne 1985, Rieth 1980b, Silva 1979). Bourrelly (1968) and Rieth (1980b) also include Asterosiphon in the Vaucheriaceae, while Christensen (1966, 1980) refers this genus to the Botridiaceae. Recently (Hori et al 1979, Yokahama et al 1980), Pseudodichotomosiphon has been shown to belong in the Xanthophyceae, rather than the Chlorophyceae, but further studies are needed to determine its relationships with Vaucheria. The genera Debsalga, Woroninia and Vaucheriopsis are not considered worthy of recognition at generic level by Blum (1972) and Rieth (1980b) and are placed in synonymy with Vaucheria. Silva (1979) considers the nomenclature of names at family level and above.

Sectional Classification

With a few exceptions (notably Brown 1929; Christensen 1952, 1969; Pecora 1978, 1980; Simons 1977), most floristic and/or monographic

accounts of Vaucheria in the twentieth century (e.g. Blum 1972, Dangeard 1939b, Gauthier-Lièvre 1955, Rieth 1980b) use a system of sections. Walz (1866) divided Vaucheria into three 'groups' and two 'subgroups', but these were not used in most nineteenth century floras (e.g. Crouan & Crouan 1867, Dupray 1887, Arechavaleta 1883). Following the formal establishment of Walz's groups as sections and subsections by Heering (1907), the infrageneric classification received wider acceptance. Between the publication of Walz (1866) and Heering (1921) there were four additional infrageneric taxa described (by Woronin 1869, Nordstedt 1879, Hansgirg 1888, Heidinger 1908), and most subsequent authors have accepted the system of Heering (1921), with modifications to include new taxa (see Table 5.1). Prior to this study, a total of 12 sections and four subsections have been described (Table 5.2).

In the present study, nine sections have been recognised (Table 5.3), six of which occur in south-eastern Australia. Features of the antheridial system have primarily been used to distinguish sections in Vaucheria; these include the presence or absence of a subtending wall-bound cavity, the position of androphores if present, the number of dehiscence pores, morphology, orientation relative to oogonia and presence or absence of antheridial pedicel. The presence or absence of gametophores, their morphology, and the distinctiveness of the oogonial fertilisation pore have also been used. These characters are analysed below.

WALL-BOUND CAVITY SUBTENDING ANTHERIDIA: In the section *Piloboloideae* (Walz) Heering, the antheridia are always subtended by a wall-bound cavity (Fig. 5.36). The antheridia of all other sections are borne on a photosynthetic portion of the siphon [which may be itself,

however, separated from the main vegetative siphon by a wall-bound cavity, as in the sections *Acrandrae* Ott & Hommersand and *Androphorae* (Nordstedt) Heering]. All south-eastern Australian plants of *Piloboloideae* could be identified on the basis of this character and no intermediate states between cavities and photosynthetic thallus were found, thus supporting the usefulness of this feature as a sectional character.

ANDROPHORES: Androphores, which are separated from the vegetative siphon by a wall-bound cavity and produce one to several antheridia, are only found in the sections *Acrandrae* and *Androphorae*.

In the section *Androphorae*, the androphores are differentiated from the vegetative siphon (often swollen), and are produced laterally (Rieth 1980b, fig. 48), while in the section *Acrandrae*, the androphores are intercalary or terminal, and little differentiated from the normal vegetative thallus (Ott & Hommersand 1974, fig. 1-8). Ott & Hommersand (1974) found that characters such as antheridial and oogonial shape and the relationship of oogonia to antheridia, also distinguished these two sections. No species of *Acrandrae* or *Androphorae* were examined in this study, but as there is no evidence to indicate that the above features are poor taxonomic characters, these two sections are maintained pending further study.

ANTHERIDIAL PORES: In most sections and subsections, antheridia dehisce through one terminal pore, but the sections *Vaucheria* [syn. *Anomalae* (Hansgirg) Heering, see p.206) and *Piloboloideae* are characterised by antheridia with one to several lateral pores. The number of pores can vary within a species (Rieth 1980b, Blum 1972], but in the section *Vaucheria* there are always two or more lateral pores and

no terminal pore, and in Piloboloideae, one or more lateral pores, in addition to usually one terminal pore.

Although this feature generally provides a useful sectional character, it can be difficult to assess in Vaucheria canalicularis (Linnæus) Christensen (section Vaucheria). In plants with discharged antheridia the distal end can become damaged, or the position and number of pores obscured (e.g. Fig. 5.122). Blum (1972) had difficulty assessing this character in dried herbarium material, leaving many specimens unidentified. In this study, as in Blum's account, V. canalicularis could be confused with V. geminata [section Corniculatae (Walz) Heering] if the antheridia were poorly preserved. Additional characters exist for separating these two species (see p.209), but with only senescent or damaged antheridia it may be impossible to refer a specimen to the correct section, and therefore difficult to identify it to species.

In spite of this difficulty with V. canalicularis and V. geminata, the number of antheridial pores appears to be a generally useful sectional character. In V. cruciata (Vaucher) de Candolle, the other species from south-eastern Australia in the section Vaucheria, the antheridia are always obviously multiporic (Fig. 5.127) and in most specimens of V. canalicularis examined, at least some antheridia were obviously biporic. The practice of preserving wet or slide material of Vaucheria species, therefore, is recommended to help reduce the practical problems associated with this character.

The section Hercynianae Rieth, not occurring in south-eastern Australia, differs from all other sections in having antheridia which lack dehiscence pores: the sperm are released after disintegration of the antheridial wall (Rieth 1980a).

Rieth (1980b) noted that antheridial pores of the section *Woroninia* (Solms-Laubach) Heering are smaller than the diameter of the antheridia, while those of the section *Tubuligerae* (Walz) Heering are large and nearly equal in diameter to the antheridia. *Vaucheria conifera* Christensen, however, has antheridia with a relatively large terminal pore, similar to those of species in the section *Tubuligerae*, but is placed in *Woroninia* on the basis of antheridial orientation and arrangement. As *V. conifera* is similar in the shape and arrangement of antheridia and oogonia to *V. velutina* and *V. dichotoma* (both in the section *Woroninia*), the size of antheridial pores appears to be a poor sectional character.

ANTHERIDIAL SHAPE: Antheridia in *Vaucheria* are variable in shape, ranging from circinate-cylindrical in the section *Corniculatae* and fusiform-cylindrical in *Piloboloideae*, to ovoid and ellipsoid in *Woroninia*. The antheridia of species in the section *Vaucheria* are particularly distinct, being deltoid-pulvinate throughout (Fig. 5.127), or distally (Fig. 5.120); that is, two or more pores terminate lateral swellings on the distal end of straight- or circinate-cylindrical antheridia. Although some antheridia in plants of *V. canalicularis* can occasionally lack this distal swelling and still be biporic (Rieth 1965a), antheridial shape is usually a useful character in distinguishing the sections *Vaucheria* and *Corniculatae* (the latter has circinate-cylindrical antheridia).

The antheridia of species in the section *Piloboloideae* also have dehiscence pores terminating lateral protuberances (Fig. 5.42), but the fundamental shape of the antheridia is fusiform-cylindrical. The antheridia in all other sections with essentially cylindrical antheridia

have a single terminal pore.

From observations made in this study, it appears that the short-cylindrical, ovoid, ellipsoid and saccate antheridia intergrade, and thus should not be used as a basis for delineating sections. Firstly, before dehiscence the saccate antheridia are similar to cylindrical antheridia (see Chapter 3, p.40, for details). Blum (1972) considered short-cylindrical and cylindrical antheridia to be essentially the same as saccate antheridia, but Rieth (1962, 1980b) maintains that the saccate morphology is distinct. Saccate antheridia are illustrated as swelling distally (Rieth 1980b, fig. 18,19) while cylindrical antheridia have parallel lateral walls (Rieth 1980b, fig. 20,21), or are sometimes a little convex in the middle. South-eastern Australian material of V. dillwynii (Weber & Mohr) C. Agardh, a species with supposedly saccate antheridia, often had almost circinate-cylindrical antheridia (Fig. 5.18), which only sometimes became flanged distally, or disintegrated, after dehiscence (Fig. 5.16). The antheridia of V. bursata, described as circinate-cylindrical, always retained this shape after dehiscence (Fig. 5.7). The prime difference between saccate and cylindrical antheridia seems to be that saccate antheridia usually do not remain cylindrical following dehiscence. Generally, when preparing a slide the empty antheridia are disrupted, but antheridia of V. dillwynii observed in situ (embedded in agar) remained cylindrical throughout their development (Fig. 5.23). Vaucheria prolifera Dangeard, another species described as having saccate antheridia, had ellipsoid antheridia which became flanged or disintegrated soon after dehiscence (Fig. 5.119). In this species it is difficult to find a mature antheridium intact. Although there is a difference in development, which should be studied further, saccate antheridia do not seem to be sufficiently distinct from

cylindrical, short-cylindrical, or ellipsoid antheridia to provide a practical diagnostic character for sections.

The difference between ovoid and cylindrical antheridia is also used as a sectional character. Although the antheridia of Corniculatae and Tubuligerae are distinctly cylindrical (usually $L/D > 2$) and the antheridia of Woroninia are ellipsoid to ovoid (usually $L/D < 2$), the antheridia of Pseudoanomalae Jao and Heeringia Blum are termed short-cylindrical: intermediate between cylindrical and ovoid. Furthermore, V. conifera has been placed in the section Woroninia on the basis of gametangial arrangement and oogonial shape, but has fusiform-cylindrical to narrowly urceolate antheridia. Generally cylindrical antheridia are not convex in the middle like ellipsoid antheridia, but there is a group of species which are similar in most other respects yet have antheridia varying from ellipsoid to cylindrical. Vaucheria prolifera has ellipsoid or saccate antheridia (Fig. 5.117B) and has been placed in Pseudoanomalae by Blum (1972) and Globiferae (Heidinger) Heering by Rieth (1980b). Vaucheria prolifera f. corniculata Rieth (1978) is similar to the type form in nearly all respects except that it has circinate-cylindrical antheridia. Therefore, V. prolifera f. corniculata cannot be referred to Pseudoanomalae or Globiferae (a section characterised by saccate antheridia) on the basis of antheridial shape. Rieth (1974b) recognised this inadequacy in the sectional system, remarking that it should be revised, but included both forms in Globiferae. In addition, V. bicornigera sp. nov., with a similar gametangial shape and arrangement to the two forms of V. prolifera, can have almost cylindrical antheridia (Fig. 5.111). To further complicate the issue, V. bicornigera is similar in other respects (see Table 5.5)

to species in Tubuligerae, which have straight-cylindrical antheridia. The integrating shapes between ovoid and cylindrical, therefore, make antheridial shape a poor sectional character.

In the section Contortae Dangeard the antheridia are variable in shape (Figs 5.2, 5.3), from contorted to straight, but are similar to, although much larger than, those of V. nanandra Christensen. The antheridia of Contortae, however, are cylindrical throughout and dehisce through a terminal pore. The difference between the antheridia of Contortae and Corniculatae does not seem to warrant its use as a taxonomic character at sectional level. In addition, the antheridia of both Contortae and Corniculatae are basically cylindrical at the proximal end, with little constriction of the walls where they join the antheridial pedicel. The antheridia of Tubuligerae and Woroninia, however, even when pedicellate, are usually constricted proximally (except sometimes in V. conifera) and the walls seldom continue straight from the antheridium to the antheridial pedicel.

The antheridia of Hercynianae are clavate and similar in size and shape to the oogonia (Rieth 1980a), features not found in any other sections. For this section, therefore, antheridial shape is a good diagnostic feature.

GAMETOPHORES: Although gametophores can be present or absent in the sections Piloboloideae, Pseudoanomalaе and Corniculatae, within most species there is no variability in this character.

In the section Corniculatae, species with gametophores are referred to the subsection Racemosae (Walz) Heering, and those without gametophores, to the subsection Sessiles (Walz) Heering. Two species may at first glance seem to cause problems in this system. Vaucheria

gardneri Collins (1907) was described as having no peduncles, but with the oogonial and antheridial pedicels arising from the same point on the siphon. If this was the case, it would be difficult to decide whether or not a gametophore was present [Hoppaugh (1930) described the subsection Radiatae for this apparently intermediate species]. However, further observations on the type material by Blum (1971) and on the variation in culture in this study (p.171), have shown that a peduncle is always present, but of variable length (see Figs 5.59-5.62). This species, therefore, can be included in the subsection Racemosae. On the other hand, some populations of V. bursata produce oogonia with relatively long pedicels arising from the antheridial pedicel (Fig. 5.6). However, as there is seldom any peduncle and at least some neighbouring gametangia are usually separate from one another, this species is considered to lack gametophores and be referable to the subsection Sessiles.

The presence of a gametophore seems to be a good character for separating the subsections Sessiles and Racemosae, but the shape of the peduncle appears to have little use as a taxonomic character. In particular, the expansion of the peduncle into a disc-like structure on which the oogonia are borne, a character used to define Corniculatae subsection Discoideae, is found to varying degrees in species in the subsection Racemosae, e.g. V. geminata (Fig. 5.68).

In the section Piloboloideae, the presence of a gametophore has not been used to subdivide the section, and as all south-eastern Australian species of Piloboloideae lacked gametophores, the distinctiveness of gametophores in this section could not be assessed.

Four species with gametophores are currently placed in the section Pseudoanomala (Jao & Ley 1947, Blum 1972, Rieth 1980b): V.

arechavaletae Magnus & Wille (in Wille 1884), V. jaoi Ley emend. Jao & Ley (1947), V. subarechavaletae Borge and V. vipera Blum (1960). Both Vaucheria arechavaletae (see Blum 1972, Heering 1907) and V. subarechavaletae (Figs. 5.98-5.100) always have gametophores, but the other two species apparently sometimes lack them.

Vaucheria vipera has both gametophores and sessile gametangia according to Blum (1960, 1972) but it is possible, as Blum points out, that there can be extensive proliferation of gametophores giving the impression of sessile gametangia. Blum (1960) suggested that V. vipera was intermediate between species with gametophores and those with lateral gametangia. However, if the antheridia are produced terminally on a siphon, usually arising perpendicular to the vegetative siphon, then the gametangia should be described as being borne on gametophores. If the antheridia are sessile and lateral, even if produced near the apex of the siphon, then the gametangia should not be considered as being borne on a gametophore. Simons & Vroman (1968) described the branching of the reproductive siphons in V. vipera as sympodial, using the terminology usually restricted to the section Piloboloideae and disregarding the term 'fruiting branch' or gametophore. Further study of this species is needed to clarify the arrangement of gametangia. Vaucheria jaoi, although described as having gametophores, resembles V. prolifera, which has sessile antheridia produced laterally but near the apex (Blum 1951, Rieth 1969). Again, further study of this species is needed to determine whether it has gametophores in the sense used in the section Corniculatae.

ANTHERIDIAL ORIENTATION AND OOGONIAL SYMMETRY: The orientation of circinate antheridia is usually variable and of no taxonomic use, but in the sections Tubuligerae and Woroninia, the orientation of antheridia is a useful character and is generally correlated with oogonial symmetry. In Woroninia, the antheridia are variously orientated but not directed towards an adjacent oogonium (Fig. 5.140), while in Tubuligerae, all antheridia have a terminal pore directed towards an adjacent oogonium (Fig. 5.107, 5.111).

The section Woroninia is also distinguished from Tubuligerae in having radially symmetrical oogonia. In Vaucheria velutina, in the section Woroninia, the antheridia are not directed towards an adjacent oogonium and the oogonia are essentially radially symmetrical, but often reflexed at the base (Fig. 5.139). Christensen (1952) considered this species (as V. thuretii Woronin) to hold a transitional position between Woroninia and Tubuligerae, but made no changes to the sectional system. Only one species in the section Tubuligerae, V. aversa Hassall, sometimes has radially symmetrical oogonia (Blum 1972, Rieth 1980b) but the antheridia are cylindrical and always directed towards the adjacent oogonium.

This relationship between antheridia and oogonia appeared to be a stable character in south-eastern Australian plants, and thus provides a useful sectional character. In most cases oogonial symmetry can be used in conjunction with the orientation of antheridia relative to oogonia.

ANTHERIDIAL PEDICELS: The curvature of antheridial pedicels was used by Walz (1866) to distinguish Corniculatae from the sections Tubuligerae and Piloboloideae. In the current study, it was found that

in some species referred to Corniculatae, the antheridial pedicels were sometimes straight (see Chapter 3, p.35, for details). However, the antheridial system (= both the antheridial pedicel and antheridium; see Fig. 1.1) was always circinate. The antheridial pedicel of Contortae was always straight, but as with Corniculatae, the antheridial system was usually curved or spiralled. The sections Heeringia and Vaucheria can also have a circinate antheridial system. In fact, most plants (except e.g. Vaucheria subarechavaletae) with pedicellate antheridia not subtended by a wall-bound cavity nor borne on an androphore, have a circinate, or at least curved, antheridial system.

The presence or absence of an antheridial pedicel was usually a distinct character in south-eastern Australian plants, but in V. bursata, the pedicel, although usually present, was sometimes (e.g. Fig. 5.9) greatly reduced in length. The antheridia, however, still arose perpendicularly from the siphon, even if the pedicel was reduced in size. In V. prolifera, a species with essentially sessile antheridia, the antheridia was sometimes borne on short pedicels (Fig. 5.116), but the antheridia arose from these at an acute angle rather than continuing perpendicularly to the siphon.

OOGONIAL SHAPE: In all sections, except Hercynianae, the ovum is apparently fertilised through a distal pore in the oogonium. In Hercynianae the ovum reportedly is released after the oogonial wall breaks down and fertilisation occurs outside the oogonium (Rieth 1974a, 1980a). In all other sections, fertilisation occurs within the oogonium.

In the sections Piloboloideae and Heeringia, the fertilisation pore can be indistinct, but in all other sections it usually terminates a

protuberance, or distal extension of the oogonium (Fig. 5.87). The oogonia in some species of Piloboloideae have distinct and even ornate pores, e.g. Vaucheria coronata Nordstedt (see Ott & Hommersand 1974, figs 18-24), while in others, e.g. V. litorea Hofman & Agardh (Fig. 5.35), there is no detectable pore. In V. uncinata, the sole representative of the section Heeringia, a number of other oogonial characters are associated with the lack of a distinctive fertilisation pore: the oogonia are radially symmetrical and globose, the oogonial wall disintegrates following fertilisation and the mature oospores are green (Blum 1972, Rieth 1980b). However, although the shape of the oogonium is distinct, there is great variation in oogonial morphology in many sections, and the breakdown of the oogonial wall is a developmental character which is not always observable. The colour of oospores and the absence of a distinct fertilisation pore seem to be good specific characters, but of less use at sectional level.

Rieth (1980b) divided the section Corniculatae subsection Racemosae into three groups based on the presence or absence of an distal oogonial cavity, and the inclination of the oogonia. Whilst this may be a useful conceptual subdivision, it is not considered worthy of formal taxonomic recognition as many specific distinctions are based on these criteria, and some intermediate states exist. For example, the distal oogonial cavity can be almost absent in some collections of V. erythrospora Christensen and V. gyrogyne sp. nov., two species usually characterised by this feature.

Oogonial characters, with the exception of symmetry as a minor character in distinguishing Woroninia, are not considered to be useful sectional characters.

CONCLUSIONS: Peduncle shape, antheridial curvature and, in some cases, antheridial shape were found to be of little diagnostic value. The other features evaluated, however, seemed to be suitable characters for distinguishing sections. As a result, the 12 sections and four subsections have been reduced to nine sections, and some circumscriptions have been emended (for diagnostic features see Table 5.3). Sections are retained primarily as an aid in identifying species, since taxa sharing a number of distinct attributes are grouped together.

The sections Acrandrae, Androphorae and Hercynianae were not represented in the south-eastern Australia flora, but the presence and shape of androphores in Acrandrae and Androphorae, and the distinctive fertilisation mechanism and gametangial morphology of Hercynianae, distinguish these sections from each other and the remaining sections in Vaucheria.

The section Pseudoanomalaе is considered to be of dubious status and each constituent species should be re-examined to decide whether gametophores are present. Those with gametophores, e.g. V. subarechavaletae, can be transferred to Racemosae, and those without, to Tubuligerae. If the concept of gametophores is unsuitable in Pseudoanomalaе, characters other than antheridial shape must be found to redefine the section or to distribute the species to other sections.

The six sections recognised in south-eastern Australia are described in the ensuing monograph, with a key provided on p.124.

KEYS AND DESCRIPTION OF SPECIES

Vaucheria de Candolle 1801: 20; Blum 1972: 6.

Synonyms:

Conferva Linnaeus 1753: 164 pro parte.

Debsalga Habeeb 1965: 1.

Ectosperma Vaucher 1803: 9.

Vaucheriopsis Heering 1921: 96.

Woroninia Solms-Laubach 1867: 366.

Thallus consisting of sparingly branched siphons with apical growth; septa generally found only as part of reproductive structures. Chloroplasts discoid and numerous; photosynthetic pigments include chlorophyll a & c, β -carotene, vaucheriaxanthin, diatoxanthin, diadinoxanthin and heteroxanthin; food reserves mainly stored as lipids.

Sexual reproduction monoecious or dioecious. Antheridia producing numerous heterokontean sperm, with one relatively short tinsel-type flagellum directed anteriorly and one long whiplash-type flagellum directed posteriorly. Oogonia with one ovum, initially multinucleate, ultimately uninucleate and separated from the thallus by a septum; fertilisation generally via a pore formed in a receptive part of the oogonial wall, and resulting in a thick-walled oospore which is usually retained within the oogonial wall.

Asexual reproduction by aplanosporangia, zoosporangia or akinetes; zoospores multinucleate with numerous pairs of unequal whiplash-type flagella.

Lectotype Species: Vaucheria disperma de Candolle (chosen by Silva 1952, p.256)

FORMAT OF SPECIES ACCOUNTS: Both the sections, and within them the species, are arranged alphabetically. The reference list for each species is not meant to be exhaustive, and it includes major or recent literature and records from Australia and New Zealand only. Further references can be found in Heering (1907) and Blum (1972). All measurements and descriptions given are based on south-eastern Australian plants. Unless stated explicitly, type material has not been examined and identifications are based on information provided in protologues and other published accounts.

The collection sites are plotted on a map of the study area (a single dot may represent a number of collections) included with the figures for each species. The high density of collections in some areas may reflect accessibility rather than a greater density of plants. For common species, not all collection sites plotted on the map are included under the heading of 'Specimens Studied', but a representative selection is made to cover the probable geographic and morphological range of the species. Although widespread through most moist habitats, Vaucheria was not detected in streams of mountain forests where human interference was minimal, and alpine highlands. The seasonality and ephemeral nature of some species, however, makes a list of sites devoid of Vaucheria misleading.

All measurements used in keys represent deliberately chosen values and most specimens will fall easily into one of the categories.

Key to the Sections Represented in South-eastern Australia

1. Wall-bound cavity subtending antheridium

.....Section Piloboloideae

1. No wall bound cavity subtending antheridium.....2
 2. Oogonia and antheridia arranged on a gametophore....3
 2. Oogonia and antheridia sessile or on isolated pedicels.....4
3. Antheridia circinate-cylindrical, dehiscing through one terminal pore.....Section Racemosae
3. Antheridia swollen distally, dehiscing through two or more lateral pores.....Section Vaucheria
4. Antheridial system consisting of a cylindrical antheridium (usually curved or circinate) and pedicel.....Section Corniculatae
4. Antheridial system consisting of sessile (rarely shortly pedicellate) antheridium; antheridia constricted proximally.....5
5. Antheridia not directed towards adjacent oogonium; oogonia radially symmetrical, but sometimes reflexed proximally.....Section Woroninia
5. Antheridia directed towards adjacent oogonium; oogonia usually bilaterally, rarely radially, symmetrical.....Section Tubuligeræ

*Section Corniculatae (Walz) Heering emend. Entwisle

Basionym:

'Group' Corniculatae 'subgroup' Sessiles Walz 1866: 144.

* Author citations for the sections of Vaucheria follow procedures outlined in article 35.2 of the International Code of Nomenclature (Voss 1983).

Synonyms:

Contortae Dangeard 1939b: 216.

Corniculatae subsection Sessiles (Walz) Heering 1907: 143.

'Group' Globiferae Heidinger 1908: 360 pro parte.

Globiferae (Heidinger) Heering 1921: 86 pro parte.

Gametangia sessile or pedicellate on vegetative siphons.

Antheridia pedicellate, cylindrical to saccate, discharging terminally; antheridial system cylindrical and circinate, contorted or rarely straight; antheridia not subtended by a wall-bound cavity. Oogonia usually sessile, bilaterally symmetrical.

Lectotype Species: Vaucheria sessilis (Vaucher) de Candolle

(chosen by Blum 1972, p.13); this species is now considered to be a synonym of V. bursata (O.F.Müller) C. Agardh (see p.134).

The subsections Racemosae and Sessiles of Corniculatae have been characterised by the presence and absence of gametophores, respectively. As concluded on p.117, this is a distinct and useful sectional character. It is unnecessarily complex, therefore, to retain these two groups at subsectional level and they are raised to sections:

Corniculatae (Walz) Heering sens. nov. (syn. Corniculatae subsection Sessiles) and Racemosae (Walz) sect. nov. (syn. Corniculatae subsection Racemosae).

The section Corniculatae has been further emended to include V. arcassonensis Dangeard, previously the sole species in the section Contortae (Dangeard 1939b, Blum 1972, Rieth 1980b), and V. dillwynii, placed in Globiferae by some authors (Hopphaugh 1930, Rieth 1980b; both as V. pachyderma Walz). The section Corniculatae is distinguished from

all other sections in having sessile oogonia, and pedicellate antheridia which form part of a cylindrical antheridial system (see Table 5.3).

Of the five species now recognised, four are known to occur in south-eastern Australia (for information on the taxonomy and nomenclature of V. borealis see Chapter 3, p.46).

Key to Species in the Section Corniculatae.

1. Oogonial walls rugose; oogonia truncate-napiform, long-axis parallel with the siphon; oospore walls 'flaky' or with many layers in transverse section.....V. dillwynii
1. Oogonial walls smooth; oogonia ovoid to ovoid-reniform, long-axis parallel with siphon or erect; oospore walls evenly textured in transverse section.....2
2. Oogonia parallel with siphon, > 130 μm longV. borealis
(not found in south-eastern Australia)
2. Oogonia parallel with siphon or erect, < 130 μm long.....3
3. Antheridia straight or contorted, > 100 μm long, irregular in size and shape.....V. arcassonensis
3. Antheridia circinate, < 100 μm long, similar in size and shape throughout the plant.....4
4. Antheridia turning through at least a full circle; oogonial long-axis and cavity usually more or less parallel with siphon.....V. nanandra

4. Antheridia turning through less than a full circle; oogonial long-axis and cavity variously directed, but seldom both parallel with siphon
V. bursata

Vaucheria arcassonensis Dangeard 1939b: 220, fig. 11. Blum 1972: 22, figs 69-72. Ott & Hommersand 1974: 383, figs 35-42. Pecora 1980: 387, fig. 2.

Type: Not designated by Dangeard (1939b).

Type Locality: Bassin d'Arcachon, Arès, France (Dangeard 1939b).

Distribution: Western Europe, North America; Western Port Bay, Victoria, Australia (see Fig. 5.5).

Specimens Studied: MEL 1049096, Cannon Creek, Western Port Bay, Victoria, Entwistle & Cullinane, 21. viii. 1985; MEL 1049097, MEL 1049098, Moody's Inlet, Western Port Bay, Victoria, Entwistle, 3. xi. 1985.

Figs 5.2-5.5

Thallus consisting of branched siphons, 24-98 μm in diameter, forming dense green mats on substrate.

Plants monoecious; gametangia sessile or pedicellate, 1 oogonium with 1 or 2 antheridia. Antheridia cylindrical, curved, contorted or straight, 100-145 μm long, 29-36 μm in diameter; antheridial pedicels straight, 24-103 μm long. Oogonia sessile or pedicellate, ellipsoid to reniform, 110-134 μm long, 60-77 μm in diameter, L/D 1.6-1.9, often recurved so that pore is directed towards siphon; oogonial wall smooth. Oospores reniform, ellipsoid or curved-rectangular, 98-122 μm long, 60-77 μm in diameter, when mature leaving a distal, and sometimes proximal, oogonial cavity; oospore walls evenly textured in transverse section, 2-5 μm thick.

Akinetes and sporangia unknown.

Diagnostic Features: Vaucheria arcassonensis is delineated from all other south-eastern Australian species of Vaucheria in having no gametophores, and in having antheridia which are pedicellate, contorted or spiralled, $> 100 \mu\text{m}$ long, and which vary considerably in size and shape throughout a population (Figs. 5.2, 5.3).

Habitat and Phenology: Vaucheria arcassonensis was collected from semi-aquatic saline habitats near to salt marsh and under mangroves in August (winter) and September (spring); plants were fertile in the field. In culture, vegetative growth occurred in media with a salinity of 6.5 o/oo, but not 0.3 o/oo: all fertile material examined came from field collections.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria arcassonensis described in the protologue (Dangeard 1939b) and by Blum (1972) and Ott & Hommersand (1974).

As Ott & Hommersand (1974) noted, there is great variability in the shape of gametangia, even on the same siphon. Although occasionally the antheridia are circinate, resembling those of V. bursata, there are usually long, contorted or straight, antheridia nearby which characterise V. arcassonensis.

The features given by Dangeard (1939b) for distinguishing V. arcassonensis from V. bursata (the latter as V. sessilis) were all observed in the south-eastern Australian material: oogonia more often pedicellate and reflexed towards the siphon and with a rounded terminal pore (Fig. 5.4), oospores almost rectangular (Fig. 5.4), antheridia

irregularly shaped and often spiralled through more than one circle (Fig. 5.2, 5.3), and the gametangia irregularly arranged. The oogonia are similar to those found in some populations of V. bursata with pedicellate oogonia (e.g. Fig. 5.6), but are usually more reflexed towards the siphon. The oospores are usually curved and rectangular to ellipsoid, rather than ovoid or ovoid-reniform as in V. bursata. The antheridia are particularly distinct, being different in shape to most, and larger than all, species in the section Corniculatae. Vaucheria nanandra Christensen, nevertheless, does have contorted antheridia turning through more than a full circle, but these are smaller in diameter and length to the antheridia of V. arcassonensis, and more tightly coiled (Figs 5.25A,B).

As the antheridia of V. arcassonensis are irregularly arranged and often long and contorted, previous authors (e.g. Dangeard 1939b, Blum 1972, Rieth 1980b, Ott & Hommersand 1974) have included this species in the monotypic section Contortae. These features, however, are not considered to be of importance at sectional level (see p.113) and V. arcassonensis is placed in the section Corniculatae as it has pedicellate antheridia and no gametophores.

Vaucheria bursata (O.F. Müller) C. Agardh 1811: 21. Christensen

1969: 26, fig. 15; 1973: 513, figs 1A-G. Heering 1907: 181. Simons 1977: 17, figs 13-14.

Basionym

Conferva bursata Müller 1788: 96, pl. 2 fig. 10.

Heterotypic Synonyms:

Ectosperma sessilis Vaucher 1803: 31, pl. 2 fig. 7.

Vaucheria repens Hassall 1843: 430; 1845: 52, pl. 6 fig. 7. Blum

1972: 15, figs 24, 36-37. Collins 1909: 424. Götz

1897: 110, figs 14,15. Teodoresco 1907: 82.

Vaucheria sessilis (Vaucher) de Candolle in Lamarck & de

Candolle 1805: 63. Blum 1972: 16, figs. 23,35. Cassie 1984:

227. Chapman 1956: 495, fig. 153a. Collins 1909: 425.

Gauthier-Lièvre 1955: 322, pl. 3 fig. 29. Götz

1897: 111, figs 17-22. Hardy 1906: 35. Hassall 1845: 55, pl.

4 fig. 2. Heering 1907: 143,213, fig. 69; 1921: 87, fig. 74.

Hoppaugh 1930: 335, pl. 24 fig. 1. Jao 1936: 738, pl. 1 fig.

4. Johnstone 1972: 326. Karling 1966: 231. Möbius

1895: 329. Rieth 1963b: 299, figs 8-12; 1980b: 58, figs. 21-

23. Sarma & Chapman 1975b: 308. Spencer 1883: 303. Teodoresco

1907: 82, figs 65-66.

Vaucheria sessilis f. clavata Heering 1907: 147, fig. 71; 1921:

88, fig. 76. Hoppaugh 1930: 336, pl. 24 figs. 3,4. Jao 1936:

739, pl. 1 fig. 6. Rieth 1980b: 60.

Vaucheria sessilis f. repens (Hassall) Hansgirg 1886: 95.

Cassie 1984: 227. Gauthier-Lièvre 1955: 322, pl. 3 fig.

28. Heering 1907: 144, fig. 68; 1921: 88, fig. 75. Hoppaugh

1930: 336, pl. 24 fig. 2. Jao 1936: 739, pl. 1 fig. 5. Rieth

1980b: 60. Sarma 1974: 87, figs. 2,4,5,15,16. Sarma &

Chapman 1975b: 308.

Misapplied Name:

Vaucheria clavata auct. non (Vaucher) de Candolle: Klebs

1896:95, fig. 2B. Blum 1972: 15, fig. 34. Götz 1897:

114, figs 23-30. Teodoresco 1907: 83.

Type: Description and illustration of Müller (1788),

according to Christensen (1973); topotype material available in

unialgal culture from Cambridge and Texas Culture collections
(Christensen pers. comm.).

Type Locality: Meinberg, Germany (Müller 1788).

Distribution: Widespread (for study area, see Fig. 5.14).

Representative Specimens Studied (from a total of 136 field collections by Entwisle, unless otherwise indicated): MEL 1049209, MEL 1049210, Seaspray, Victoria, 30.ix.1983; MEL 1049221, Five Mile Creek, Woodend, Victoria, 23.i.1984; MEL 1049099, MEL 1049235, Diamond Creek, Eltham, Victoria, 28.iv.1984; MEL 1049236, Onkaparinga River, Clarendon, South Australia, 4.viii.1983; MEL 1049208, Tambo River, Ensay, Victoria, 17.x.1984; MEL 1049100, Menzies Road, Kangaroo Ground, Victoria, Macauley, 9.ix.1984; MEL 1049211, Tambo River, Bark Sheds, Bruthen, Victoria, 17.x.1984; MEL 1049212, Skenes Creek, Skenes Creek township, Victoria, 28.viii.1984; MEL 1049213 p.p., Greenvale Reservoir, Victoria, 22.viii.1984; MEL 1049214 p.p., Stony Creek, Glenmaggie-Licola Road, Victoria, 18.viii.1984; MEL 1049215 p.p., La Trobe River, Traralgon, Victoria, 18.viii.1984; MEL 1049216 p.p., Fords Creek, Mansfield, Victoria, 22.vii.1984; MEL 1049217 p.p., Merri Creek, Clifton Hill, Victoria, 24.vi.1984; MEL 1049218, Ovens River, Porepunkah, Victoria, 22.vii.1984; MEL 1049219, Happy Valley Creek, Myrtleford, Victoria, 22.vii.1984; MEL 1049101, MEL 1049220, Lake Guy, Bogong Village, Victoria, 16.x.1984; MEL 1049223 p.p., Running Creek, Myrtleford-Mt Beauty Road, Victoria, 16.x.1984; MEL 1049224, Lake Linlithgow, Victoria, 4.x.1984; MEL 1049226, Werribee River, Bacchus Marsh, Victoria, 27.v.1983; MEL 1049133, Mitchell River, Bairnsdale, Victoria, 30.ix.1983; MEL 1049150, Lake Bullen Merri, Victoria, 2.viii.1983; NSW A3699, NSW A3700, Caves Beach, Jervis Bay, New South Wales, May, 23.vii.1974; MELU 728, St Leonard's Bay, Wilsons Promontory, Victoria, Ducker, 9.viii.1963.

Figs 5.6-5.14

Thallus consisting of sparingly branched siphons, 29-84(-115) μm in diameter, forming dense green mats on substrate.

Plants monoecious; gametangia sessile or pedicellate, in bisexual groups of 1-2 oogonia on opposite sides of 1 antheridium. Antheridia circinate-cylindrical, turning through less than a full circle, 36-89 μm long, 17-31 μm in diameter; antheridial pedicel straight or curved distally, 5-132 μm long. Oogonia usually sessile, long-axis making an angle of 0-90° with siphon, ovoid to ovoid-reniform, 67-130 μm long, 53-96(-103) μm in diameter, L/D 1.0-1.5(-1.7); oogonial wall smooth.

Oospores similar in size and shape to oogonia, mature oospore leaving oogonial cavity directed at an angle of -90° to 50° with siphon; oospore wall evenly textured in transverse section, 2-7 μm thick.

Sporangia terminal on siphons, obovoid to claviform, 230-320 μm long, 75-105 μm in diameter.

Diagnostic Features: Vaucheria bursata is delineated from other south-eastern Australian species of Vaucheria in having ovoid to ovoid-reniform oogonia not borne on gametophores, oogonial walls smooth (Fig. 5.13), oospore walls evenly textured in transverse section (Figs. 5.6-5.9), and in having pedicellate antheridia, $< 100 \mu\text{m}$ long, turning through less than a full circle (Fig. 5.7), and similar in size and shape throughout the plant.

Habitat and Phenology: Vaucheria bursata was collected from freshwater (rarely saline), terrestrial to aquatic habitats; fertile plants were found throughout the year. In culture, vegetative growth occurred in media with salinities of 0.3-16 o/oo, but not 30 o/oo; all fertile material examined came from ASP-V media with salinities of 0.3-6.5 o/oo and soil/water media. Maximal growth and reproduction occurred in media with salinity of 0.3 o/oo, at 15°C and $35\text{-}50 \mu\text{mol/m}^2/\text{s}$ (see Chapter 2).

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria bursata described in the protologue (Müller 1788, as Conferva) and by Christensen (1969, 1973).

Three isolates (from MEL 1049235, MEL 1049236 and MEL 1049237) were studied in a series of culture experiments and compared with 19 field populations (see Chapter 3). From this work, two growth forms of V.

bursata were recognised. The first growth form consisted of plants (Figs. 5.9, 5.12) usually with a single oogonium with each antheridium, relatively short antheridial pedicels (5-101 μm), and oogonia with pore usually directed parallel with, or towards, the siphon. The second growth form consisted of plants often with paired oogonia, relatively long antheridial pedicels (55-130 μm) and oogonia with pores directed away from the siphon (Figs 5.6-5.8). These two groups were not given any taxonomic recognition as they overlapped in all measured characters, and some field populations could not be satisfactorily referred to either group.

Sporangia were often formed in culture (Fig. 5.11), and although no flagella were observed and all germinated in situ in agar, they resemble the zoosporangia illustrated by Christensen (1969) and became globular after release in soil/water media. Zoosporangia are frequently reported from V. bursata (e.g. Dippel 1856, Klebs 1896, Götz 1897; all as V. sessilis).

Galls similar to those found by Christensen (1969) and Simons (1977) were found in some specimens. They were probably caused by ~~the rotifers~~, Proales spp. (e.g. Fig. 5.10) and Zygorhizium^{zi} vaucheriae Rieth (see Rieth 1980b and Christensen 1969).

No voucher material was found for Hardy's (1906) record of V. bursata (as V. sessilis) from the Treasury Gardens, Melbourne, but this is an easily recognisable species, and one which would grow in such a locality.

The plants described here have been previously referred to V. sessilis, V. repens or V. clavata sensu Klebs (see Blum 1972), or to forms of V. sessilis (see Heering 1907, 1921). These three taxa are now placed in synonymy with V. bursata, the earliest name available for

these plants (Christensen 1969, 1973). Ectosperma clavata Vaucher (1803, p.34, pl.3 fig. 10) was described from plants with zoosporangia, but no gametangia, and Christensen (1969) concluded that this species is, at least in part, synonymous with V. fontinalis (Linnaeus) Christensen [section Tubuligerae (Walz) Heering sens. nov.]. Most authors using the name V. clavata (e.g. Götz 1897, Blum 1972) refer to plants similar to those described by Klebs (1896, p.95, fig. 2B). Vaucheria sessilis f. clavata Heering (1907) refers to the same taxon described by Klebs (1896) and, therefore, is also placed in synonymy with V. bursata.

The disposition of a number of other taxa referable to the section Corniculatae should also be reassessed following the studies in Chapter 3. Vaucheria antarctica Reinsch (1890, p.361, pl. 3 figs 5-7) is similar in most respects to V. bursata but differs in having a many-layered oospore wall like V. dillwynii. Authentic material of V. antarctica should be studied to clarify the relationships among these three species.

In the protologue of V. hookeri Kützing (1856, p.21, pl. 58. figs 3a,b) the oogonia illustrated in fig. 3b are ovoid-reniform and similar in size to those of V. repens (Kützing 1856, pl. 58 fig. 1), but with the long axis almost parallel with the siphon, the oogonial pore directed strongly towards the siphon and the associated antheridial pedicels relatively short. In pl. 58 fig. 3a, however, the oogonia are more globose, and more like those of V. dillwynii. A comparison of the type collections of V. hookeri and V. bursata should be made to clarify the relationships between the two species.

Vaucheria orthocarpa Reinsch (1887, p.191, pl. 8 figs 1-6) is

similar to V. bursata, and in particular, culture isolate 325 studied in Chapter 3 (see also Figs 5.6-5.8).. In fig. 4 of Reinsch (1887), the oogonium arises from the antheridial pedicel as occurred frequently in some treatments of isolate 325. In figs 2 & 3^{of Reinsch (1887)} the oospore wall is multilayered and appears to be thicker than was measured in the south-eastern Australian plants. In the measurements given, however, the oospore wall is 6-8 μm thick, which is only a little outside the range of 4-7 μm measured in this study. The seven layers distinguished by Reinsch were not observed in any specimens of the V. bursata complex studied here, but flaky or multi-layered oospore walls were diagnostic of V. dillwynii. The oogonial wall, however, was not illustrated as rugose so presumably it is smooth as in V. bursata. In agreement with Christensen (1969), this species may be best synonymised with V. bursata, but culture studies and a comparison of the relevant type material are needed to assess the importance of oogonial and oospore wall characters.

Islam (1965, p.52, pl.4 figs 13-15) described V. sessilis var. sylhetensis from plants with oogonia orientation, siphon diameter and oogonial size similar to those of V. repens, but with many-layered or lamellated oospore walls like V. orthocarpa. The texture of the oogonial wall was not described but seems to be smooth, rather than rugose, in the illustrations provided. As all the features used, except oospore wall structure, were found to have little diagnostic value in the V. bursata complex, the disposition of this taxon also depends on the results of culture and field studies on plants with multilayered oospore walls but the oogonial long axis not parallel with the siphon.

In the protologue of V. orthocarpa var. major Smith (1932, p.190), this variety was said to be similar to the description and illustration

in Reinsch (1887) of the type variety, but with larger oogonia and oospores. The oogonia are 147-175 μm long, much larger than any measured in V. bursata in this study and judgement is therefore reserved on this taxon. Teodoresco (1907), however, described a population with oogonia 137-175 μm long and similar in orientation to V. orthocarpa, and included them in V. sessilis.

Chapman (1956, p.495, fig. 153b) distinguished V. pseudosessilis from V. sessilis in having broader siphons, 96-105 μm , single rather than paired oogonia and unspotted ripe oospores. In the current study, one of the field populations of V. bursata (MEL 1049226) had vegetative siphons 62-101 μm in diameter and it was concluded from the experimental studies that siphon diameter was a variable and poor taxonomic character. The number of oogonia associated with each antheridium was also shown to be variable, both by Rieth (1963b) and in the current study, and of no taxonomic value. It is unclear what the term 'spotted' means in regard to the mature oospores. Although the rugose oogonial walls of V. dillwynii have been described as spotted (Hoppaugh 1930), all south-eastern Australian populations of V. bursata had smooth oogonial walls. The spotting may refer to pigment spots in the oospore cytoplasm, but these are also present in V. bursata. A comparison of the type collections of V. pseudosessilis and V. bursata will probably show the two to be conspecific.

Vaucheria sessilis var. iowense Prescott (1938, p.7, figs 1,2) is distinguished from the type variety in having bilaterally arranged and crowded gametangia, often with a series of oogonia near a single antheridium. The orientation of the oogonia was variable, the pore being directed parallel or perpendicular-erect to the siphon, and the thallus was frequently septate. From the results of the current study

(see Chapter 3), none of these features seem to be useful diagnostic characters and an examination of the type collections will probably show that this variety is superfluous.

Vaucheria sessilis var. monogyna W. West & G.S. West (1897, p.235) is similar in nearly all respects to V. bursata and a comparison of the type collections will almost certainly show that this variety is also superfluous.

Vaucheria dillwynii (Weber & Mohr) C. Agardh 1811: 21. Blum 1972: 15, fig. 16. Chapman et al 1957: 729. Christensen 1969: 25, fig. 14; 1973: 515, figs 1H,I. Collins 1909: 423. Hooker 1855: 261.

Basionym:

Conferva dillwynii Weber & Mohr 1803: 12, pl. 16.

Heterotypic Synonyms:

Vaucheria pachyderma Walz 1866: 146, pl. 12 figs 1-6. Cassie 1984: 226. Couch 1932: 285, figs 20-25. Gauthier-Lièvre 1955: 320, pl. 1 figs 3-7. Heidinger 1908: 318, pl. 19 figs 1-5. Heering 1907: 151,206, fig. 74. Hoppaugh 1930: 334, pl. 24 figs 6,7. Rieth 1956a: 151, pl. 2 figs 18-20,25-27; 1980b: 49, fig. 18. Sarma 1973: 168, figs 4,5,13,14; 1974: 87, figs 6,17,27,28. Sarma & Chapman 1975a: 233, pl. 1-8.

Vaucheria sessilis var. pachyderma (Walz) Hansgirg 1888: 233.

Lectotype: Description and illustration by Dillwyn (1802), but see Christensen (1973).

Type Locality: Norden, Germany; according to Blum (1972).

Distribution: Widespread (for study area, see Fig. 5.20).

Representative Specimens Studied (from a total of 15 field collections by Entwistle): MEL 1049234 p.p., Barwon River, Forrest, Victoria, 28.viii.1984; MEL 1049231 p.p., Lake Wallace, Edenhope, Victoria, 3.x.1984; MEL 1049232, Morses Creek, Bright, Victoria, 22.vii.1984; MEL 1049233 p.p., Royal Botanic Gardens, South Yarra, Victoria, 4.vi.1984.

Figs 5.15-5.24

Thallus consisting of sparingly branched siphons (36-)46-72 μm in diameter, forming stringy green mats on substrate; narrowing colourless rhizoids often present.

Plants monoecious; gametangia sessile or pedicellate, in bisexual groups of 1 oogonium with 1 antheridium. Antheridia circinate-cylindrical, turning through less than $1/2$ a circle, 53-60 μm long, 26-34 μm in diameter; walls usually flaring or disintegrating after dehiscence; antheridial pedicel straight or curved distally, 36-84(-96) μm long. Oogonia sessile, truncate-napiform, long-axis making an angle of -10° to 10° with siphon; oogonia 101-150 μm long, 79-120 μm in diameter, L/D 1.2-1.5; oogonial walls rugose. Oospores similar in size and shape to oogonia; mature oospore leaving an oogonial cavity directed at an angle of -70° to -30° with siphon; oospore walls 'flaky', or many layered, in transverse section, 8-14 μm thick.

Akinetes and sporangia unknown.

Diagnostic Features: Vaucheria dillwynii is delineated from other south-eastern Australian species of Vaucheria in having no gametophores and in having oogonia which are truncate-napiform (Figs 5.15, 5.16) and with rugose walls (Figs 5.15, 5.17, 5.19, 5.21); oospore walls flaky or with layers in transverse section (Fig. 5.19); and in having pedicellate antheridia 100 μm long and similar in size and shape throughout the plant.

Habitat and Phenology: Vaucheria dillwynii was collected from freshwater, terrestrial to semi-aquatic habitats; plants were fertile in the field, and found during May-October (winter-spring). In culture, vegetative growth occurred in media with salinities of 0.3-6.5 o/oo, but not 30 o/oo; all fertile material examined came from ASP-V media with salinities of 0.3-6.5 o/oo, and soil/water media.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria dillwynii described by Christensen (1969, 1973) and Rieth (1980b, as V. pachyderma).

Although Rieth (1962, 1980b) uses antheridial morphology to distinguish V. dillwynii (as V. pachyderma) from V. borealis and V. bursata, the results of the study in Chapter 3 indicate that the differences between saccate and cylindrical antheridia are not sufficiently distinct in all cases. If the antheridia are disintegrated or flanged distally (Fig. 5.16), the plants are probably referable to V. dillwynii, rather than V. bursata, but if they remain cylindrical (Fig. 5.18) even following dehiscence, the plants may be referable to any species in the section Corniculatae (the development of antheridia in V. borealis could not be adequately studied here, but see Chapter 3, p.40). It was found, however, that the truncate-napiform oogonia with their rugose walls, and the flaky textured, or many layered, oospore walls (in transverse section) served to distinguish V. dillwynii from all other species in the section Corniculatae. Generally, the oogonia of V. dillwynii are smaller than those of V. borealis and larger than those of V. bursata, V. arcassonensis and V. nanandra, but there is a large overlap in the length and diameter ranges.

Some stages following oospore germination in situ were photographed

(Figs 5.22-5.24) from V. dillwynii growing in agar. All oospores expanded and broke through the distal surface of the oogonium, as was reported for this species by Rieth (1956b), then developed into two siphons (Fig. 5.22). The red-brown pigment spot, observed in nearly all species in this study except those in Woroninia and Piloboloideae, migrates along one of the growing siphons (Figs 5.23, 5.24) and eventually vanishes. The function of this pigment spot is unknown.

Weber & Mohr (1803) based the name V. dillwynii on plants described by Dillwyn (1802) and on material collected by themselves. The oogonia illustrated by Dillwyn [1802, as misapplied V. frigida (Roth) C. Agardh] are similar in shape to the plants from south-eastern Australia referred to V. dillwynii. The specimens examined by both Dillwyn (1802) and Weber & Mohr (1803) are now destroyed or lost (Christensen 1973). Heering (1907), however, confirmed that the plants collected by Weber & Mohr were also referable to V. pachyderma, a commonly used name for this taxon (e.g. Hoppaugh 1930, Rieth 1980b). On the basis of Heering's judgement and the illustration of Dillwyn (1802), Christensen placed V. pachyderma in synonymy with V. dillwynii, and his conclusions are adopted here.

The 'brain-like' pattern on the oospore wall of V. pachyderma var. cebrina Guerrero (1931, p.638, fig. 8) is probably equivalent to the rugose pattern of the oogonial wall observed in south-eastern Australian populations of V. dillwynii. In the illustrations, the oospore wall has a similar flaky appearance and the outer layer but one, looks pitted. These two outer layers, together, may constitute the oogonial wall, creating a similar patterning to that observed under light microscopy in this study. A comparison of the type collections will probably show that this variety should not be recognised.

Vaucheria pachyderma var chittagonensis Islam (1965, p.51, pl. 6 figs 1-19) differs from V. dillwynii (as V. pachyderma) in having a scrobiculate oospore wall. Islam (1965) also notes characterising features such as the oogonia being occasionally pedicellate and the antheridia and oogonia resembling V. borealis. The scrobiculate oospore wall probably refers to the oogonial wall, which is illustrated (Islam 1965: pl. 6 figs 15,18) as scrobiculate or rugose, making this variety referable to V. dillwynii (see also Sarma & Chapman 1975a). Most of the oogonia illustrated are similar in shape to those of V. dillwynii (although some are more obovoid like V. borealis) and the oospore walls are many layered. As the other distinguishing features used by Islam (1965) are not considered to be useful taxonomic characters, a study of the type material will probably show that this variety is superfluous.

Vaucheria pronosperma Islam (1965, p.51, pl. 2 figs 7-11) differs from V. dillwynii in having ovate to subglobose oogonia with a broad oogonial cavity directed towards the siphon, and several oil globules inside the mature oospore. In addition, the oospore walls of V. pronosperma have > 3 layers but they are not easily distinguished (Islam 1965). Most of the diagnostic characters for this species are found at least sometimes in V. dillwynii, and the oogonia illustrated (Islam 1965, pl. 2 figs 7-10) are slightly oblique, but essentially truncate-napiform in shape. A comparison of the type material of these two species will probably show the two to be conspecific.

Vaucheria nanandra Christensen (in preparation for Aust. J. Bot.)

Holotype: ADU (Christensen pers. comm.).

Type Locality: Kirk Point, via Point Wilson, Victoria (Christensen pers. comm.).

Distribution: South-eastern Australia (see Fig. 5.30).

Representative Specimens Studied (from a total of 32 field collections by Entwisle) : MEL 1049102 p.p., Lake Corangamite, Victoria, 13.vi.1984; MEL 1049044, MEL 1049136, Lake Corangamite, Victoria, 29.viii.1983; MEL 1049103, Lake Corangamite, Victoria, 13.x.1983; MEL 1049390 p.p., Taillem Bend-Ashville Road, South Australia, 8.viii.1983; MEL 1049406, North Beach Road, via Wallaroo-Port Broughton Road, South Australia, 5.viii.1983; MEL 1049104, Barr Creek, Kerang-Cohuna Road, Victoria, 20.vii.1984; MEL 1049137, Toora Beach, Victoria, 24.vi.1983.

Figs 5.25-5.30

Thallus consisting of sparingly branched siphons, 53-91(-103) μm in diameter, forming dense green mats on substrate.

Plants monoecious; gametangia sessile or pedicellate, in bisexual groups of 1-2 oogonia on opposite sides of 1 antheridium. Antheridia circinate-cylindrical to helical, turning through at least an entire circle, 35-60 μm long, 12-17(-19) μm in diameter; antheridial pedicels straight or curved distally, 19-48 μm long. Oogonia transverse-obovoid, long-axis making an angle of $0-20(-40)^{\circ}$ with siphon, 89-127 μm long, 72-101 μm in diameter, L/D 1.1-1.3; oogonial wall smooth. Oospores similar in shape and size to oogonia; mature oospores leaving an oogonial cavity directed at an angle of -30° to 20° with siphon; oospore walls evenly textured in transverse section, 6-7 μm thick.

Akinetes and sporangia unknown.

Diagnostic Features: Vaucheria nanandra is delineated from other south-eastern Australian species of Vaucheria in having antheridia $< 70 \mu\text{m}$ long, pedicellate, curved through at least a full circle (Figs 5.25A,B) and not borne on a gametophore, and in usually having the long axis of the oogonium and the distal cavity both parallel to the siphon (Figs 5.26, 5.27, 5.29).

Habitat and Phenology: Vaucheria nanandra was collected from saline, terrestrial to semi-aquatic habitats; plants were fertile in the field, and found during June-November (winter-spring). In culture, vegetative growth occurred in media with salinities of 0.3-16 o/oo, but not 30 o/oo; all fertile material examined came from ASP-V media with salinities of 0.3-6.5 o/oo and soil/water media. Maximal growth and reproduction occurred at 15°C and 35-50 $\mu\text{mol/m}^2/\text{s}$ (see Chapter 2).

Remarks: The plants studied were concordant with the plants of Vaucheria nanandra described by Christensen (pers. comm.).

The antheridia of V. nanandra turn through at least an entire circle, while those of V. bursata, V. dillwynii and V. borealis only turn through a quarter to three-quarters of a circle (the antheridia of V. arcassonensis are contorted or straight, and $> 100 \mu\text{m}$ long).

Vaucheria nanandra also has narrower antheridia (generally $< 17 \mu\text{m}$) than other species in the section Corniculatae. Occasionally, the twisting of the antheridia in V. nanandra can make it appear swollen distally, but no antheridia were observed which were flanged distally, even after dehiscence, like is sometimes found in V. dillwynii. In addition to these antheridial features, the oogonia of V. nanandra are smaller than those of V. borealis, but similar in size to those of V. arcassonensis, V. bursata and V. dillwynii. The orientation of oogonia, however, is different in these three latter species. The oogonial long-axis in V. nanandra is close to parallel with the siphon, similar to that of V. dillwynii and some populations of V. bursata (e.g. MEL 1049221) but the pore is also usually directed parallel to the siphon (see however Fig. 5.28); not towards it as in V. dillwynii and those populations of V. bursata with oogonia parallel to the siphon.

Based on measurements from an isolate of MEL 1049102 grown at 5°C, 35-50 $\mu\text{mol}/\text{m}^2/\text{s}$, 0.3 o/oo; 15-20°C, 110-130 $\mu\text{mol}/\text{m}^2/\text{s}$, 0.3 o/oo; and 15°C, 30-40 $\mu\text{mol}/\text{m}^2/\text{s}$ 6.5 o/oo; the effect of salinity and temperature on the diagnostic characters of V. nanandra appears to be negligible.

Ecologically, V. nanandra is also distinct, being found only in saline areas, and usually in salt marshes with V. erythrospora. Vaucheria bursata, V. dillwynii and V. borealis are generally restricted to freshwater habitats, only rarely occurring at the edge of saline areas, while V. arcassonensis grows in saline areas, but only coastally and often under mangroves.

Section Piloboloideae (Walz) Heering 1907: 169.

Basionym:

'Group' Piloboloideae Walz 1866: 144.

Gametangia borne on gametophores or pedicellate on siphons.

Antheridia cylindrical, with one terminal and one to many lateral discharge pores; antheridia subtended by a wall-bound cavity. Oogonia radially or bilaterally symmetrical.

Type Species: Vaucheria piloboloides Thuret (see Walz 1866, p.144).

The section Piloboloideae is distinguished from all other sections in having a wall-bound cavity subtending the antheridia ^{as well as} multiporic, fusiform-cylindrical antheridia (see Table 5.3). It may be useful, in the future, to subdivide this relatively large section which includes a diverse array of species, but as it is poorly represented in south-eastern Australia, no attempt was made in the current study. Of the 12 species worldwide (Blum 1972, Rieth 1980b), three are known to occur in

south-eastern Australia.

Key to the South-eastern Australian species in the section Piloboloideae

1. Oogonia not subtended by a wall bound cavity; no proximal mass of protoplasm left by mature oospore
.....V. longicaulis
1. Oogonia subtended by a wall bound cavity; proximal mass of protoplasm left by mature oospore.....2
2. Antheridia < 500 µm long, with almost cylindrical protuberances, subtending cavity L/D > 2
.....V. glomerata
2. Antheridia > 500 µm long, with short conical protuberances, subtending cavity L/D < 2
.....V. litorea

Vaucheria glomerata Blum & Womersley 1955: 713, figs 1-9, 12-14.

Holotype: ADU (A19793)

Type Locality: Port Willunga, St Vincent's Gulf, South Australia.

Distribution: Coastal south-eastern Australia (see Fig. 5.33).

Specimens Studied: A19102, Port Willunga, South Australia, Womersley, 1.ii.1953; A46258, A46230, Crawfish Rock, Western Port Bay, Victoria, Watson, 17.xi.1974; A19793, Port Willunga, South Australia, Womersley, 26.ix.1954 (holotype); A56407, Nora Creina, South Australia, Womersley, 22.ii.1985. [The measurements given in the following description are essentially those of Blum & Womersley (1955), except where observations from the herbarium material made it necessary to extend some of the size ranges.]

Figs 5.31-5.34

Thallus consisting of sparingly branched siphons, 19-50 µm in diameter, forming dark green mats on substrate.

Plants dioecious; gametangia produced terminally on siphons.

Antheridia borne singly or in monopodial clusters, cylindrical to fusiform, 117-208 μm long, 18-29 μm in diameter, 1 terminal pore and 1-2 lateral pores borne on almost cylindrical protuberances, 10-25 μm long; antheridia subtended by a wall-bound cavity, 60-120(-244) μm long, 18-28(-44) μm in diameter, L/D 2.4-6.5; antheridial pedicels usually smaller in diameter than attached vegetative siphon. Oogonia usually sessile or shortly pedicellate following subsequent sympodial growth, often in unilateral series, claviform, 142-235 μm long, 86-160 μm in diameter; oogonia subtended by a wall-bound cavity, 41-110 μm long, 45-60 μm in diameter. Oospores globose to ellipsoid, 85-160 μm in diameter, leaving a mass of protoplasm in a proximal oogonial cavity; oospore wall 6-15 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria glomerata is delineated from other south-eastern Australian species of Vaucheria in having oogonia subtended by a wall-bound cavity and containing a proximal mass of protoplasm when the oospore matures (Fig. 5.31), and in having antheridia < 500 μm long, with almost cylindrical protuberances, and subtended by a wall-bound cavity with L/D > 2 (Figs 5.32, 5.34).

Habitat and Phenology: All collections of Vaucheria glomerata were from intertidal mudflats in February (summer), September and November (spring); at least some of the material in each collection was fertile in the field. No material was grown in culture.

Remarks: The material of Vaucheria glomerata deposited in ADU was concordant in most respects with the protologue (Blum & Womersley 1955).

In A19102, however, antheridia were borne both singly and in monopodial clusters (Fig. 5.32), while Blum & Womersley (1955) only observed single antheridia in material taken from this collection. The absence of reflexed oogonia in V. glomerata, noted by Blum & Womersley (1955), is not a useful distinguishing character since some south-eastern Australian collections of V. litorea, a species which normally has reflexed oogonia, had almost straight oogonia (Figs 5.35, 5.37). Vaucheria glomerata, however, is easily distinguished from V. litorea, the only other species in south-eastern Australia with a wall-bound cavity subtending the oogonia, by the diagnostic characters listed above and in having antheridial pedicels thinner than the adjacent vegetative siphon (Fig. 5.34).

Vaucheria litorea Hofman & C. Agardh in C. Agardh 1823: 463. Blum 1972: 26, figs 84,85. Blum & Womersley 1955: 716, figs 18-26. Christensen 1952: 177, figs 2 h,i. Dangeard 1939b: 247, fig. 20. Heering 1907: 172,200, fig. 98. Nordstedt 1879: 180, pl. 2 figs 1-6. Ott & Hommersand 1974: 376, figs 9-13. Rieth 1956a: 148, figs 24,25,42,43; 1980b: 119, figs 51,52 A-B.

Type: Not designated by Hofman & C. Agardh in C. Agardh (1823).

Type Locality: Odense Fjord, Funen, Denmark; according to Blum (1972).

Distribution: Europe, North America, U.S.S.R.; south-eastern Australia (see Fig. 5.38).

Specimens Studied (collected by Entwisle): MEL 1049199(female plants), MEL 1049200(male plants), Lake Bunga, Lakes Entrance-Lake Tyers Road, Victoria, 1.x.1983; MEL 1049201, Glenelg River, Nelson, 3.x.1984.

Thallus consisting of sparingly branched siphons, 62-103(-127) μm in diameter, forming thick dark green mats on substrate.

Plants dioecious; gametangia produced terminally on siphons, but becoming lateral following sympodial growth. Antheridia borne singly or in sympodial clusters, cylindrical to fusiform, 576-1008 μm long, 96-125 μm in diameter, with 1 terminal pore and 1-4 lateral pores borne on conical protuberances, 12-48 μm long; antheridia subtended by a wall-bound cavity, 67-96 μm long, 57-77 μm in diameter, L/D 0.3-1.5.

Oogonia usually sessile following subsequent sympodial growth, in unilateral series, claviform, 248-464 μm long, (163-)211-268 μm in diameter; oogonia subtended by a wall-bound cavity, 29-48 μm long, 77-116 μm in diameter. Oospores globose, 172-250 μm in diameter, leaving a mass of protoplasm in a proximal oogonial cavity; mature oospores not seen.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria litorea is delineated from other southeastern Australian species of Vaucheria in having oogonia subtended by a wall-bound cavity and containing a proximal mass of protoplasm when oospore matures (Fig. 5.37), and in having antheridia $> 500 \mu\text{m}$ long, with short conical protuberances, and subtended by a wall-bound cavity with L/D < 2 (Fig. 5.36, 5.40).

Habitat and Phenology: Vaucheria litorea was collected from upper intertidal mudflats in October (spring); all plants were sterile in the field. In culture, vegetative growth occurred in media with salinities of 0.3-30 o/oo; all fertile culture material examined came from media with a salinity of 6.5 o/oo.

Remarks: The south-eastern Australian plants were concordant in most respects with the plants of Vaucheria litorea described by Rieth (1956a) and Ott & Hommersand (1974).

They differed in having oogonia which were usually not, or little, reflexed (Figs 5.35, 5.37). If they were reflexed (Fig. 5.39), it was not through an angle of nearly 90° as illustrated by the above two authors. While both C. Agardh (1823) and Nordstedt (1879) referred to the reflexing of the oogonia as diagnostic for this species, the south-eastern Australian plants resemble V. litorea in all other respects. The size and shape of the gametangia, the sympodial arrangement of these gametangia and the formation of a cell bound cavity subtending the oogonia, are all consistent with the descriptions of V. litorea in the literature. In addition, the oogonia appear sessile after the subsequent sympodial growth, and give the characteristic arrangement shown in Fig. 5.35.

Vaucheria litorea is most easily distinguished from V. longicaulis in having larger antheridia (see Fig. 5.36), a proximal mass of cytoplasm after oospore maturation and a wall-bound space subtending the oogonia. In addition, the oogonia are borne on pedicels $< 300 \mu\text{m}$ long, and are usually almost sessile following sympodial growth. Vaucheria glomerata, the only other south-eastern Australian species in the section Piloboloideae, has oogonia with a proximal mass of cytoplasm after oospore maturation, and subtended by a wall-bound cavity, but differs from V. litorea in the diagnostic characters given above. Furthermore, although V. litorea can produce antheridia in clusters (Fig. 5.40), they are sympodial rather than monopodial as in V. glomerata, and the pedicels subtending the antheridia in V. glomerata are thinner than the attached vegetative siphons (Blum & Womersley

1955).

Rieth (1956a) found that V. litorea usually grew in areas of low salinity (< 5 o/oo), while the south-eastern Australian plants were collected from marine waters. In culture, however, vegetative growth occurred in media with salinities of 0.3-30 o/oo.

Vaucheria longicaulis Hoppaugh 1930: 332, figs 1-3. Blum 1972: 26, fig.

88. Islam 1979: 167, figs 1-32. Ott & Hommersand 1974: 378, figs 46-50. Pecora 1977: 28, figs 8-10. Taylor 1952: 274, figs 1-11.

Heterotypic Synonyms:

Vaucheria longicaulis var. bengalensis Islam 1974: 90.

Vaucheria longicaulis var. orientalis Islam 1965: 55, pl. 8 figs 6-10, pl. 9 figs 1-18.

Type: Not designated by Hoppaugh (1930).

Type Locality: Elkhorn Slough, Monterey County, U.S.A. (Hoppaugh, 1930).

Distribution: North America, South America, Asia; coastal south-eastern Australia (see Fig. 5.46).

Specimens Studied: MEL 1049202, Stony Creek, Spotswood, Victoria, Entwisle, 22.viii.1984; MEL 1049203, Dynon Bridge, Moonee Ponds Creek, North Melbourne, Victoria, Entwisle, 3.ix.1985; MEL 1049204, Nelson Lagoon, Victoria, Womersley, 15.x.1985.

Figs 5.41-5.46

Thallus consisting of sparingly branched siphons, 24-60 μm in diameter, forming thick dark green mats on substrate.

Plants dioecious; gametangia produced terminally on siphons.

Antheridia borne singly or arranged sympodially, cylindrical to fusiform, 270-520(-720) μm long, 38-101 μm in diameter, with 1 terminal pore and 1-4 lateral pores borne on conical protuberances, 7- 100(-190)

μm long; antheridia subtended by a wall-bound cavity, 29-48 μm long, 30-35 μm in diameter, L/D 1.2-4.1. Oogonia arranged sympodially, claviform, 210-326 μm long, 96-170 μm in diameter, often with an incomplete septum in the mid-region, not subtended by a wall-bound cavity; oogonial pedicels over 300 μm long. Oospores globose to ellipsoid, 125-165 μm long, 105-134 μm in diameter, not leaving a mass of protoplasm in proximal oogonial cavity; oospore walls ca 2 μm thick.

Aplanosporangia terminal on siphons, obovoid to claviform, 192-272 μm long, 77-96 μm in diameter. Akinetes unknown.

Diagnostic Features: Vaucheria longicaulis is delineated from other south-eastern Australian species of Vaucheria in having no wall-bound cavity subtending the oogonia, no proximal mass of protoplasm left by the mature oospore (Fig. 5.41) and in having antheridia subtended by a wall-bound cavity and often with conical protuberances up to 190 μm long (Figs 5.42, 5.43).

Habitat and Phenology: Vaucheria longicaulis was collected from upper sublittoral and eulittoral mudflats in August (winter), September and October (spring); no plants were sexually reproductive in the field. All fertile material examined came from media with a salinity of 6.5 o/oo or crude culture.

Remarks: The south-eastern Australian plants were concordant in most respects with the plants of Vaucheria longicaulis described in the protologue (Hoppaugh 1930) and by Taylor (1952) and Islam (1979).

In common with the plants described by Hoppaugh (1930), the south-eastern Australian material had oogonia borne terminally on elongate lateral branches following sympodial growth (see Fig. 5.45), and with no subtending wall-bound cavity. The south-eastern Australian plants differed in having 1-4, rather than 3-12, lateral pores on the antheridia, and generally shorter oogonia and antheridia. Islam (1979) however, recorded that in the literature, the number of antheridial pores ranges from 1-6(-10) and Taylor (1952) found 3-4 lateral pores on most antheridia in a collection from the type locality. Although the gametangia measured by Hoppaugh (1930) are smaller than those found in this study, Islam (1979) gave the length of the oogonia as 248-278 μm , and the antheridia 292-510 μm , which are closer to the size ranges found here. In addition, a few antheridia measured in the current study were up to 720 μm long.

Taylor (1952) also found that V. longicaulis has generally narrower siphons and shorter antheridia than V. litorea. Measurements of siphons and antheridia in south-eastern Australian plants included a similar distinction. The absence of a protoplasmic mass in the proximal cavity of oogonia distinguishes V. longicaulis from V. litorea and V. glomerata. Vaucheria glomerata also differs from V. longicaulis in having glomerate clusters of short antheridia generally with cylindrical rather than conical protuberances.

Five additional collections (MEL 1049205, MEL 1049206, Glenelg River, Nelson, Victoria, Entwisle, 3.x.1984; MEL 1049207, Lake King, Lakes Entrance, Victoria, Entwisle, 1.x.1983; MEL 1049387, MEL 1049388, MEL 1049389, Pine Point, South Australia, Entwisle, 8.viii.1985; MEL 1049744, Tooradin, Victoria, Entwisle, 3.ix.1985; A47258, Nooan, The Coorong, South Australia, Robertson,

27.viii.1976) had antheridia resembling those of V. longicaulis, and some also had elongate oogonial pedicels, but no oogonia. In the absence of mature oogonia, no positive determination could be made. Even in identified collections of V. longicaulis, antheridia were generally produced profusely while oogonia were only rarely seen.

The aplanosporangia found in this study were similar in size and shape to those described by Taylor (1952).

Blum (1971, p. 193, figs 13-19) described V. longicaulis var. mucronii, which differs from the type in having shorter, 149-300 μm , and curved antheridia which are frequently bifurcate and oogonia often subtended by a wall-bound cavity. The south-eastern Australian plants had some antheridia of a similar size and a few (Fig. 5.43) could be considered bifurcate. In the same material, however, there also were longer antheridia (Fig. 5.85), similar in shape to the type variety. No wall-bound cavities were observed subtending the oogonia, but a perforated, or incomplete, septum was found midway along the oogonia. The structure of this septum is discussed by Blum (1971) and it has been commonly observed in the type variety (Blum 1971, Ott & Hommersand 1974, Taylor 1952).

In addition to V. litorea, V. glomerata and V. longicaulis there is another dioecious species (not found in south-eastern Australia) in the section Piloboloideae, V. compacta (Collins) Collins. This species is distinguished from the others in having smaller antheridia, 84-228 μm long, and no wall-bound cavity subtending the oogonia (Blum 1972).

Islam (1979) placed V. longicaulis var. orientalis (= V. longicaulis var. bengalensis; but see Islam 1974) in synonymy with V. longicaulis var. longicaulis, after finding that the variation in a collection of the type variety from Iraq, included the features

previously considered to be distinctive of V. longicaulis var. bengalensis.

Section Racemosae (Walz) Entwistle sect. nov.

Basionym:

'Group' Corniculatae 'subgroup' Racemosae Walz 1866: 144.

Synonyms:

Corniculatae subsection Racemosae (Walz) Heering 1907: 141.

Corniculatae subsection Discoideae Venkataraman 1961: 89.

Corniculatae subsection Radiatae Hoppaugh 1930: 332.

Heeringia Blum 1971: 189.

Vaucheriosis Heering 1921: 96.

Gametangia gametophoris insidentia. Antheridia pedicellata, cylindrica, arcuata ad circinata, non ^{interstitiis in ambus} parietibus ^{circum datais} subtenta, singulari terminali poro. Oogonia radialiter vel bilateraliter congruentia.

Gametangia borne on gametophores. Antheridia pedicellate, cylindrical, curved to circinate, with 1 terminal discharge pore; antheridia not subtended by a wall-bound cavity. Oogonia radially or bilaterally symmetrical.

Lectotype Species: Vaucheria terrestris (Vaucher) de Candolle;

this species was chosen from those examined by Walz (1866) as the other species ^{names} are misapplied or less representative of the section Racemosae.

The subsection Racemosae of Corniculatae has been raised to sectional level (see p.126) and includes, following Blum (1972) and Rieth (1980b), Corniculatae subsection Discoideae, a monotypic

subsection characterised by the presence of a disc-like expansion in the peduncle, and Corniculatae subsection Radiatae, also monotypic and characterised by the apparent absence of a peduncle. The section *Heeringia* is rejected and *V. uncinata* transferred back to the section *Racemosae* (see Walz 1866), as the distinguishing oogonial characters are considered to be important at species but not sectional level, and the antheridia are monoporic and terminate a gametophore (see Table 5.3). *Vaucheria subarechavaletae* also shares these antheridial characters and is referred to the section *Racemosae*. Of the 21-25 species worldwide (Blum 1972, Rieth 1980b; as subsection *Racemosae*), ten are known to occur in south-eastern Australia.

Key to South-eastern Australian Species in the Section *Racemosae*

1. Mature oospores not leaving a distal oogonial cavity; distal end of oogonia obtuse.....2
1. Mature oospores usually leaving a distal oogonial cavity; distal end of oogonia attenuate, often reflexed or oblique.....7
 2. Oogonia erect; antheridial pedicels usually erect, at least proximal end straight.....3
 2. Oogonia pendent or perpendicular to the peduncle; antheridial pedicels pendent, or only little extended beyond the peduncle, usually curved throughout.....5
3. Oogonia radially symmetrical; antheridia always straight.....*V. subarechavaletae*

3. Oogonia bilaterally symmetrical; antheridia usually curved or circinate.....4
4. Oogonial pedicels curved, distal end parallel with antheridial pedicel; antheridial pedicels usually straight.....V. gardneri
4. Oogonial pedicels straight, making an acute angle with peduncle; antheridial pedicels usually curved distally.....V. geminata
5. Oogonia almost radially symmetrical around oogonial pedicel, with no distal prominence.....V. uncinata
5. Oogonia bilaterally symmetrical, with distal prominence.....6
6. Gametophores with only 1 oogonium, borne distally to antheridium; mature oospore walls > 5 μ m thick; oogonia often > 100 μ m long.....V. frigida
6. Gametophores with 1 or more oogonia (if 1 oogonium, it is borne laterally to antheridium); oospore walls < 5 μ m thick; oogonia almost always < 100 μ m long.....V. prona
7. Oogonial pedicels erect, almost parallel with antheridial pedicel; antheridial pedicels usually straight.....V. gardneri
7. Oogonial pedicels more or less transverse to peduncle, or pendent; antheridial pedicels at least in part circinate.....8
8. Oogonia pendent.....V. erythrospora
8. Oogonia erect or transverse to peduncle.....9

9. Oogonial plane of symmetry transverse to peduncle; oogonia $> 80 \mu\text{m}$ long.....V. gyrogyna
9. Oogonial plane of symmetry erect and parallel to peduncle; oogonia $< 80 \mu\text{m}$ long.....10
10. Oogonial cavities circinate-cylindrical, directed towards oogonial pedicel; septum present in peduncle.....V. lii
10. Oogonial cavities conical, reflexed, but not directed towards oogonial pedicel; septum absent in peduncle.....V. pseudogeminata

Vaucheria erythrospora Christensen 1956: 275, figs 1a-d, 2. Blum 1972:

17, fig. 38. Ott & Hommersand 1974: 384, figs 43-45. Pecora 1977: 28, figs 4,5; 1980: 388, fig. 5. Rieth 1980b: 74, fig. 29.

Homotypic Synonym:

Vaucheria hamata f. salina Rieth 1956a: 135, text fig. 5-7, pl. 1 figs 7, 8.

Holotype: Not designated by Rieth (1956a) or Christensen (1956).

Type Locality: Artern, East Germany (Rieth 1956a).

Distribution: Northern Europe, eastern U.S.A., Asia; widespread in saline habitats throughout south-eastern Australia (see Fig. 5.52).

Representative Specimens Studied (from a total of 85 field collections by Entwistle): MEL 1040059, MEL 1049060, MEL 1049061, St Leonards Lake, Victoria, 15.vi.1983; MEL 1049077, MEL 1049144, MEL 1049145, MEL 1049146, Onkaparinga River, Port Noarlunga, South Australia, 4.vii.1983; MEL 1049147, MEL 1049148, Barker Inlet, North Adelaide, South Australia, 5.vii.1983; MEL 1049152, Port Davis, South Australia, 6.viii.1984; MEL 1049153, Ashville-Meningie Road, South Australia, 8.viii.1984; MEL 1049045, MEL 1049062, Lake Corangamite, Victoria, 29.viii.1983; MEL 1049135 p.p., Lake Tyers, Victoria, 1.x.1983; MEL 1049063, MEL 1049064, Stingray Point, Mallacoota, 1.x.1983; MEL 1049065, MEL 1049066, MEL

1049067, Natimuk Lake, Victoria, 12.vi.1984; MEL 1049068, Nine Mile Creek, Kerang-Cohuna Road, Victoria, 23.vii.1984; MEL 1049069 p.p., MEL 1049070, Piccaninny Barr Creek, Kerang-Cohuna Road, 20.vii.1984; MEL 1049071, MEL 1049072, MEL 1049073, Richardson River, Donald, Victoria, 5.iii.1984; MEL 1049074, Salt Lake, Lake Charm township, Victoria, 4.viii.1984; MEL 1049075 p.p., MEL 1049078, Lake Hawthorn, Merbein-Mildura Road, Victoria, 2.x.1984; MEL 1049409, The Corrong, Magrath Flat, South Australia, 8.viii.1983; MEL 1049112, Natimuk Lake, Victoria, 12.vi.1984.

Figs 5.47-5.52

Thallus consisting of sparingly branched siphons, rarely spiralled; siphons 28-64 μm in diameter, forming dense green mats on substrate.

Plants monoecious; gametophores consisting of 1-2 oogonia borne laterally to 1 antheridium; peduncles 96-384 μm long, 27-52 μm in diameter. Antheridia circinate-cylindrical, 27-48 μm long, 12-17 μm in diameter; antheridial pedicels circinate, 36-53 μm long. Oogonia pendent, ovoid-reniform, (66-)72-94 μm long, 48-74 μm in diameter, L/D 1.2-1.4(-1.6), with attenuate, sometimes oblique, apex; oogonial pedicels 10-24 μm long. Oospores ellipsoid to ovoid-reniform, 53-79 μm long, 48-74 μm in diameter, leaving a distal oogonial cavity when mature; distal cavity conical, (5-)10-23 μm long; oospore wall 1-3 μm thick.

-like fungal infections

Akinetes~~x~~ formed in vegetative thallus by production of cross walls, usually separated wall-bound cavities. Sporangia unknown.

Diagnostic Features: Vaucheria erythrospora is delineated from other south-eastern Australian species of Vaucheria in having gametophores bearing pendent oogonia (Figs 5.47, 5.48, 5.50) with a distal cavity left by the mature oospore (Figs 5.49A-C, 5.50).

Habitat and Phenology: Vaucheria erythrospora was collected from terrestrial to semi-aquatic habitats near saline rivers, channels, and

lakes, and from coastal and inland salt marshes (usually with V. nanandra); plants were found in May-November (autumn-spring) and were fertile in the field in June-October (winter-spring). In culture, vegetative growth occurred in media with salinities of 0.3-30 o/oo; all fertile material examined came from media with salinities of 2-6.5 o/oo. Maximal vegetative growth and gametangial production in culture occurred at a temperature of 15°C, and light irradiance of 35-50 $\mu\text{mol}/\text{m}^2/\text{s}$ (see Chapter 2).

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria erythrospora described by Christensen (1956) and Rieth (1956a, as V. hamata f. salina).

Vaucheria prona Christensen, like V. erythrospora, has pendent oogonia and if mature oospores are not found, the two species may be difficult to separate. Christensen (1956) and Rieth (1956a) noted that V. erythrospora also differs from V. prona in having more loosely coiled antheridia but this was not observed in the south-eastern Australian material. Rieth (1956a), using the 'ratio of radii' method for measuring antheridial curvature (see Chapter 4, p.81), compared the results of Blum (1953) for V. prona Christensen (as V. hamata sensu Götz) and V. frigida C. Agardh (as V. terrestris sensu Götz) from U.S.A., with V. erythrospora (as V. hamata f. salina) collected from Germany. Rieth (1956a) concluded that his material represented a form of V. prona rather than V. frigida. Christensen (1956) reinterpreted these results and concluded that since the mean of the antheridial measurements for V. erythrospora lay between the ranges of V. prona and V. frigida, the plants need not be included in either species on this account.

In this study, the length of the antheridium was used to measure the antheridial curvature and it was found that the antheridia of V. erythrospora (see Fig. 5.49D), 27-48 μm long, were usually more tightly coiled than both V. prona, 38-65(-77) μm long, and V. frigida, 38-67(-79) μm long. Blum (1972) found similar antheridial lengths in North American material of V. prona, 30- 65 μm , but did not take measurements of V. erythrospora [using the description from Rieth (1956a), which did not include this dimension]. The length of antheridia in V. frigida, 64-93 μm , were longer than those measured in this study. The variation in antheridial length, and hence degree of coiling, makes this character of doubtful use in distinguishing V. erythrospora.

Both Christensen (1956) and Rieth (1956a) found a red-brown layer in the oospore walls of V. erythrospora and this has been subsequently observed by Ott & Hommersand (1974) and Pecora (1980). This colouration was evident in field and culture material from south-eastern Australia, but was not observable in stained preparations.

Plants collected near the Wimmera River, Jeparit, Victoria (MEL 1049079 p.p.) had grey oospore walls $> 3 \mu\text{m}$ thick and oogonial cavities up to 30 μm long. The oogonial cavities were often strongly reflexed and hence similar to those of V. adunca Jao (1939). In all other respects, however, the gametophores resembled those of V. erythrospora. As no material of this collection survived for study in culture, it has not been included in the description given here.

The salinity of Lake Corangamite, Victoria, a site with a dense cover of V. erythrospora, can reach 28 o/oo (Williams 1981), and Pecora (1977) measured salinities of 1-25 o/oo in North American habitats of this alga. In culture, V. erythrospora grew and reproduced in media with salinities of 0.3-30 o/oo. Rieth (1956a) found V. erythrospora

in habitats with salinities of 9-15 o/oo and grew it in culture media with a salinity of 15 o/oo. It can thus be considered a euryhaline alga.

The absence of this species from freshwater habitats, therefore, seems not to result from an intolerance of low salinities. As it was collected from inland, in addition to coastal, saline habitats, the possibility of a 'seawater' requirement is negated. Generally, V. erythrospora was found above the permanent water level, and only submerged in very high tides or floods. This is a similar habitat to that described by Ott & Hommersand (1974). Reproduction in this species was restricted to the colder months (see also Christensen 1956) and even sterile plants were not found in the study area during summer.

The akinetes sometimes contained spherical (?fungal) structures (Fig. 5.51), similar to those observed in V. racemosa (Vaucher) de Candolle (as V. uncinata Kützinger) by Randhawa (1939), but these did not appear to have any reproductive function.

Vaucheria erythrospora was originally described as Vaucheria hamata f. salina Rieth. Christensen (1956) raised it to species level, which required the introduction of a new epithet erythrospora as the name V. salina had been used previously (see Heering 1907, p. 212). This change of rank has been supported by Rieth (1980b).

Vaucheria frigida (Roth) C. Agardh 1824: 173. Christensen 1969: 16, fig. 9; 1970: 466, figs 12-15. Blum 1972: 19, figs 44,45,60.

Basionym:

Conferva frigida Roth 1797: 166.

Heterotypic Synonyms:

Ectosperma hamata Vaucher 1803: 27, pl. 2 fig. 3.

Ectosperma multicornis Vaucher 1803: 33, pl. 3 fig. 9.

Vaucheria brevicaulis Blum 1951: 445, figs 7-11.

Vaucheria hamata (Vaucher) de Candolle in Lamarck & de Candolle
1805: 63. non V. hamata sensu Götz 1897.

Vaucheria pseudohamata Prescott 1953: 468, pl. 1.

Misapplied Name:

Vaucheria terrestris auct. non (Vaucher) de Candolle: Götz

1897: 120, figs 35-37. Blum 1953: 490, figs 12,13,43-53.

Cassie 1984: 227. Chapman et al, 1957: 729. Gauthier-

Lièvre 1955: 323, pl. 3 figs 33-36. Rieth 1965b: 151,

figs 26-33; 1980b: 87, fig. 36. Sarma 1974: 88, figs

9,11,12,14,20,26. Sarma & Chapman 1975b: 309.

Holotype: Dillenian Herbarium, OXF; but see Christensen (1968).

Type Locality: London, England; according to Blum (1972).

Distribution: Widespread (for study area, see Fig. 5.57).

Specimens Studied (from a total of 51 field collections by
Entwistle): MEL 1049268, MEL 1049080, Avoca River, Elmhurst-
Amphitheatre Road, Victoria, 12.vi.1984; MEL 1049255,
Irrigation Channel, Sea Lake-Woomalang Road, Victoria,
4.viii.1984; MEL 1049256, Irrigation Channel, Swan Hill-Sea
Lake Road, Victoria, 4.viii.1984; MEL 1049258 p.p., Glenelg
River, Lower Glenelg National Park, Victoria, 3.x.1984; MEL
1049259 p.p., Running Creek, Myrtleford-Mt Beauty Road,
Victoria, 16.x.1984; MEL 1049260, Murray River, Merbein-Mildura
River-Road, Victoria, 2.x.1984; MEL 1049261, Lake Corangamite,
Wool Wool, Victoria, 28.viii.1984; MEL 1049262, Lake George,
Beachport, Victoria, 15.vi.1983; MEL 1049081, Queenscliff,
Victoria, 15.vi.1983; MEL 1049263, Lake Connnewarre Game
Reserve, Barwon Heads, Victoria, 15.vii.1983; MEL 1049888,
Piccaninnie Ponds Conservation Park, South Australia,
3.viii.1983; MEL 1049889, The Coorong, Woods Well, South
Australia, 8.viii.1983; MEL 1049264, Campbells Creek, Yapeen,
Victoria, 9.viii.1983; MEL 1049265, Lake Beeac, Victoria,
29.viii.1983; MEL 1049266, Corringale Creek, Corringale-
Newmerella Road, South Australia, 1.x.1983; MEL 1049267,
Campbells Creek, Yapeen, Victoria, 17.ix.1983.

Thallus consisting of sparingly branched siphons, 29-62(-86) μm in diameter, forming dense green mats on substrate; narrowing colourless rhizoids often present.

Plants monoecious ; gametophores consisting of 1 oogonium borne distally to 1 antheridium; peduncle 20-340(-670) μm long, (31-)41-72(-85) μm in diameter distally. Antheridia circinate-cylindrical, 38-67(-79) μm long, 12-29(-34) μm in diameter; antheridial pedicel pendent, circinate. Oogonia transverse to peduncle or slightly pendent, globose to dimidiate-globose, 72-158 μm long, 58-144 μm in diameter, L/D 1-1.4, fertilisation pore directed towards vegetative siphon; oogonial pedicels erect, 12-38(-48) μm long. Oospores same size and shape as oogonia, but extruding through fertilisation pore into distal protuberance; oospore wall 8-16 μm thick, usually with flaky texture in transverse section.

Akinetes and sporangia unknown.

Diagnostic Features: Vaucheria frigida is delineated from other south-eastern Australian species of Vaucheria in having gametophores with one, large (often $> 100 \mu\text{m}$) oogonium borne distally to the antheridium (Fig. 5.53), a thick ($> 5 \mu\text{m}$) oospore wall which is flaky in transverse section (Fig. 5.55), and oospores with a large distal protuberance (Figs 5.54, 5.56).

Habitat and Phenology: Vaucheria frigida was collected from freshwater to saline, terrestrial to aquatic habitats; plants were found from June-November (winter-spring) and were fertile throughout this period. In culture, vegetative growth occurred in media with salinities of 0.3-16 o/oo, but not 30 o/oo; all fertile material examined came from media

with salinities of 0.3-6.5 o/oo.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria frigida described by Christensen (1969) and Blum (1972).

One isolate (from MEL 1049268) was studied in a series of culture experiments and compared with 15 field populations of V. frigida, and V. prona (see Chapter 4). From the results of this study, V. frigida was recognised as a distinct species which probably includes a number of variants differing only in the size of gametangia, gametophores and siphons.

Christensen (1968, 1969) has discussed the identity of V. frigida, concluding that if legitimate [depending on the correct application of article 13 and (Christensen per. comm.) the 'Guide for the determination of types, T4.e', in the International Code of Botanical Nomenclature (Voss 1983)], it is synonymous with V. hamata (Vaucher) de Candolle (non V. hamata sensu Götz). The description of Conferva frigida by Roth (1797) was based partly on a description of plants now referable to both V. frigida and V. dillwynii by Dillenius (1741), and partly on material now referable to Schizogonium murale Kützinger (Christensen pers. comm.) examined at the time. If V. frigida (Roth) C. Agardh is shown to be illegitimate, there are two other names available for this species.

Vaucheria hamata (Vaucher) de Candolle, described as Ectosperma hamata in 1803, is the earliest, but may be confused with V. hamata sensu Götz (= V. prona), used extensively in the literature (e.g. Gauthier-Lièvre 1955; Islam 1984; Blum 1953; Rieth 1965a, 1980b) for a different taxon. Since V. hamata has been widely

misapplied, it may be rejected under article 69.1 of the International Code of Botanical Nomenclature (Voss 1983). Vaucheria frigida Agardh (1824), however, is a legitimate and unambiguous name for this species, and considered by Christensen (1968) to be the best replacement.

Vaucheria terrestris sensu Götz has been used extensively (e.g. Gauthier-Lièvre 1955; Blum 1953, Rieth 1965a, 1980b; Sarma 1974) for plants referable to V. frigida (see Christensen 1968, 1969).

Vaucheria terrestris (Vaucher) de Candolle, however, is used by Christensen (1969) for a taxon distinct from V. frigida (see below). In any case, V. frigida (Roth) C. Agardh is an earlier name than V. terrestris, and is adopted here.

The synonyms of V. frigida listed by Blum (1972) and Christensen (1969) are all accepted here but the disposition of a number of other names should be considered following the studies in Chapter 4.

Vaucheria mu()lleola Skuja (1964, p.338, pl. 65 figs 21-24) resembles V. frigida in gametophore shape and oogonial orientation, but has a sculptured oospore wall and a short distal oogonial cavity. The sculpturing may refer to the flaky texture noted in oospore walls in the current study, but the illustrations by Skuja are difficult to interpret. The suitability of oogonial cavity features as taxonomic characters should be assessed in culture isolates, and type material of V. mu()lleola should be examined to determine whether the two species are distinct.

Christensen (1969) has concluded that V. terrestris (Vaucher) de Candolle (in Lamarck & de Candolle 1805, p.62) is specifically distinct from V. terrestris sensu Götz (= V. frigida in this study). The plants Christensen (1969) referred to V. terrestris (Vaucher) de

Candolle were intermediate between V. frigida and V. prona: the orientation of oogonia in V. terrestris resembles that found in V. frigida, but the size of gametangia and the size and shape of gametophores are more like V. prona. In the present study, the orientation of oogonia, but not the other characters, was found to be a useful diagnostic character in the V. prona complex. Furthermore, the large size range of oogonia in V. frigida includes values similar to those measured from published illustrations of V. terrestris (see Table 4.5). The oospore walls illustrated by Christensen (1969, fig. 8) seems to be relatively thick compared with V. prona, but no indication of oospore wall texture is given for any of the V. prona complex illustrated by Christensen. None of the illustrations of V. terrestris, however, include oospores with a large distal protuberance like that found in V. frigida. Christensen (1969) suggested that it may be better to reduce V. terrestris to a subspecific category in V. frigida, while Simons (1977) found that V. terrestris and V. frigida could not be adequately distinguished from each other. Further study, therefore, is needed to assess the taxonomic position of V. terrestris (Vaucher) de Candolle.

Rieth (1980b) has interpreted the variation in size of plants allied to V. frigida in a different manner. Vaucheria terrestris sensu Götz is distinguished from V. prona in having one oogonium produced distally to the antheridium, therefore including plants referred to V. frigida in this study. Rieth (1980b) recognises three varieties of V. terrestris sensu Götz, and V. terrestris var. terrestris is referable to both V. frigida and V. terrestris (Vaucher) de Candolle (in the sense of Christensen 1969) on the basis of oogonial size. The other two varieties are considered below.

Vaucheria terrestris var nuoliae Skuja (1964, p.336, pl. 65

figs 17-20) is distinguished from the type variety in having a reticulate-scrobiculate pattern of the middle layer of the oospore wall, larger oospores, and antheridial pedicels originating from a different part of the gametophore. The reticulate-scrobiculate pattern is poorly illustrated by Skuja (the same illustration is reproduced in Rieth 1980b), and could possibly refer to the flaky texture of the oospore wall noted in south-eastern Australian plants of V. frigida. The oogonia and oospores of V. terrestris var. nuoljæ are 148-212 μm long and 93-130 μm in diameter, longer than measured in V. frigida in the current study, but similar in diameter. In two of the three gametophores illustrated by Skuja, the peduncle is reflexed near the insertion of the antheridial pedicel, but otherwise the arrangement and orientation of antheridia and oogonia are not unusual in V. frigida. It is probable, therefore, that this variety is unnecessary but further study of the oospore wall and oogonial shape are needed.

Vaucheria terrestris var. major (Wille) Rieth (1965b, p.158, fig. 27) is distinguished from the type variety in having larger oospores and broader siphons: the oogonia are 145.5-226 μm long and 106-174 μm in diameter, and the siphons, 41.5-151 μm in diameter. [Nordstedt (1888, p.22) described V. terrestris f. megacarpa from New Zealand with oospores 220 μm long and 160 μm in diameter, and this may be an earlier name for the plants referable to V. terrestris var. major.] Although these dimensions are generally larger than those found in V. frigida from south-eastern Australia, or recorded in the literature (see Table 4.5), it may be more suitable to include V. terrestris var. major, V. frigida and V. terrestris in a single species including a range of growth forms only differing in the size of gametangia and siphons. As the two extremes in size were not examined in the current study, no taxonomic

conclusions can be reached here.

Vaucheria terrestris Lyngbye emend Walz, used by Heering (1907, p.160, fig. 85; 1921, pp.90,219, fig. 80), includes plants referable to V. frigida, but with oogonia up to 211 μ m long and 103 μ m in diameter. This taxon may include plants referable to either V. terrestris var. nuoliae or V. terrestris var. major, and its disposition also depends on culture studies and a comparison of the relevant type collections.

Vaucheria undulata Jao (1936, p.741, pl.3 figs 12, 13) is similar to V. frigida in oospore shape and orientation, but has undulating siphons. Rieth (1968) found two types of undulation in siphons of Vaucheria: either spiralled, as in V. undulata and occasionally in V. racemosa (as V. walzii Rothert), or regularly constricted, as occasionally found V. canalicularis (Linnæus) Christensen (as V. woroniniana Heering) and V. dichotoma (Linnæus) Martius. In the current study, spiralled siphons were observed rarely in V. prona, V. canalicularis and V. litorea, and regular constrictions were seen in V. uncinata Kützing (when placed in media with salinities > 2 o/oo, see Fig. 5.104). The presence or absence of any kind of undulating siphons, therefore, may be of little use in delineating taxa since they can be induced in a number of species. In the absence of spiralled siphons, the plants referred to V. undulata by Jao (1936), Blum (1953, 1972) and Gauthier- Lièvre (1955) would be included in V. frigida; those plants referred to V. undulata by Christensen & Lind (1960), Sarma (1974) and Rieth (1980b), to V. prona; and the plants described by Simons (1978), possibly to V. geminata (Vaucher) de Candolle. The undulation of siphons, therefore, needs to be critically studied in culture to determine whether or not it is influenced by the environment.

Vaucheria gardneri Collins 1907: 201, figs 2,3; 1909: 428. Blum 1971: 190, figs 1-4; 1972: 18, figs 41,42. Hoppaugh 1930: 342, fig. 15.

Heterotypic Synonyms:

Vaucheria gardneri f. tenuis Collins 1907: 201; 1909: 428.

Vaucheria gardneri var. tenuis (Collins) Hoppaugh 1930: 343, fig. 16.

Vaucheria geminata f. pedunculata (Arechavaleta) Heering 1907: 158, figs 81-83 *pro parte, according to Blum 1972.*

Lectotype: NY.

Type Locality: Berkeley, California, U.S.A. (Silva pers. comm.; Blum 1971).

Distribution: California, U.S.A.; Victoria, Australia (see Fig. 5.64).

Specimens Studied: MEL 1049082, MEL 1049083, MEL 1049084, MEL 1049085, Campbells Creek, Yapeen, Victoria, Entwisle, 2.vi.1984; MEL 1049086 p.p., MEL 1049183 p.p., Silver Creek, Beechworth, Victoria, Entwisle, 21.vii.1984; MEL 668196, Berkeley, California, Gardner, 15.iv.1905 (isotype).

Figs 5.58-5.65

Thallus consisting of sparingly branched siphons, 36-55 μm in diameter, forming dense green mats on substrate.

Plants monoecious; gametophores consisting of 1-2 oogonia borne laterally to 1 antheridium; peduncles 12-230 μm long, 19-42 μm diameter. Antheridia circinate-cylindrical to short straight-cylindrical, 31-70 μm long, 20-24 μm in diameter; antheridial pedicels erect, straight or rarely curved at apex, 48-82 μm long. Oogonia reniform to dimidiate-ovoid, or ovoid, flattened or concave on adaxial side, 74-110(-130) μm long, 62-75 μm in diameter, L/D 1.2-1.6, with a distal prominence; plane of oogonial symmetry usually perpendicular to the oogonial pedicel and parallel to the plane of the antheridial

curvature; oogonial pedicels erect, curved, 41-90 μm long, distal end almost parallel with antheridial pedicel. Oospores same size and shape as oogonia, sometimes leaving a small distal oogonial cavity when mature; oogonial cavity conical, $< 10 \mu\text{m}$ long; oospore wall 4-5 μm thick.

Sporangia and akinetes not seen.

Diagnostic Features: Vaucheria gardneri is delineated from other south-eastern Australian species of Vaucheria in having gametophores with erect oogonia; curved oogonial pedicels with distal end parallel with the antheridial pedicel; and erect, usually straight antheridial pedicels (Figs 5.59, 5.60, 5.62).

Habitat and Phenology: Vaucheria gardneri was collected from two semi-terrestrial freshwater drainage ditches in June-July (winter), and was sterile in the field. In culture, vegetative growth occurred in media with salinities of 0.3-6.5 o/oo; all fertile culture material examined came from ASP-V media with a salinity of 0.3-2 o/oo and soil/water media.

Remarks: The south-eastern Australian plants were concordant in most respects with the isotype material examined (MEL 668196) and the plants of Vaucheria gardneri described by Collins (1907, 1909) and Blum (1972).

The collection from Yapeen, Victoria, was studied in detail in culture. The gametangia produced after 26 and 45 days (Figs 5.60-5.62), in ASP-V and soil/water media, were typical of V. gardneri as the peduncles were short, 12-70 μm , and the oogonial and antheridial pedicels long, 41-70 μm and 75-82 μm respectively. Further culturing in

ASP-V, however, induced a change in the gametophore morphology (Fig. 5.59). After 114 days in culture the length of most peduncles increased, to 72-230 μm , while the antheridial pedicels were reduced to 48-64 μm long (the oogonial pedicels did not vary appreciably in length). In addition, the angle at which the oogonial pedicels were borne became more acute after 114 days (Fig. 5.59).

As a consequence of these changes in the gametophore, the plants no longer resembled the type material of V. gardneri. Collins (1907) described the oogonial pedicels as being arranged around the peduncle at an angle of about 45° , and borne directly on the vegetative siphon (a re-examination of the lectotype by Blum (1971) and an isotype in this study, has shown that short peduncles are present). The south-eastern Australian plants from older cultures can have much longer peduncles and oogonial pedicels borne at more acute angles to those of the type material. However, there were some gametophores in the older cultures similar to those of the type material. The influence of culture conditions on these morphological changes was not ascertained. In addition, the number of oogonia in each gametophore varied from 1-2 in the south-eastern Australian plants. In the lectotype there are 1-3 oogonia with 1 antheridium (Blum 1971), unless there is adventitious production of gametophore, and Collins (1907) recorded 2-4 in the same material.

In many respects, V. gardneri resembles V. longata Blum (1953, p. 492, figs 15, 32-38). The oogonia are similar in size and shape (Figs 5.58A-C, 5.63, 5.65), and the antheridial pedicel length is comparable. Vaucheria longata differs, however, in having shorter oogonial pedicels, 7-20 μm long in the illustrations of Blum (1953), borne almost at a right angle to the peduncle. Christensen (1956) illustrated plants with

oogonial pedicels up to 50 μm long, and these were observed in material of V. longata (No. 6556, Hestefælleden, Denmark, Christensen, 9.iii.1945) kindly supplied by Dr Tyge Christensen. The oogonial pedicel, however, was orientated similarly to that illustrated by Blum (1953) for the North American plants. Vaucheria gardneri, on the other hand, had gametophores bearing oogonial pedicels at an angle of 45° , or less, and the oogonial pedicel usually distally erect (Figs 5.58A, 5.65). An oogonial cavity was sometimes left by the mature oospores of V. gardneri (Fig. 5.58B), but not always (Fig. 5.58A, 5.65).

Blum (1972) confirmed the identity of the Californian collections of this species (described by Collins 1907), but was unable to corroborate the reports (Prescott 1938) from Illinois and Iowa. No other published records of this species have been found.

Smith (1944) recorded small spherical structures, 5.5-6.5 μm in diameter, which he termed microaplanospores, in the siphons and pedicels of V. gardneri. These were not observed in the south-eastern Australian plants.

The synonyms listed here are taken from Blum (1971, 1972). ^{According to} Heering (1907), Vaucheria geminata f. pedunculata (Arechavaleta) Heering includes

V. gardneri, V. geminata var. martialis Teodoresco [with long oogonial pedicels, but oogonia and antheridia typical of V. geminata (Vaucher) de Candolle] and V. longipes Collins [with peduncles 1-6 mm long and considered by Blum (1972, p.17) to be as species inquirenda]. In the protologue of V. pedunculata Arechavaleta (1883, p.25, pl. 6 fig. 5), plants from Uruguay similar to V. gardneri are described, but without studying the relevant material no assessment of this species can be made.

Vaucheria gardneri f. tenuis was apparently described from a

collection of V. gardneri with adventitious gametophores (Blum 1971), and therefore is not recognised as a distinct taxon.

Vaucheria geminata (Vaucher) de Candolle in Lamarck & de Candolle 1805:

62. Bailey 1893: 25. Cassie 1984: 226. Chapman et al 1957: 729.

Hoppaugh 1930: 338, figs 8,9. Jao 1936: 740, pl. 2 figs 10,11.

Möbius 1892: 436. Playfair 1917: 212. Simons 1977: 31, fig.

24. Sarma 1974: 88, figs 7,8,10,24,25.

Basionym:

Ectosperma geminata Vaucher 1803: 29, pl. 2 fig. 5.

Holotype: Not designated by Vaucher (1803).

Type Locality: Not designated by Vaucher (1803); material collected from near Geneva, Switzerland.

Distribution: Widespread (for study area, see Fig. 5.70).

Specimens Studied (collected by Entwistle): MEL 1049087, Rocklands Reservoir, Cherrypool, Victoria, 26.v.1983; MEL 1049088, MEL 1049089, Lake Narracan, Yallourn, Victoria, 19.viii.1984; MEL 1049090 p.p., MEL 1049245, Bulga National Park, Victoria, 19.viii.1984; MEL 1049091, MEL 1049092, Fire dam, Mount Beauty-Bogong Road, Victoria, 16.x.1984; MEL 1049093 p.p., Mount Beauty Reservoir, Victoria, 16.x.1984; MEL 1049094, MEL 1049095, Patrick Lawler Drinking Water Spring, Mt Beauty-Bright Road, Victoria, 16.x.1984; MEL 1049149 p.p., MEL 1049169 p.p., Bembridge, Tyabb-Tooradin Road, Victoria, 21.viii.1985.

Figs 5.66-5.71

Thallus consisting of sparingly branched siphons, (48-)58-96 μm in diameter, forming thick green mats on substrate; narrowing rhizoids often present.

Plants monoecious; gametophores consisting of 1-2 oogonia borne laterally to 1 antheridium; peduncles 172-364 μm long, 48-84 μm in diameter distally. Antheridia circinate-cylindrical, (60-)70-108 μm long, 24-41 μm in diameter; antheridial pedicels erect, curved distally (often also laterally), (60-)70-108 μm long, usually surpassing

apex of oogonia. Oogonia erect, ellipsoid to ovoid, flattened on adaxial side, 96-110 μm long, 77-96 μm in diameter, L/D 1.1-1.3(-1.4), with a small distal prominence; oogonial pedicels 28-86 μm long.

Oospores same size and shape as oogonia, leaving no oogonial cavity when mature; oospore wall 1-3 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria geminata is delineated from other south-eastern Australian species of Vaucheria in having gametophores with erect oogonia (Figs 5.66, 5.67, 5.69) borne on almost straight oogonial pedicels making an acute angle with the peduncle (Figs 5.66, 5.67, 5.69), and in having monoporic antheridia borne on erect pedicels, only curved distally (Figs 5.66-5.69).

Habitat and Phenology: Vaucheria geminata was found in semi-terrestrial to aquatic freshwater habitats in May (autumn), August (winter) and October (spring); plants were fertile in the field except for two collections in October (MEL 1049091 & MEL 1049093). This species is apparently restricted to areas of high rainfall (> 700 mm/yr). In culture, vegetative growth occurred in media with salinities of 0.3-4 o/oo, but not in 16-30 o/oo; all fertile culture material examined came from ASP-V media with a salinity of 0.3 o/oo and soil/water media.

Remarks: The south-eastern Australian plants were concordant in most respects with the plants of Vaucheria geminata described in the protologue (Vaucher 1803) and by Hoppaugh (1930), Jao (1936) and Rieth (1980b).

In the protologue of Vaucheria geminata, Vaucher (1803, as Ectosperma) stated that this species resembled V. canalicularis [as Ectosperma cespitosa, see Christensen (1969) for details of synonymy], but had oogonial pedicels forming a cross shape with the antheridium, and oogonia concave on the adaxial side and borne on lateral gametophores (in some populations, V. canalicularis often produces gametophores terminally on the vegetative siphons). As noted by Christensen (1969), there is a discrepancy between the oogonia of V. geminata described and those illustrated in Vaucher (1803), the latter being convex rather than concave on the adaxial side. Similarly, the illustrated gametophores have oogonial pedicels slightly erect rather than perpendicular to the antheridium (as in a regular cross). The south-eastern Australian plants (see Fig. 5.67) had gametophores similar to those of V. geminata illustrated in Vaucher (1803, p. 2 fig. 5), and with erect oogonia generally flattened on the adaxial side.

Christensen (1969), however, on the basis of observations on material collected from near the type locality, concluded that V. geminata referred to plants with shorter and thinner peduncles and oogonia either erect or in a plane transverse to the peduncle. These plants do not resemble V. canalicularis, but are more similar to V. prona Christensen and V. verticillata Meneghini sensu Kützinger. Gauthier-Lièvre (1955) and Rieth (1965b) included in V. geminata, plants almost certainly referable to V. prona, V. taylorii Blum and V. verticillata. Rieth (1980b), however, more clearly and narrowly delineated V. geminata, referring many of the growth forms illustrated in Rieth (1965b) to one of the above species. Vaucheria geminata sensu Rieth (1980b) includes plants similar to those found in south-eastern Australia. It seems appropriate, therefore, to use the name V. geminata

for the plants described here until this taxon is more clearly circumscribed.

Vaucheria taylorii Blum (1971, p.191, figs 5-12) is similar to V. geminata but includes plants with 3-8, and only rarely 2, oogonia on each gametophore (Blum 1971,1972). The south-eastern Australian plants had 1-2 oogonia per gametophore (the number of oogonia per gametophore never exceeded 2 in either field and culture material) but the diameter of siphons and the size of antheridia and oogonia were similar to those found in V. taylorii. In addition, the distal end of the peduncle was often inflated (e.g. Fig. 5.68) as Blum (1971) observed in gametophores bearing a whorl of oogonia. Hoppaugh (1930) gametophores of V. taylorii bearing 4 to 6 oogonia on the same siphon, and adjacent to, some bearing only 2. She concluded that the number of oogonia per gametophore is an extremely variable character in this species and should not be used to distinguish a variety or form. An examination of North American plants of V. taylorii (MEL 1049151, Fort Knox, Kentucky, U.S.A., Christensen, 29.vii.1962) in this study showed them to be similar in nearly all respects, except the number of oogonia per gametophore, to V. geminata. A re-examination of the type material of V. taylorii and a study of both species in culture is needed to assess whether the two species should be considered conspecific. Vaucheria prona (Figs 5.83-5.90) has oogonia variously directed, but not erect, and also has circinate antheridial pedicels which are not proximally straight and erect as in V. geminata. Vaucheria verticillata, although having erect oogonia and antheridial pedicels, has thin elongate oogonial pedicels and peduncles (Rieth 1980b: 81, fig. 32). It is also distinguished by having gametophores with more than two oogonia, but it may be more suitable to include plants similar to those

illustrated by Christensen (1969), with only one or two oogonia, in this species. Again, an evaluation of taxonomic characters in species with erect oogonia is needed before these species concepts can be properly evaluated.

The similarities between V. geminata and V. canalicularis (in the section Vaucheria) are discussed on p.209. They are included in different sections on the basis of antheridial morphology: the former has circinate monoporic antheridia (Fig. 5.71), while the latter has antheridia with a deltoid-pulvinate apex and two lateral pores (Fig. 5.120).

Phillipson (1935, p.281, fig. 27) described and illustrated a species found on garden soil at Melbourne University, Victoria, which he called V. hamata (Vaucher) Lyngbye. Lyngbye (1819, p.77, pl. 20) illustrated plants of V. hamata with one large oogonium distal to the antheridium, which are now referable to V. frigida (Blum 1972). The illustration by Phillipson (1935, fig. 27), however, shows a gametophore with two erect oogonia, similar to V. geminata as delineated here. There is no voucher material of this record, but it is tentatively included in V. geminata.

Vaucheria gyrogya Entwisle sp. nov.

Thallus filis siphonaceis ramosis 43-79(-96) μ m diametro stoream viridem facientibus.

Plantae monoeciae; gametophoris antheridio terminali et oogoniis lateralib^{us} 1-2(-3), pedunculo 48-108 μ m longitudine, 39-70 μ m diametro. Antheridia circinata, 50-65 μ m longitudine, 12-26 μ m diametro, pedicello circinato 38-84 μ m longitudine. Oogonia reniformia, parte

distali parum protracta leviter reflexa, plano congruentiae ad pedunculum perpendiculari axe longo ad antheridium parallelo, 89-120 μm longitudine, 70-98 μm diametro, rationibus longitudinis:diametri 1.1-1.4; ubi oogonia duo adsunt, eorum poro fecundationis versus se hiant, pedicello 24-48 μm longitudine. Oosporae reniformes ad ovoideas, rationibus longitudinis:diametri ad oogonia similibus, maturitate plerumque cavitatem oogonialem distalem conicam 14-32 μm longitudine, ^{relinquentes} parietibus 2-5 μm crassitie.

Sporangia akinetaque ignota.

Holotypus: MEL 1049158; this includes slides, and wet and dry preserved material, of the sterile field collection and subsequent culture isolates.

Type Locality: Bourne Creek, Kilcunda, Victoria.

Distribution: Coastal western Victoria, Australia (see Fig. 5.78).

Representative Specimens Studied (from a total of 14 field collections by Entwistle): MEL 1049161, MEL 1049162, MEL 1049163, Clydebank Morass, Avon River mouth, Victoria 30.ix.1983; MEL 1049164, Bemm River, Sydenham Inlet, Victoria, 1.x.1983; MEL 1049165, MEL 1049166, Stingray Point, Mallacoota, Victoria, 1.x.1983; MEL 1049167, Fisherman's Landing, Lake Tyers, Victoria, 1.x.1983; MEL 1049168, Port Welshpool Victoria, 3.x.1983; MEL 1049158, MEL 1049159, MEL 1049160, Bourne Creek, Kilcunda, Victoria, 31.iii.1984; MEL 1049132, Dowd Morass, Golden Beach-Longford Road, Victoria, 30.ix.1983.

Figs 5.72-5.78

Thallus consisting of sparingly branched siphons, 43-79(-96) μm in diameter, forming dense green mats on substrate.

Plants monoecious; gametophores consisting of 1-2(-3) oogonia borne laterally to 1 antheridium; peduncle 48-108 μm long, 39-70 μm in diameter. Antheridia circinate-cylindrical, 50-65 μm long, 12-26 μm in diameter; antheridial pedicels circinate, 38-84 μm long. Oogonia elongate-reniform, 89-120 μm long, 70-98 μm in diameter, L/D 1.1-1.4,

with a slightly deflexed, attenuate distal portion; plane of oogonial symmetry usually transverse to the peduncle and long-axis parallel with antheridium, fertilisation pores opening towards each other if 2 oogonia present; oogonial pedicels 24-48 μm long. Oospores elongate-reniform to ovoid, same length and diameter as oogonia, usually leaving a distal oogonial cavity when mature; oogonial cavity conical, 14-32 μm long; oospore walls 2-5 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria gyrogya is delineated from other south-eastern Australian species of Vaucheria in having gametophores with the oogonial plane of symmetry transverse to the peduncle, the oogonial long-axis parallel to the antheridium (Figs 5.72-5.75), and a distal oogonial cavity left by mature oospores (Fig. 5.77).

Habitat and Phenology: Vaucheria gyrogya was found in terrestrial to semi-terrestrial habitats near estuarine rivers and salt marshes, and in supralittoral to upper eulittoral mudflats; plants were collected in March (autumn), June (winter), September and October (spring) and were fertile in the field during the last two months. In culture, vegetative growth occurred in media with salinities of 0.3-16 o/oo, but not 30 o/oo; all fertile culture material examined came from media with a salinity of 0.3-6.5 o/oo.

Remarks: The diagnostic features of Vaucheria gyrogya and the other species in the section Racemosae with distal oogonial cavities are summarised in Table 5.4.

In some slides of V. gyrogya (where the gametophores were distorted

by the coverslip), and rarely in agar, the oogonia appeared to be erect (Fig. 5.76), resembling those of V. pseudogeminata Dangeard (Fig. 5.92). Vaucheria gyrogyna, however, can also be distinguished by the larger oogonia (> 80 μm long). V. alaskana Blum (not found in this study) has erect oogonia, similar in size to those of V. gyrogyna, but with a distal cavity left in a reflexed tubular papilla, 8-13 μm long. The oogonia of V. gyrogyna have a conical oogonial cavity which is 14-32 μm long.

The morphology of V. gyrogyna was similar in plants grown in culture media with salinities of 0.3-6.5 o/oo, but under some conditions the mature oospore did not leave a distal oogonial cavity. The number of oospores occupying the entire oogonium did not seem to be correlated with salinity, light or temperature. Even when the oogonium had no oogonial cavity, the distal end was attenuated and deflexed (Figs 5.72, 5.76), distinguishing V. gyrogyna from species such as V. prona, which always have no oogonial cavity and an obtuse distal portion.

The epithet gyrogyna refers to the structure of the gametophores: the oogonia appear to orbit in a plane transverse to the peduncle.

Vaucheria lii Rieth 1963a: 583, figs 1-6; 1963b: 309, fig. 15; 1980b: 69, fig. 26. Blum 1972: 19, fig. 40. Luykx & Laval 1977: 3, figs 1-4. Pecora 1978: 138, figs 1, 2.

Type: Not designated by Rieth (1963a).

Type Locality: Not designated by Rieth (1963a); V. lii nom. nud. in Rieth (1959^a) was based on material collected from Kleiner Hsingan, China, one of the two localities listed in Rieth (1963a).

Distribution: North America, China, Europe; Mornington Peninsula, Victoria, Australia (see Fig. 5.81).

Specimen Studied: MEL 1049169 p.p., Bembridge, Tyabb-Tooradin Road, Victoria, Entwisle & Cullinane, 21.viii.1985.

Figs 5.79-5.81

Thallus consisting of sparingly branched siphons, 21-29 μm in diameter, intermingled with dense green mats of other Vaucheria species.

Plants monoecious; gametophores consisting of 1-2 oogonia borne laterally to 1 antheridium; peduncle 48-340 μm long, 18-28 μm in diameter, with septum midway, or gametophores terminal on vegetative siphon. Antheridia circinate-cylindrical, 40-58 μm long, 14-17 μm in diameter, turning through at least an entire circle; antheridial pedicels erect, distally circinate, 36-55 μm long. Oogonia erect, ellipsoid-reniform to ovoid, (45-)55-67 μm long, (29-)34-41 μm in diameter, L/D 1.4-1.9, with strongly reflexed, attenuate distal portion; oogonial pedicels 24-36 μm long, disintegrating proximally when oospore mature. Oospores ellipsoid to reniform, (43-)55-60 μm long, (29-)34-41 μm in diameter, leaving an almost circinate-cylindric distal cavity when mature, 15-25 μm long; oospore walls 1-2.5 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria lii is delineated from other south-eastern Australian species of Vaucheria in having gametophores bearing erect oogonia with a circinate distal cavity left by the mature oospore (Fig. 5.79), a septum in the peduncle (Fig. 5.80) and the pedicel still attached to released oospores (Fig. 5.79).

Habitat and Phenology: Vaucheria lii was collected from a freshwater swamp in August (winter); plants were fertile in the field. All specimens studied came from this field collection.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria lii described in the protologue (Rieth 1963a). [This species was described without a latin diagnosis in Rieth (1959a, p.223, figs 1,2), and remained a nomen nudum until Rieth (1963a).] One of the most distinctive features of V. lii is the mechanism of oospore liberation (see Rieth 1963a, 1963b; Luykx and Laval 1977), where the oogonial pedicel is ruptured at the peduncle and remains with the released oospore (Fig. 5.79).

(as nom. nud.)

Vaucheria prona Christensen 1970: 250, figs 1,2; 1969: 18, fig. 10.
Blum 1972: 20, figs 53-55,62.

Misapplied Name:

Vaucheria hamata auct. non (Vaucher) de Candolle: Götz
1897: 118, figs 31-33. Blum 1953: 487, figs 16,17,54-66. Cassie
1984: 226. Gauthier-Lièvre 1955: 325, pl. 3 figs 37-
40,41,45. Heering 1907: 159, fig. 84; 1921: 90,197, fig. 81.
Jao 1936: 742, pl. 3 figs 14,15. Rieth 1965b: 159, figs 35,36;
1980b: 93, fig. 39. Sarma 1973: 168, figs 1-3,9,11,13. Sarma &
Chapman 1975b: 308.

Holotype: C (Christensen 1970).

Type Locality: Kongelunden, Amager, Denmark (Christensen 1970).

Distribution: Widespread (for study area, see Fig. 5.82).

Representative Specimens Studied (from a total of 162 field collections by Entwisle, unless otherwise indicated): MEL 1049269, MEL 1049170, Flowerdale Mineral Springs, Flowerdale, Victoria, 24.i.1984; MEL 1049233 p.p., Royal Botanic Gardens, South Yarra, Victoria, 4.vi.1984; MEL 1049238 p.p., MEL 1049239 p.p., Gunbower Creek, Gunbower, Victoria, 20.vii.1984; MEL 1049240 p.p., Salt Creek, Berri, South Australia, 2.x.1984; MEL 1049154, MEL 1049241, Falls Creek Township, Victoria, 16.x.1984; MEL 1049244, MEL 1049155, Livingstone Creek, Omeo, Victoria, 17.x.1984; MEL 1049243, Iguana Creek, Bairnsdale-Cobbannah

Road, Victoria, 18.x.1984; MEL 1049245, Bulga National Park, Victoria, 19.viii.1984; MEL 1049246, Clifton Hill, Victoria, 3.vi.1984; MEL 1049247, Yarriambiack Creek, Warracknabeal, Victoria, 5.viii.1984; MEL 1049248 p.p., Diamond Creek, Diamond Creek township, Victoria, 28.iv.1983; MEL 1049171, Dales Creek, Greendale, Victoria, 13.vi.1984; MEL 1049172, Thompson River, Erica-Walhalla Road, Victoria, 19.viii.1984; MEL 1049249 p.p., Lake Glenmaggie, Glenmaggie, Victoria, 18.viii.1984; MEL 1049250 p.p., Bool Lagoon, Apsley, Victoria, 3.x.1984; MEL 1049251, Murray River, Renmark, Victoria, 2.x.1984; MEL 1049252, Boundary Creek, Gellibrand-Colac Road, Victoria, 28.viii.1984; MEL 1049173 p.p., MEL 1049174 p.p., Jackson Creek, Organ Pipes National Park, Victoria, 22.viii.1984; MEL 1049175, Thompson River, Walhalla, Victoria, 19.viii.1984; MEL 1049176, Wimmera River, Jeparit, 5.iii.1984; MEL 1049177, Lake Charm, Kerang-Swan Hill Road, Victoria, 4.viii.1984; MEL 1049178, Mount Emu Creek, Skipton, Victoria, 4.x.1984; MEL 1049179 p.p., Ovens River (west branch), Harrietville, Victoria, 16.x.1984; MEL 1049180, MEL 1049253, German Creek, Mt Beauty-Bright Road, Victoria, 16.x.1984; MEL 1049216 p.p., Fords Creek, Mansfield, Victoria, 22.vii.1984; MEL 1049254 p.p., Charlies Creek, Colac, Victoria, 28.viii.1984; MEL 1049181 p.p., Running Creek, Myrtleford-Mt Beauty Road, Victoria, 16.x.1984; MEL 1049182 p.p., Kiewa River, Running Creek-Mt Beauty Road, Victoria, 16.x.1984; MEL 1049183 p.p., Silver Creek, Beechworth, Victoria, 21.vii.1984; MEL 1049184, Royal Botanic Gardens, South Yarra, 31.viii.1984. NSW A3708, Gordon, New South Wales, Lucas, vii.1914. MEL 665076, Hume River, Victoria, Jephcott, 1886.

Figs 5.82-5.90

Thallus consisting of sparingly branched siphons, 19-125 μm in diameter, rarely spiralled, forming dense green mats, usually closely appressed to substrate.

Plants monoecious; gametophores consisting of 1-3(-4) oogonia borne laterally to 1 antheridium; peduncle 48-432(-685) μm long, 24-79(-96) μm in diameter distally. Antheridia circinate-cylindrical, 38-65(-77) μm long, 12-19(-24) μm in diameter; antheridial pedicel circinate. Oogonia variously directed, but not erect, ovoid-reniform, 48-101 μm long, (36-)48-82(-94) in diameter, L/D 1.0-1.5, distal prominence directed towards peduncle; oogonial pedicels erect or pendent, 12-96(-115) μm long. Oospores same shape and size as oogonia; oospore wall 1.5-4 μm thick, evenly textured in transverse section.

Akinetes formed in vegetative thallus by septa, usually separated

by wall bound cavities. Aplanosporangia unknown and zoosporangia not seen.

Diagnostic Features: Vaucheria prona is delineated from other south-eastern Australian species of Vaucheria in having gametophores with 1 or more, usually pendent, oogonia $< 100\ \mu\text{m}$ long [if only 1, it is lateral to the antheridium (Fig. 5.86)]; oospore walls $< 5\ \mu\text{m}$ thick and evenly textured in transverse section (Fig. 5.83); and no oogonial cavity left by mature oospores.

Habitat and Phenology: Vaucheria prona was collected from freshwater, terrestrial to semi-aquatic habitats; fertile plants were found throughout the year. In culture, vegetative growth occurred in media with salinities of 0.3-6.5 o/oo, but not 15-30 o/oo; all fertile material examined came from ASP-V media with salinities of 0.3-6.5 o/oo and soil/water media.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria prona described in the protologue (Christensen 1970) and by Blum (1972) and Rieth (1980b, as V. hamata sensu Götz).

Two isolates (from MEL 1049233 p.p. and MEL 1049269) were studied in a series of culture experiments and compared with 17 field populations of V. prona, and V. frigida (see Chapter 4). From this work, two growth forms of V. prona were recognised, but not given formal taxonomic recognition. The first growth form (see Figs 5.84, 5.86) was characterised by short oogonial pedicels, < 0.8 times as long as the oogonia, and 1-2 oogonia per gametophore. The second growth form (see Figs 5.83, 5.85, 5.88-5.90) had longer oogonial pedicels, > 0.8 times as

long as the oogonia, and (1-)2-3(-4) oogonia per gametophore. There were populations with characters intermediate between these two groups, and even some populations with a combination of long pedicels and 1(-2) oogonia. In addition, collections MEL 1049244 and MEL 1049243 from montane areas, had relatively large oogonia and siphons, but with size ranges that overlapped those of the studied isolates. Therefore, all populations with one or more oogonia, $< 100 \mu\text{m}$ long, with thin oospore walls and oogonia, if single, lateral to the antheridium, have been referred to V. prona.

Zoosporangia have been reported in V. prona (as V. hamata sensu Götz) by de Puymaly (1922), but were not observed in any south-eastern Australian material. Akinetes were observed by Gauthier-Lièvre (1954) in the place of oogonia in V. prona (as V. hamata sensu Götz), but the akinetes observed in this study were formed in the vegetative siphons, and similar to those reported by Randhawa (1939, 1942b).

Populations of V. prona with more than two oogonia per gametophore, and long oogonial pedicels can be similar to V. racemosa (Vaucher) de Candolle (in Lamarck & de Candolle 1805, p.61). Vaucheria racemosa is characterised by the presence of 2-6(-7) oogonia per gametophore and has relatively long oogonial pedicels (Christensen 1969, Blum 1972). It differs from V. prona, however, in producing oogonia in opposite rows along the peduncle. Even if there are three oogonia, two are borne on one side and one on the other. In V. prona the third oogonium arises distally to the antheridium (Figs 5.85, 5.89). Although the peduncles of V. racemosa illustrated by most authors (e.g. Blum 1972; Götz 1897, as V. uncinata) are usually $< 80 \mu\text{m}$ long, Christensen (1969, fig. 12) and Rieth (1980b, fig. 41, as V. walzii) illustrated plants with

peduncles up to 200 μ m long. If only two oogonia are borne per gametophore, it may be difficult to separate V. racemosa from V. prona. Studies of V. racemosa in culture and field populations, therefore, are needed to clarify the relationships between these two species.

Some populations of V. prona can have erect oogonial pedicels (Fig. 5.84), similar to those illustrated by Christensen (1969, fig. 6) for V. geminata. As noted on p.176, the circumscription of V. geminata varies between authors and some (e.g. Christensen 1969) include plants referable to V. prona as delineated here.

Christensen (1970) described V. prona to dispel the confusion concerning the correct application of V. hamata. The name V. hamata has been commonly used (e.g. Götz 1897; Heering 1921; Hoppaugh 1930) for plants which have usually two pendent oogonia and in this sense, is considered by Christensen (1969, 1970) to be conspecific with V. prona [the plants described by Vaucher (1803) as Ectosperma hamata are considered by Christensen (1969, 1970) to be referable to V. frigida].

Vaucheria pseudogeminata Dangeard 1939b: 214, fig. 9. Blum 1972: 18, figs 43, 65. Christensen 1969: 20, fig. 11. Gauthier-Lièvre 1955: 329, pl. 4 figs 46-49. Pecora 1980: 90, fig. 8. Rieth 1975: 160, text figs 1-4, pl. 1 figs 1-4; 1980b: 66, fig. 25.

Type: Not designated by Dangeard (1939b).

Type Locality: Not designated by Dangeard (1939b); material collected from Floirac and Guethary, France.

Distribution: North America, northern Africa, Europe; south-eastern Australia (see Fig. 5.95).

Specimens Studied (collected by Entwistle): MEL 1049225, Mullum Mullum Creek, Eltham, Victoria, 7.iv.1983; MEL 1049358, Robe, South Australia, 11.viii.1983; MEL 1049359 p.p., Onkaparinga River, Clarendon, South Australia, 4.viii.1983; MEL 1049185

p.p., MEL 1049186, Stony Creek, Toorloo Arm, Lakes Entrance-Nowra Nowra Road, 1.x.1983; MEL 1049187 p.p., Serpentine Creek, Serpentine, Victoria, 20.vii.1984; MEL 1049188 p.p., Calder River, Otway Ranges, Victoria, 28.viii.1984; MEL 1049189, MEL 1049258 p.p., Glenelg River, Lower Glenelg National Park, Victoria, 3.x.1984; MEL 1049190, Stokes River, Dartmoor-Casterton Road, Victoria, 4.x.1984; MEL 1049191, Wandella Creek, Kerang, Victoria, 23.vii.1984.

Figs 5.91-5.95

Thallus consisting of sparingly branched siphons, 22-77(-93) μm in diameter, forming dense green mats on substrate.

Plants monoecious; gametophores consisting of 1-2 oogonia borne laterally to 1 antheridium; peduncles 76-192 μm long, 23-47(-66) μm in diameter, or gametophores terminal on vegetative siphon. Antheridia circinate-cylindrical, 28-55 μm long, 12-17 μm in diameter; antheridial pedicels circinate, 43-70 μm long. Oogonia erect, reniform, 53-79 μm long, 38-62 μm in diameter, L/D 1.2-1.4(-1.9), with a slightly reflexed apex; oogonial pedicels 24-38(-65) μm long. Oospores ovoid to reniform, same length and diameter as oogonia, leaving a distal oogonial cavity when mature; oogonial cavity conical, 9-25 μm long; oospore walls 1-2.5 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria pseudogeminata is delineated from other south-eastern Australian species of Vaucheria in having gametophores bearing erect oogonia with a conical distal cavity left by mature oospore (Figs 5.91, 5.92, 5.93A,B).

Habitat and Phenology: Vaucheria pseudogeminata was collected from semi-terrestrial freshwater habitats in April (autumn), July, August (winter) and October (spring); plants were fertile in the field except in April (autumn). In culture, vegetative growth occurred in media with

salinities of 0.3-6.5 o/oo, but not 16-30 o/oo; all fertile culture material examined came from media with salinities of 0.3-2 o/oo.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria pseudogeminata described in the protologue (Dangeard 1939b) and by Blum (1972) and Rieth (1980b).

Although Blum (1972) considered V. erythrospora as possibly synonymous with V. pseudogeminata, these two species are distinguished on the basis of oogonial orientation: the oogonia are pendent in V. erythrospora and erect in V. pseudogeminata. In addition, the oogonia of V. pseudogeminata have a slightly reflexed apex (Figs 5.91, 5.92, 5.93A,B), while in V. erythrospora the apex is usually oblique (see Figs 5.49A,C) and only rarely reflexed (see Fig. 5.49B). Rieth (1975) noted that in V. pseudogeminata adventitious gametophores were produced from the oogonial pedicel, while in V. erythrospora they usually arose from the peduncle. This was supported by observations on the south-eastern Australian material (see e.g. Fig. 5.94). Rieth (1975) also mentioned the distinctive red-brown oospore wall of V. erythrospora. The oospore wall of V. pseudogeminata was greyish in both culture and field material collected from south-eastern Australia.

There also appears to be ecological differences between these two species. Vaucheria erythrospora is restricted to saline areas, while V. pseudogeminata is usually found in freshwater habitats. Blum (1972), however, has recorded V. pseudogeminata from brackish habitats in North America.

The only other south-eastern Australian species of the section Racemosae with an oogonial cavity left by the mature oospore is V. gyrogya. This species is similar to V. pseudogeminata except for the

orientation and larger dimensions of the oogonia (see Table 5.4).

Vaucheria gyrogya was only found in saline habitats.

Vaucheria subarechavaletae Borge 1901: 12, pl. 1 fig. 2. Heering 1907: 168.

Type: Not designated by Borge (1901).

Type Locality: Rio Pescado, Argentina (Borge 1901).

Distribution: Argentina; Western Port Bay, Victoria, Australia (see Fig. 5.96).

Specimens Studied: MEL 1049192, Crib Point, Victoria, Australia, Entwisle & Cullinane, 21.viii.1985.

Figs 5.96-5.100

Thallus consisting of sparingly branched siphons, 28-34 μm in diameter, forming sparse green mats on substrate.

Plants monoecious; gametophores consisting of (0-)1 oogonium borne laterally to 1(-2) antheridium; peduncle 24-96 μm long, 28-34 μm in diameter. Antheridia straight-cylindrical, 84-145 μm long, 28-41 μm in diameter, L/D 3-4; antheridial pedicel 120-192 μm long, continuing straight from the peduncle. Oogonia erect, globose, radially symmetrical, ca 125 μm long, 93-144 μm in diameter; oogonial pedicels ca 84-144 μm long. Oospores not seen.

Akinetes and sporangia unknown.

Diagnostic Features: Vaucheria subarechavaletae is delineated from all other south-eastern Australian species of Vaucheria in having gametophores with straight antheridia, > 80 μm long (Fig. 5.97); erect oogonial pedicels, > 40 μm long; and radially symmetrical oogonia (Fig. 5.100).

Habitat and Phenology: Vaucheria subarechavaletae was collected from under mangroves in August (spring); plants were sterile in the field. In culture, limited vegetative growth and production of gametangia occurred in liquid ES media.

Remarks: The south-eastern Australian plants were concordant with the plants described in the protologue of Vaucheria subarechavaletae (Borge 1901).

The shape of the gametophores and gametangia (Figs 5.98-5.100) are similar to those of V. arechavaletae Magnus & Wille (Wille 1884). Borge (1901) distinguished V. subarechavaletae from V. arechavaletae in having more globose and larger oogonia (106-127 μm cf. 56-58 μm in diameter) and much longer antheridia [the antheridia illustrated for V. arechavaletae in Wille (1884) and Blum (1951) have a L/D 1-2, while Borge (1901) described the antheridia of V. subarechavaletae as having L/D 3-5]. The south-eastern Australian plants corresponded closely in size and shape of gametangia to those described and illustrated by Borge (1901).

The only other species found in south-eastern Australia, with long oogonial pedicels and erect oogonia, was V. gardneri. Vaucheria gardneri, however, has bilaterally symmetrical oogonia, < 90 μm in diameter, and usually curved antheridia, < 80 μm long.

Vaucheria subarechavaletae has been included previously (Jao & Ley 1947, Venkataraman 1961, Starmach 1972, Rieth 1980b) in the section Pseudoanomalaе, but based on an evaluation of sectional characters in the current study (see particularly p.118), it seems to be better placed in the section Racemosae. The presence of a gametophore is considered to be more important at sectional level than the curvature of the antheridium.

The only previously published record of V. subarechavaletae is from the type locality, where it grew on a riverbank in inland mountains (Borge 1901). In south-eastern Australia it consisted of sparse, erect siphons in a saline habitat near the coast. In spite of this habitat difference, and the lack of mature oogonia and oospores, this is a distinctive species which cannot be confused with any other described species of Vaucheria.

Vaucheria uncinata Kützting 1856: 21, pl. 60 fig. 1. Blum 1953:

479, figs 1-11; 1972: 22, figs 21,67,68. Non Vaucheria uncinata sensu Götz/1897.

Heterotypic Synonyms:

Vaucheria arrhyncha Heidinger 1908: 362, pl. 4 figs 10-17.

Luther 1953: 3, Fig. 1. Rieth 1963c: 457, figs 1-10; 1980b: 31, pl. 56.

Vaucheriopsis arrhyncha (Heidinger) Heering 1921: 96, fig. 92.

Jao 1947: 269.

Holotype: L; according to Blum (1953).

Type Locality: Freiburg, Germany (Kützting 1856).

Distribution: Widespread (for study area, see Fig. 5.103).

Specimens Studied (collected by Entwistle): MEL 1049193, Yarra River, Yarra Glen, Victoria, 24.i.1984; MEL 1049194, MEL 1049195, MEL 1049196, MEL 1049197, Yarra River, Warburton, Victoria, 13.ii.1984; MEL 1049198, Yarra River, Yarra Glen, Victoria, 13.ii.1984.

Figs 5.101-5.104

Thallus consisting of sparingly branched siphons, 68-150 μm in diameter, forming dense mats; narrowing colourless rhizoids usually present.

Plants monoecious; gametophores consisting of 1-2 oogonia borne

laterally to 1 antheridium; peduncle 120-480 μm long, 44-65 μm in diameter. Antheridia cylindrical to short circinate-cylindrical 50-60 μm long, 24-26 μm in diameter, disintegrating soon after dehiscence; antheridial pedicels circinate, 45-90 μm long. Oogonia pendent, globose to ovoid, 108-180 μm long, 95-144 μm in diameter, L/D 1.0-1.3, lacking distal prominence, long-axis perpendicular to the oogonial pedicel; oogonial pedicels circinate, becoming wider towards distal end, 70-150 μm long. Oospores same shape and size as oogonia, leaving no oogonial cavity when mature; oospore wall 1-2 μm thick; oogonial wall disintegrating after fertilisation.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria uncinata is delineated from all other south-eastern Australian species of Vaucheria in having gametophores with radially symmetrical, pendent oogonia $> 100 \mu\text{m}$ long and with no distal prominence (Figs 5.101-5.102).

Habitat and Phenology: Vaucheria uncinata was collected from aquatic to semi-aquatic sites (in and near rivers) during January and February (summer); plants were fertile in the field in both months. In culture, 'normal' vegetative growth and reproduction occurred in media with a salinity of 0.3 o/oo, but not 2-30 o/oo.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria uncinata described by Blum (1953, 1972), Christensen (1986b) and Rieth (1963c, as Vaucheria arrhyncha).

In addition to the shape of the oogonia, the size and colour of oospores have been used to characterise this species. Vaucheria

uncinata has relatively large oogonia and their length in south-eastern Australian material, 108-180 μm , is comparable to that reported in the literature for this species. Most species in the section Racemosae have oogonia 120 μm long, but V. frigida, can have oogonia up to 158 μm long. The oospores of V. uncinata remain vivid green, even when fully mature, while those of other species of Vaucheria become grey or yellow-brown. As with V. erythrospora, the distinct colour of the oospore was evident in culture and field material, but not after staining. The disintegration of the oogonial and antheridial walls after fertilisation also distinguishes V. uncinata from others with gametophores. In other species in the section Racemosae, the oogonial wall remains with the mature oospore, even after its release, and the antheridial wall remains intact after dehiscence.

Christensen (1986b) describes a similar species, V. incurva Christensen, which has been found in Australia and Greece. Vaucheria incurva has smaller oospores, 30-60 μm long, and peduncles which are longer, narrower and more curved than those of V. uncinata. None of the plants collected in this study were referable to V. incurva.

Ghose & R^{andhawa} (1933) and R^{andhawa} (1939) found akinetes in plants referred to V. uncinata, but from the gametophores illustrated the plants were probably referable to V. racemosa.

Vaucheria uncinata was unable to grow 'normally' in ASP-V media with a salinity > 2 o/oo. In media of 2-6.5 o/oo salinity (and 0.3 o/oo if 0.19 mg tris was added, raising the pH) the thallus grew very slowly and was constricted at irregular intervals (Fig. 5.104). Similar constrictions have been observed by Rieth (1968) in other species of Vaucheria, and they resemble the siphons of Dichotomosiphon tuberosus (A. Braun) Ernst during akinete formation [illustrated in Bold & Wynne

(1985, fig. 3.143d)]. The plants found in flowing water (MEL 1049198) were sterile in the field, while the two collections from near the river were fertile. Collections of the aquatic plants in subsequent years were also sterile. The inability of this species to tolerate salinities > 2 o/oo and/or pH > 7.5 , may account for its restriction to primarily aquatic habitats. In terrestrial habitats, the varying moisture content of the substrate could result in a variable salinity and pH (see also Christensen 1986b).

There are three areas of confusion concerning the synonymy of Vaucheria uncinata. Firstly, Kützinger (1856) and Götz (1897) used the name V. uncinata for two different taxa. Kützinger illustrated, but incompletely described, plants similar to those collected in this study. The morphology and size (relative to the other plants illustrated) of the Kützinger plants has left little doubt as to their identity. Götz (1897) however, described plants which are referable to V. racemosa (Vaucher) de Candolle. This interpretation of the Götz plants has been proposed by both Christensen (1969) and Blum (1953), and is evident from Götz's illustrations. The literature is confused with records of V. uncinata sensu Götz, labelled as V. uncinata Kützinger; these include Dangeard (1939b, p.206, fig. 7), Heering (1921, p.92, fig. 82), Hoppaugh (1930, p.340, fig. 14), Li (1936, p.101, fig. 9) and Teodoresco (1907, p.85, figs 67-68).

A second problem arises from the publication of another name, V. arrhyncha, for the Kützinger taxon. This name was proposed by Heidinger (1908) to include a collection of plants from the type locality of V. uncinata. Blum (1953) studied the type material of V. uncinata and confirmed the synonymy of these two species. The later

name, V. arrhyncha, has been accepted by some authors (e.g. Rieth 1980b) since Kützing's description is inadequate, there are plants referable to V. uncinata included in other Kützing type specimens, and the illustrations of this species by Kützing shows smaller oogonia than are usually observed. The latter point seems largely invalid as specimens collected in this study, and those recorded by Rieth (1980b), include some specimens with oogonia similar in size to those illustrated by Kützing. Blum (1953) also pointed out that, relative to the other illustrations of Vaucheria by Kützing, the oogonia of V. uncinata are larger. So, based on the conclusions of Blum (1953) and Christensen (1986b) that the Kützing description is adequate, and an examination of the relevant literature, the name V. uncinata is adopted for this species.

The final area of confusion concerns the generic placement of this species. Heering (1921) erected a monotypic genus, Vaucheriopsis, to accommodate this species, based on the findings of Heidinger (1908). Whitford (1943) listed the following distinctive characters for Vaucheria uncinata (as Vaucheria arrhyncha): starch rather than oil as a storage product, green mature oospores with a single oospore membrane, no expulsion of protoplasm at fertilisation, and no prominence on the oogonia. The first character has not been subsequently confirmed, and Whitford (1943) found oil in the siphons. Using pigment analysis by spectrophotofluorimetry (Rowan, pers. comm.), the presence of Chlorophyll C in this species has been confirmed, giving further evidence for a typical Chrysophyte metabolism. Whitford also noted that there were two thin oospore membranes, similar to those of other Vaucheria species. The oogonial morphology, with no distal prominence and a long-axis perpendicular to the pedicel, and the persistent green

colour of the oospores, make this a distinctive species. However, as noted by Whitford, these features do not warrant its separation into a new genus. The extent to which the extrusion of protoplasm at fertilisation occurs throughout the genus is not known, and its relevant taxonomic weighting is therefore doubtful. The disintegration of the oospore wall coupled with the distinctive oogonial morphology are used at species level in this study, and are considered to have no importance at sectional or generic level.

Section Tubuligerae (Walz) Heering emend. Entwistle

Basionym:

'Group' Tubuligerae Walz 1866: 144.

Synonyms:

Tubuligerae (Walz) Heering 1907: 132.

'Group' Globiferae Heidinger 1908: 360 pro parte.

Globiferae (Heidinger) Heering 1921: 86 pro parte

Gametangia sessile on siphon. Antheridia more or less parallel to the siphon, cylindrical, ellipsoid or saccate, constricted proximally, with pore directed towards adjacent oogonia; antheridia not subtended by a wall-bound cavity. Oogonia bilaterally, or rarely radially, symmetrical.

Lectotype Species: Vaucheria sericea Lyngbye; this species is chosen ^{here} from those examined by Walz (1866) as it is in accordance with the intentions of Blum (1972, p.11) who chose V. fontinalis [V. sericea is given as a synonym of V. fontinalis by Blum (1972)].

Tubuligerae is emended to include V. bicornigera and V. prolifera.

The variability in antheridial morphology in V. prolifera (see Rieth

1974b, 1978), and the similarity between V. bicornigera and both V. prolifera and Tubuligerae, made this change necessary. Tubuligerae can no longer be characterised by antheridial shape or pore size, but is now distinguished in having sessile antheridia directed towards adjacent oogonia (Table 5.3). Globiferae, previously characterised by the presence of saccate antheridia (Heering 1921, Rieth 1980b), and including V. dillwynii and V. prolifera, has been rejected, as the difference between saccate and ellipsoid or cylindrical antheridia seems to be a poor sectional character. Of the seven species now referable to the section Tubuligerae worldwide (Blum 1972, Rieth 1980b), three are known to occur in south-eastern Australia.

Key to the South-eastern Australian Species in the Section Tubuligerae

1. Oospore globose, leaving a peripheral oogonial cavity; antheridia $> 70 \mu\text{m}$ long.....V. aversa
1. Oospore ellipsoid, obovoid or reniform; oogonial cavity distal or absent; antheridia $< 70 \mu\text{m}$ long
.....2
2. Gametangia in opposite pairs; antheridia L/D
 > 2.0V. bicornigera
2. Gametangia unilateral; antheridia L/D < 2.0
.....V. prolifera

Vaucheria aversa Hassall 1843: 429. Blum 1972: 12, fig. 31. Cassie 1984: 226. Dangeard 1939b: 195, figs 2p,q. Heering 1907: 133, 180, figs 60, 61; 1921: 84, fig. 71. Rieth 1963b: 291, figs 1-3; 1980b: 46, figs 17b-h, 17A. Sarma 1974: 87, figs 1, 3, 18, 19, 21. Sarma & Chapman 1975b: 308.

Holotype: Not designated by Hassall (1843); Koster (1969) lists BM as housing the collections of Hassall.

Type Locality: Vicinity of Cheshunt, England (Hassall 1843).

Distribution: Widespread in most countries; Victoria, Australia (see Fig. 5.108).

Representative Specimens Studied (from a total of 11 field collections by Entwisle): MEL 1049105 p.p., Silver Creek, Beechworth, Victoria, 21.vii.1984; MEL 1049106, Ovens River, Myrtleford, Victoria, 22.vii.1984; MEL 1049 p.p., Lake Nillahcootie, Victoria, 22.vii.1984; MEL 1049108 p.p., Lake Glenmaggie, Victoria, 18.viii.1984; MEL 1049109 p.p., Tyers River, Moe-Erica Road, Victoria, 19.viii.1984; MEL 1049090 p.p., Bulga National Park, Victoria, 19.viii.1984; MEL 1049110, Gellibrand River, Gellibrand, Victoria, 28.vii.1984.

Figs 5.105-5.108

Thallus consisting of sparingly branched siphons, 34-72 μm in diameter, forming dense green mats on substrate.

Plants monoecious; gametangia sessile, in bisexual groups of 1(-2) oogonium with 1 antheridium on each side. Antheridia reflexed at base, orientated parallel to siphon and directed towards adjacent oogonium, fusiform to straight-cylindrical, 72-96 μm long, 22-29 μm in diameter, L/D 2.5-3.8. Oogonia globose, 113-156 μm long, 96-132 μm in diameter, L/D 1.1-1.3, with reflexed apex directed towards siphon. Oospores globose to ellipsoid, 77-103 μm long, 40-101 μm in diameter, L/D 1.0-1.2(-2.4), leaving a distal and peripheral oogonial cavity when mature; long-axis of oospore irregularly orientated; oospore wall 3-4 μm thick.

Akinetes unknown; sporangia not seen.

Diagnostic Features: Vaucheria aversa is delineated from other south-eastern Australian species of Vaucheria in having no gametophores, and in having straight-cylindrical antheridia, > 70 μm long (Figs 5.106, 5.107), and directed towards a globose oogonium with a peripheral

cavity left by the mature oospore (Fig. 5.105, 5.106).

Habitat and Phenology: Vaucheria aversa was collected from terrestrial to semi-terrestrial freshwater habitats in July and August (winter); all plants were fertile in the field. This species is apparently restricted to areas of high rainfall (> 700 mm/yr). Plants did not grow in culture media with salinities of 2-6.5 o/oo; all fertile material examined came from ASP-V media with salinity of 0.3 o/oo, crude cultures or field material.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria aversa described in the protologue (Hassall 1843) and by Blum (1972) and Dangeard (1939b).

In common with plants of V. aversa collected from New Zealand (Sarma 1974) and the Gulf of Mexico (Pecora 1980), all oogonia observed had reflexed distal portions (Figs 5.105-5.107), the oogonia therefore "...resembling a bird's head..." (Hassall 1843, p.429). Plants collected in Europe (Rieth 1980b) and North America (Blum 1972) contained some oogonia with erect distal portions.

Birckner (1912) recorded zoosporangia in V. aversa, but none were found in the south-eastern Australian plants.

There are no widely used synonyms for V. aversa, but Blum (1972) listed V. pulchella Arechavaleta (1883, p.26, fig. 8) as a probable synonym. The gametangia illustrated by Arechavaleta are similar to those observed in plants of V. aversa from south-eastern Australia, and a comparison of type collections will probably show the two to be conspecific.

Vaucheria bicornigera Entwisle sp. nov.

Thallus filis siphonaceis ramosis 24-65 μm diametro stoream viridem facientibus.

Plantae monoeciae; gametangiis vel sessilibus vel tumori parvo insidentibus, apice fili lateraliter prodientibus, in paribus bisexualibus (raro oogoniis 0 vel 2 simul cum antheridio uno) pari altero tali plerumque oppositis, ordinem irregularem paribus oppositis ad quatuor facientibus. Antheridia ellipsoidea ad cylindrico-fusiformia, interdum curva, 29-50 μm longitudine, 12-23 μm diametro, rationibus longitudinis:diametri 2.1-2.7. Oogonia sub antheridiis portata, obovoidea, adaxialiter plana vel concava, axe longo ad filum parallelo, 68-98 μm longitudine, 34-55 μm diametro, rationibus longitudinis:diametri 2.1-2.7. Oosporae aut oogoniis similes aut reniformes cavitatem^m oogonialem^m distalem^m ^{relinquentes} 62-98 μm longitudine, 34-55 μm diametro, rationibus longitudinis:diametri 1.5-2.5, parietibus 4-5 μm crassitie.

Sporangia akinetaque ignota.

Holotypus: MEL 1049111; this includes slides, and wet and dry preserved material, of the field collection and subsequent culture isolates.

Type Locality: Daylesford Mineral Spring, Daylesford Lake, Victoria.

Distribution: Victoria, Australia (see Fig. 5.109).

Specimens Studied (collected by Entwistle): MEL 1049114 p.p., Dales Creek, Greendale, Victoria, 30.v.1983; MEL 1049111, MEL 1049112 p.p., MEL 1049113, Daylesford Mineral Spring, Daylesford Lake, Victoria, 23.i.1984; MEL 1049115 p.p., Serpentine Creek, Serpentine, Victoria, 20.vii.1984; MEL 1049054 p.p., Calder River, Otway Ranges, Victoria, 28.viii.1984.

Figs 5.109-5.115

Thallus consisting of sparingly branched siphons, 24-65 μm in diameter, forming green mats on substrate.

Plants monoecious; gametangia sessile or borne on small swellings, produced laterally at the apex of the siphon in bisexual pairs (rarely 0 or 2 oogonia with 1 antheridium), usually opposite another pair of gametangia, up to 4 of these opposite pairs arranged in an irregular series. Antheridia elongate-ellipsoid to cylindrical-fusiform, curved to almost straight, 29-50 μm long, 12-23 μm in diameter, L/D 2.1-2.7. Oogonia borne subapically to the antheridia, elongate-obovoid, flattened or concave on adaxial side, 68-98 μm long, 34-55 μm in diameter, L/D 1.5-2.5, long-axis usually parallel with siphon. Oospores same shape as oogonia, or reniform, 62-98 μm long, 34-55 μm in diameter, L/D 1.5-2.5, leaving a distal oogonial cavity when mature; oospore wall 4-5 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria bicornigera is delineated from other south-eastern Australian species of Vaucheria in having no gametophores, antheridia with L/D > 2.0 and directed towards an adjacent oogonium (Fig. 5.111), and in having opposite pairs of gametangia produced at the apex of the siphon (Fig. 5.115).

Habitat and Phenology: Vaucheria bicornigera was collected from semi-terrestrial habitats throughout the year, but was only fertile in the

field during July (winter). In culture, vegetative growth occurred in media with salinities of 0.3-16 o/oo, but not 30 o/oo; all fertile culture material examined came from media with a salinity of 0.3 o/oo.

Remarks: A comparison of Vaucheria bicornigera with similar species in the section Tubuligerae is presented in Table 5.5.

The bilateral arrangement of gametangia found in V. bicornigera (Figs 5.111-5.115) is commonly observed in V. fontinalis (Linnæus) Christensen and is diagnostic of both V. jonesii Prescott and V. bilateralis Jao. Vaucheria bicornigera differs from these species, however, in having oogonia orientated parallel to the siphon (Figs 5.111-5.115) and shorter antheridia produced at the apex of siphons. In addition, the oogonia of the V. jonesii are much larger than those of V. bicornigera, and the oospores of V. bilateralis are more globose. Vaucheria globulifera W.West & G.S.West also has bilaterally arranged gametangia, but the oospores are again globose, the oogonia truncate (cf., Fig. 5.110), and the antheridia broader and apparently not produced apically.

The antheridia are produced apically in V. prolifera var. prolifera f. prolifera Dangeard and V. prolifera var. prolifera f. corniculata Rieth, but these two forms have unilaterally, rather than bilaterally arranged gametangia and a larger oogonial L/D. In addition, V. bicornigera differs from V. prolifera var. prolifera f. prolifera in having elongate-ellipsoid to cylindrical-fusiform antheridia (Fig. 5.111), with a L/D 2.1-2.7, rather than ovoid or ellipsoid antheridia, with a L/D 1.2-1.8. Vaucheria prolifera var. prolifera f. corniculata has antheridia of a similar size and shape to those of V. bicornigera,

but they are circinate rather than straight or slightly curved.

The epithet bicornigera refers to the hornlike appearance of the two opposite antheridia (see Figs 5.111, 5.115).

Vaucheria prolifera Dangeard 1939a: 297, figs A-E; 1939b: 222, fig. 13.

Gauthier-Lièvre 1955: 319, figs 14-19. Pecora 1977: 28, figs 11-13. Rieth 1969: 252, figs 1-5, pl. 41; 1980b: 51, figs 19q-s. Simons 1977: 17, pl. 11 fig. 2.

Holotype: Not designated by Dangeard (1939a, 1939b).

Type Locality: Tresses-Mélac, France (Dangeard, 1939b).

Distribution: Europe, North and Central America, North Africa; Victoria, Australia (see Fig. 5.118).

Specimens Studied (from a total of 9 field collections by Entwisle): MEL 1049116 p.p., Irrigation channel, Nathalia-Cobram Road, Victoria, 21.vii.1984; MEL 1049117 p.p., Boggy Creek, Mt. Hotham-Omeo Road, Victoria, 17.x.1984; MEL 1049105 p.p., Silver Creek, Beechworth, Victoria, 23.vii.1984; MEL 1049118 p.p., Morses Creek, Bright, Victoria, 23.vii.1984; MEL 1049119 p.p., Swifts Creek, Swifts Creek Township, Victoria, 17.x.1984; MEL 1049120 p.p., Port Welshpool, Victoria, 28.v.1985.

Figs 5.116-5.119

Thallus consisting of sparingly branched siphons, 22-31 μm in diameter, forming green mats on substrate.

Plants monoecious; gametangia sessile, in unilateral, bisexual pairs. Antheridia ovoid, ellipsoid or saccate, 27-35 μm long, 15-29 μm in diameter, L/D 1.2-1.8, disintegrating soon after dehiscence, produced laterally at apex of siphon, sometimes in a unilateral series. Oogonia ovoid to ovoid-reniform, 48-72 μm long, 36-48 μm in diameter, L/D 1.2-1.6, long-axis parallel to siphon. Oospores reniform to ellipsoid,

flattened on adaxial side, 48-62 μm long, 36-48 μm in diameter, L/D 1.2-1.5, sometimes leaving distal oogonial cavity when mature; oospore wall 2-3 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria prolifera is delineated from other south-eastern Australian species of Vaucheria in having no gametophores, antheridia with L/D < 2.0 and directed towards an adjacent oogonium with an oogonial cavity distal or absent when oospore matures, and in having unilaterally arranged gametangia produced at apex of the siphon (Figs 5.116, 5.117A,B, 5.119).

Habitat and Phenology: Vaucheria prolifera was collected from terrestrial to semi-aquatic sites in June, July, August (winter) and October (spring); plants were fertile in the field during July, August (winter) and October (spring). Plants did not grow in culture media with salinities of 2-6.5 o/oo; all fertile material examined came from crude culture or field material.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria prolifera described by Dangeard (1939a, 1939b), Rieth (1969, 1980b), Pecora (1977) and Simons (1977).

As with some collections of V. bicornigera, there were only fragments of V. prolifera among other species of Vaucheria. Even in MEL 1049117, with the greatest number of gametangia, the antheridia were difficult to observe as most had already dehisced and disintegrated (Figs 5.116, 5.119). There ~~were~~ ^{antheridia observed} sufficient, however, to confirm that they were ovoid, ellipsoid, or saccate in shape, and not different from those

recorded by other authors.

For a comparison of V. prolifera with the other species in the section Tubuligerae, see Table 5.5.

Section Vaucheria

Synonyms:

Anomalae [as an unspecified infrageneric taxon] Hansgirg 1888: 234.

Anomalae (Hansgirg) Heering 1907: 164.

Gametangia borne on gametophores. Antheridia straight or curved, expanded distally to deltoid-pulvinate, with 2-4 lateral discharge pores; antheridia not subtended by a wall-bound cavity. Oogonia radially or bilaterally symmetrical.

Type Species: Vaucheria disperma.

Although this section has been previously (e.g. Heering 1921, Blum 1972, Rieth 1980b) called Anomalae, it includes the type species of Vaucheria, V. disperma [now considered to be a synonym of V. canalicularis; see Christensen (1969)], and following article 22 of the International Code of Botanical Nomenclature (Voss 1983) the autonym must be used.

The section Vaucheria is delineated as in Blum (1972) and Rieth (1980b), both of whom use the name Anomalae. It is distinguished from all other sections in having multiporic antheridia not subtended by a wall-bound cavity (see Table 5.3), and of the three species worldwide (Rieth 1980b), two are known to occur in south-eastern Australia.

Key to South-eastern Australian Species in the Section *Vaucheria*

1. Antheridia straight or curved, < 40 μm long;
oogonia < 70 μm long.....V. cruciata
1. Antheridia circinate, > 40 μm long; oogonia > 70 μm
long.....V. canalicularis

Vaucheria canalicularis (Linnæus) Christensen 1968: 466, figs 7-11; 1969: 5, figs 3-5. Blum 1972: 24, figs 64, 80-83.

Basionym: Conferva canalicularis Linnæus 1753: 1164.

Heterotypic Synonyms:

Ectosperma cespitosa Vaucher 1803: 28, pl. 2 fig. 4.

Ectosperma ovata Vaucher 1803: 25, pl. 2 fig. 1.

Vaucheria disperma de Candolle 1801: 21.

Vaucheria woroniniana Heering 1907: 165, figs 89,90. Dangeard 1939b: 227, Fig. 14. Gauthier-Lièvre 1955: 316, figs 11-13. Heering 1907: 165, figs 89,90; 1921: 93,183, fig. 85. Rieth 1956a: 139, figs 8-10; 1965a: 495, figs 1,2; 1980b: 102, fig. 43.

Misapplied Name:

Vaucheria geminata auct. non (Vaucher) de Candolle: Götz 1897: 126, figs 45-49.

Lectotype: Description by Dillenius (1741) of Conferva rivulorum capillacea, densissime congestis ramulis (chosen by Christensen 1968).

Type Locality: Not designated by Linnæus (1753) or Christensen (1968).

Distribution: Widespread (for study area, see Fig. 5.126).

Representative Specimens Studied (from a total of 25 field collections by Entwistle): MEL 1049046, Sailor's Spring, Leonards Hill, Victoria, 23.i.1984; MEL 1049047, MEL 1049048, Glenluce Springs, via Vaughan Springs, Victoria, 23.i.1984; MEL 1049255, Irrigation channel, Sea Lake-Woomalang Road, Victoria, 4.viii.1984; MEL 1049049 p.p., Werribee River, Bacchus Marsh, Victoria, 13.vi.1984; MEL 1049050, Field River, via Happy Valley Reservoir, South Australia, 7.viii.1983; MEL 1049051, Lake Tutchwop, Lake Boga, Victoria, 11.xi.1983; MEL 1049052, Yarra River, Warrandyte, Victoria, 18.xi.1983; MEL 1049053 p.p., MEL 1049134 p.p., Goulburn River, Seymour-Hume Highway Road, Victoria, 14.x.1983; MEL 1049054 p.p., Calder River, Otway Ranges, Victoria, 28.viii.1984; MEL 1049055, Lake Mombeong, Nelson, Victoria, 4.x.1984.

Figs 5.120-5.126

Thallus consisting of sparingly branched siphons, (31-)45-67(-86) μm in diameter, forming dense green mats on substrate; narrowing colourless rhizoids often present.

Plants monoecious; gametophores consisting of 1-2 oogonia borne laterally to 1 antheridium; peduncles 60-200 μm long, 47-80 μm in diameter, or gametophores terminal on vegetative siphons. Antheridia usually surpassing the apex of oogonia, circinate, 50-75 μm long, 23-31 μm in diameter at base, with deltoid-pulvinate apex, 31-72 μm in diameter, and 2(-3) lateral pores; antheridial pedicels straight or little curved at apex, 96-144 μm long. Oogonia erect, ellipsoid, sometimes flattened on on adaxial side, (62-)77-120(-139) μm long, (21-)53-91 μm in diameter, L/D (1.1-)1.3-1.6(-2.0), with small distal prominence; oogonial pedicels 5-36 μm long. Oospores same shape and size as oogonia; oospore walls 2-5 μm thick.

Aplanosporangia obovoid, 106-127 μm long, 70-96 μm in diameter, terminal on vegetative siphons; akinetes unknown.

Diagnostic Features: Vaucheria canalicularis is delineated from other south-eastern Australian species of Vaucheria in having gametophores with biporic, circinate antheridia > 40 μm long (Figs 5.120, 5.125) and

oogonia > 70 μm long.

Habitat and Phenology: Vaucheria canalicularis was found in terrestrial to semi-aquatic, freshwater habitats; plants were fertile in the field throughout the year. In culture, vegetative growth occurred in media with salinities of 0.3-16 o/oo, but not 30 o/oo; all fertile culture material examined came from media with a salinity of 2 o/oo.

Remarks: The south-eastern Australian plants were concordant with the plants of Vaucheria canalicularis described by Christensen (1968, 1969).

Vaucheria canalicularis and V. geminata (section Racemosae) share many attributes, including the orientation and size of oogonia, the shape and size of the gametophores, and in some populations, apparently similar antheridial shape. The antheridia of V. canalicularis have two lateral pores on a deltoid-pulvinate distal swelling (Figs 5.120, 5.121, 5.124, 5.125), while those of V. geminata are monoporic and circinate-cylindrical throughout (Figs 5.66, 5.68, 5.71). In some south-eastern Australian specimens, however, the antheridia of V. canalicularis appeared to be monoporic after the distal portion of the senescent antheridia disintegrated. This, coupled with the often poor perspective offered in all but the ventral view of antheridia, obscured the number of pores and the swollen apex. At least some biporic antheridia can generally be found after an extensive search of material, but many (Fig. 5.122) may be indistinguishable from those of V. geminata. There are additional characters which also separate the two species. The antheridia of V. canalicularis (Figs 5.122, 5.125) are more tightly coiled than those of V. geminata (Figs 5.66, 5.68, 5.71),

circinate antheridial length $< 70 \mu\text{m}$ and $> 70 \mu\text{m}$ respectively, and the oogonia of V. canalicularis are generally more elongate, L/D 1.3-1.6 compared with 1.1-1.3(-1.4) in the latter species.

Christensen (1969) recorded aplanosporangia similar in size and shape to those observed in the south-eastern Australian plants (Fig. 5.123).

Rieth (1956a) recorded V. canalicularis from saline habitats and found that it grew normally in culture media with 'no added salt' to media with a salinity of 15 o/oo. The ability of V. canalicularis to tolerate salinities up to 15 o/oo in culture was confirmed in this study, although no plants were found in saline habitats.

The nomenclature and synonymy of V. canalicularis given by Christensen (1968, 1969) are adopted here. Previously V. woroniniana was the most commonly used name for this taxon (e.g. Dangeard 1939b, Gauthier-Lièvre 1955) and Rieth (1976, 1980b) continues to use this heterotypic synonym.

Vaucheria cruciata (Vaucher) de Candolle in Lamarck & de Candolle 1805:

62. Blum 1972: 24, fig. 79. Christensen 1969: 13, fig. 7.

Basionym:

Ectosperma cruciata Vaucher 1803: 30, pl. 2 fig. 6.

Heterotypic Synonym:

Vaucheria debaryana Woronin 1880: 425, pl. 7. Dangeard 1939b: 225, figs 140, p. Heering 1907: 167, fig. 91; 1921: 95, 186, fig. 85. Jao 1936: 743, figs 16-19. Rieth 1956a: 153, figs 14, 15; 1965a: 502, Figs 5-7; 1980b: 106, fig. 45.

Type: Not designated by Vaucher (1803).

Type Locality: Not designated by Vaucher (1803); material collected from near Geneva, Switzerland.

Distribution: Widespread throughout the world; not common in south-eastern Australia (see Fig. 5.131).

Specimens Studied (collected by Entwistle): MEL 1049056, Yarra River, Yarra Bend Golf Course, Victoria, 1.i.1984; MEL 1049057 p.p., Greendale Reservoir, Greendale, Victoria, 22.viii.1984; MEL 1049058, Duck Creek, Hordern Vale-Aire River Mouth Road, Victoria, 28.viii.1984; MEL 1049076, Bundaleer Reservoir, via Spalding, South Australia, 10.viii.1985.

Figs 5.127-5.131

Thallus consisting of sparingly branched siphons, 14-34 μm in diameter, closely adhering to substrate.

Plants monoecious; gametophores consisting of 1-2 oogonia borne laterally to 1 antheridium; peduncles 60-200 μm long, 14-33 μm in diameter, or gametophores terminal on vegetative siphons. Antheridia straight or slightly curved, deltoid-pulvinate, 19-24 μm long, 26-41 μm in diameter, 2(-3) lateral pores; antheridial pedicels 40-72 μm long. Oogonia erect, ellipsoid to globose, 43- 67 μm long, 38-48 μm in diameter, L/D 1.1-1.2(-1.4), with a papillate or discoid distal prominence; oogonial pedicels 5-31 μm long. Oospores same size and shape as oogonia; oospore walls ca 1 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria cruciata is delineated from the other south-eastern Australian species of Vaucheria in having gametophores with biporic, straight or little curved antheridia < 40 μm long (Fig. 5.127-5.130) and oogonia < 70 μm long.

Habitat and Phenology: Vaucheria cruciata was found in semi-aquatic habitats and semi-terrestrial areas of farmland. Collections were made

in January (summer) and August (winter); plants were sparsely fertile in the field in August. In culture, vegetative growth occurred in media with salinities of 0.3-6.5 o/oo; all fertile material examined came from media with a salinity of 0.3 o/oo.

Remarks: The plants collected from south-eastern Australia were concordant with the plants of Vaucheria cruciata described in the protologue (Vaucher 1803, as Ectosperma) and by Christensen (1969). The biporic antheridia in V. cruciata are more readily observable than those of V. canalicularis, and are unlikely to be confused with the monoporic antheridia found in species of the section Racemosae.

This species may be more widespread in south-eastern Australia, but due to its small size, it could easily be overlooked in field collections. Cullinane (1976) found V. cruciata (as V. debaryana) growing on Lithothamnion calcareum (Pallas) Areschoug, in the upper intertidal zone, whereas all south-eastern Australian collections were from freshwater habitats.

Christensen (1969), following a study of plants from the type locality, argued that although Vaucher inaccurately described and illustrated the antheridia of V. cruciata, the size, general appearance and habit of the plants make their identity obvious. Vaucheria debaryana has been used subsequently (e.g. Heering 1907; Rieth 1965a, 1980b) for the same taxon and Christensen (1969) placed it in synonymy with V. cruciata.

Section Woroninia (Solms-Laubach) Heering 1907: 138.

Basionym:

Woroninia Solms-Laubach 1867: 366 (as a genus).

Synonym:

Woroninia [as an unspecified infrageneric taxon] (Solms-Laubach)

Woronin 1869: 160.

Gametangia sessile on siphons. Antheridia ellipsoid, ovoid, fusiform-cylindrical or narrowly urceolate, constricted proximally, with pore not directed towards an adjacent oogonium; antheridia not subtended by a wall-bound cavity. Oogonia radially symmetrical (but sometimes reflexed proximally).

Type Species: Vaucheria dichotoma (Linnæus) Martius (see Solms-Laubach 1867, p.366).

The section Woroninia includes the same species as in Rieth (1980b) and Blum (1972), plus V. conifera Christensen, and is distinguished from all other sections of Vaucheria in having no gametophores and in having sessile antheridia not directed towards an adjacent oogonium (Table 5.3). Of the five species worldwide, two are known to occur in south-eastern Australia.

Key to the South-eastern Australian Species in the Section Woroninia

1. Antheridia fusiform-cylindrical to narrowly urceolate, > 100 µm long.....V. conifera
1. Antheridia ovoid to ellipsoid, < 100 µm long
.....V. velutina

Vaucheria conifera Christensen (in preparation for Aust. J. Bot.)

Holotype: ADU (Christensen pers. comm.)

Type Locality: Garden Island, Adelaide, South Australia
(Christensen pers. comm.).

Distribution: Coastal south-eastern Australia (see Fig. 5.132).

Specimens Studied (collected by Entwistle): MEL 1049121, MEL 1049122, Bass River, Bass, Victoria, 20.iv.1983; MEL 1049123, Newhaven, Victoria, 27.vi.1983; MEL 1049124, MEL 1049125, Betka River, Mallacoota, Victoria, 2.x.1983; MEL 1049126, Tarwin River, Tarwin Lower, 31.iii.1984. MEL 1049407, MEL 1049408, Chinaman's Creek, Red Cliff Point, South Australia, 10.viii.1985.

Figs 5.132-5.136

Thallus consisting of sparingly branched siphons, 34-62 μm in diameter, forming dense or open green mats on substrate.

Plants dioecious. Antheridia sessile, borne laterally at right angles to siphons, rarely terminally; antheridia fusiform-cylindrical to narrowly-urceolate, straight, 120-154 μm long, 34-50 μm in diameter, dehiscing through large terminal pore, sometimes with recurved margin. Oogonia sessile, usually erect, ovoid to ellipsoid, 117-180 μm long, 86-156 μm in diameter, proximally obtuse. Oospores globose, 94-108 μm in diameter, leaving a distal and proximal oogonial cavity; oospore wall 2-2.5 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria conifera is delineated from other south-eastern Australian species of Vaucheria in having no gametophores and in having fusiform-cylindrical to narrowly-urceolate antheridia $> 100 \mu\text{m}$ long (Figs 5.134, 5.133) borne on a separate siphon to the oogonia.

Habitat and Phenology: Vaucheria conifera was collected from intertidal mudflats and estuarine rivers in March, April (autumn), June, August (winter) and October (spring); all plants were sterile in the field. In culture, vegetative growth occurred in media with salinities of 2-30

o/oo; all fertile material examined came from media with a salinity of 6.5-30 o/oo.

Remarks: The Victorian plants were concordant in most respects with the plants of Vaucheria conifera from South Australia described by Christensen (pers. comm.).

In some collections of V. velutina the oogonia were erect, rather than typically oblique, and closely resembled those of V. conifera. The oogonia of Vaucheria conifera, however, were generally relatively wide at the base and obtuse (Fig. 5.135, 5.136), rather than acute as in V. velutina C. Agardh (Christensen pers. comm.). The antheridia of V. conifera were more distinctive in size and shape compared with those of V. velutina which were ellipsoid to ovoid and only 46-96 μm long. In addition, the antheridia of V. conifera had a relatively large terminal opening (see Fig. 5.133), similar to that found in many species in the section Tubuligerae, while the antheridia of V. velutina dehisced through a pore which is substantially smaller than the diameter of the antheridia (e.g. Fig. 5.141).

Although in the plants studied, V. conifera was always apparently dioecious and V. velutina monoecious, Christensen (1986a) has reported apparently dioecious variants of V. velutina. Vaucheria dichotoma (section Woroninia), not found in the current study, is usually dioecious, but in this species the oospores fill the oogonium, and are much larger [210-340 μm in diameter (Blum 1972)] than those of V. conifera. Furthermore, the antheridia of V. dichotoma are ellipsoid to ovoid and similar to those of V. velutina, rather than elongate as in V. conifera.

In collections grown in ASP-V (salinity 6.5 o/oo) agar media, only

oogonia were observed, and rarely antheridia, while MEL 1049407 was grown in liquid ES & Iodine & liver broth and produced abundant antheridia and few oogonia.

Vaucheria velutina C. Agardh 1824: 312. Christensen 1973: 516.

Gallagher and Humm 1981: 185, figs 2,3. Nordstedt 1878: 176.

Pecora 1980: 390, fig. 10. Watts 1887: 137.

Heterotypic Synonyms:

Vaucheria thuretii Woronin 1869: 158. Blum 1972: 11, fig. 30.

Christensen 1952: 183, fig. 4r. Dangeard 1939b: 190, figs 1M-P. Knutzen 1973: 173, figs 9a,b. Heering 1907: 140, 220, fig. 67; 1921: 83, fig. 69. Ott & Hommersand 1974: 383, figs 31-34. Pecora 1977: 29, fig. 14. Rieth 1956b: 282, pl. 4 fig. 3-6. Chapman 1956: 495.

Holotype: LD; according to Christensen (1973).

Type Locality: Gråen, Sweden (C. Agardh 1824).

Distribution: Widespread (for study area, see Fig. 5.142).

Specimens Studied (collected by Entwisle, unless otherwise indicated): MEL 1049127, Tarwin River, Inverloch-Tarwin Road, Victoria, 31.iii.1984; MEL 1049128, Tarwin River, Tarwin Lower, Victoria, 31.iii.1984; MEL 1049129, Bass River, Bass, Victoria, 31.iii.1984; MEL 1049130, Rhyll Inlet, Rhyll, Victoria, 31.iii.1984; MEL 1049131, Clinton Conservation Park, Port Wakefield-Clinton Road, South Australia, 8.viii.1985; A52911, Port Clinton, South Australia, Womersley, 18.ix.1981; A55088, Coobowie-Edithburg Road, South Australia, Brock, 17.iii.1984; A20068, American River Inlet, Kangaroo Island, South Australia, Womersley, 6.ii.1956.

Figs 5.137-5.142

Thallus consisting of sparingly branched siphons, 26-70 μ m diameter, forming dense green mats on substrate.

Plants monoecious; antheridia in groups near to one or more oogonia. Antheridia erect or oblique, ellipsoid to ovoid, 46-96 μ m

long, 36-50 μm in diameter, narrowing acutely to a distal dehiscence pore. Oogonia erect or reflexed at base, ellipsoid to obovoid, 134-240 μm long, 106-190 μm in diameter, proximally acute; oogonia usually with elongate, erect, distal papillae. Oospores globose, 154-202 μm in diameter, leaving a distal and proximal oogonial cavity; oospore wall 2-5 μm thick.

Sporangia and akinetes unknown.

Diagnostic Features: Vaucheria velutina is delineated from other south-eastern Australian species of Vaucheria in having no gametophores and in having groups of ovoid to ellipsoid antheridia, < 100 μm long (Figs 5.140, 5.141), on the same siphon as the oogonia, but not all directed towards an adjacent oogonium.

Habitat and Phenology: Vaucheria velutina was collected from semi-aquatic intertidal mudflats in February (summer), March (Autumn), August (winter) and September (spring); plants were fertile in the field in all months. In culture, vegetative growth occurred in media with salinities of 2-30 o/oo; all fertile material examined came from media with a salinity of 6.5 o/oo.

Remarks: The south-eastern Australian plants were concordant in most respects with the plants of Vaucheria velutina described by Christensen (1952, as V. thuretii; 1973), Rieth (1956b, as V. thuretii) and Blum (1972, as V. thuretii).

The oogonia of V. velutina are usually reflexed at the base (Fig. 5.139) and directed towards an adjacent group of antheridia (Christensen 1986a), and this was true for all the plants collected from South

Australia. The Victorian collections, however, often included plants with erect or only slightly deflexed oogonia (Figs 5.137, 5.138). Christensen (1986a) described V. velutina var. separata to include plants similar to the type variety but dioecious and with erect oogonia. He considers this taxon to be a "means of reference" for such plants, but not a solution to the taxonomic problems associated with V. velutina. Although the Victorian plants often have erect oogonia, they are monoecious and similar in all other respects to the South Australian plants, and are included in V. velutina var. velutina. This conclusion is supported by the variation observed by Christensen (1986a) in plants of V. velutina from the British Isles grown in crude culture media with salinities of 20 and 30 o/oo. These contained some siphons with only antheridia or only oogonia, and the oogonia were sometimes not reflexed. The Victorian plants, with both erect and reflexed oogonia, were grown in media with salinities of 3-6.5 o/oo.

The oogonia of V. velutina from Victoria varied from obovoid (Figs 5.137, 5.139), as is commonly found in this species (Christensen 1952, as V. thuretii), to ellipsoid (Fig. 5.138), which is similar to the oogonia found in V. conifera. The base of the oogonium, however, was usually acute rather than obtuse, and similar to that found in V. velutina by Christensen (1952, as V. thuretii). Vaucheria conifera is also distinguished from V. velutina in having long cylindrical antheridia borne on different siphons to the oogonia.

Vaucheria velutina has been recorded from Australia by Watts (1887), in a list of freshwater algae from Victoria, but there are no collection details. The determination was made by Kützinger in 1882 (D.Sinkora pers. comm.) and there is no specimen lodged at MEL. Chapman (1956) recorded this species (as V. thuretii) from salt marshes and

mangrove swamps in New Zealand, and all collections of V. velutina made in the current study were from saline habitats.

Nordstedt (1878) concluded that V. velutina and V. thuretii probably referred to the same taxon, but the synonymy was not formally made until Christensen's (1973) examination of the type material of both species.

Table 5.1 Sectional classifications used in selected published accounts (horizontal rows represent sections apparently including the same type species, but not necessarily of the same circumscription).

Table 5.1.

Walz 1866	Heering 1921	Blum 1972	Rieth 1980b	Current study (see Table 5.3 for details)
'Group' Corniculatae ¹	Corniculatae	Corniculatae	Corniculatae	Corniculatae
'Subgroup' Sessiles	subsect. Sessiles	subsect. Sessiles	subsect. Sessiles	R. (to Corniculatae) ²
'Subgroup' Racemosae	subsect. Racemosae	subsect. Racemosae	subsect. Racemosae	Racemosae
'Group' Tubuligerae	Tubuligerae	Tubuligerae	Tubuligerae	Tubuligerae
'Group' Piloboloideae	Piloboloideae	Piloboloideae	Piloboloideae	Piloboloideae
S.U.	Globiferae	R. (to Pseudoanomala and subsect. Sessiles)	Globiferae	R. (to Corniculatae and Tubuligerae)
S.U.	Woroninia	Woroninia	Woroninia	Woroninia
S.U.	Anomala	Anomala	Anomala	Vaucheria
S.U.	S.U.	Pseudoanomala	Pseudoanomala	?
S.U.	S.U.	Contortae	Contortae	R. (to Corniculatae)
S.U.	S.U.	Heeringia	Heeringia	R. (to Racemosae)
S.U.	S.U.	N.C.	Androphorae	Androphorae
S.U.	S.U.	S.U.	Acandrae	Acandrae
S.U.	S.U.	S.U.	Hercynianae	Hercynianae

S.U. = Section undescribed at time of publication, R. = Rejected, N.C. = Not considered in publication. ¹All taxa are sections unless otherwise indicated. ²Species have been referred to the section(s) included within parentheses.

Table 5.2 Data from published accounts (protologues,
Blum 1972 and Rieth 1980b) of the sections of
Vaucheria.

Table 5.2.

Infra-generic taxon and protologue	Antheridia subtended by wall-bound cavity	Androphore (L)ateral, (I)ntercalary, (T)erminal or absent (-).	Number of antheridial pores	Antheridial shape - (C)ylindrical, (D)eltoid-pulvinate, (F)usiform, (Cl)avate, (O)void to ellipsoid, (Ci)rcinate, (S)accate, (St)raight, (Co)ntorted, (Cu)rved	Gametophores	Antheridia directed towards adjacent oogonium	Antheridial pedicel (S)traight, (C)urved or Absent (-)	Disc-like swelling in peduncle	Distinct oogonial fertilisation pore
Acrandrae Ott & Hommersand 1984: 373.	-	I,T	1	St,Cu,C	-	-	S	NA	+
Androphorae Nordstedt 1879: 188.	-	L	1	Cu,C	-	-	S,-	NA	+
Contortae Dangeard 1939b: 216	-	-	1	Co,C	-	-	S	-	+
Corniculatae Walz 1866: 143	-	-	1	Ci,C	+, -	NA	C	+, -	+
Discoideae Venkataraman 1961: 10	-	-	1	Ci,C	+	NA	C	+	+
Globiferae Heidinger 1908: 360	-	-	1	S	-	NA	C,-	NA	+
Heeringia Blum 1971: 189	-	-	1	Cu,S,C	+	NA	C	-	-
Hercynianae Rieth 1980a: 446	-	-	0 ¹	Cl	+	NA	-	-	-
Piloboloideae Walz 1866: 144	+	-	1-7	C,F	+, -	NA	NA	NA	+, -
Pseudoanomalae Jao & Ley 1947: 106	-	-	1	C	+, -	+, -	S,C,-	-	+
Radiatae Hoppaugh 1930: 332	-	-	1	Ci,C	+, -	NA	C	-	+
Racemosae Walz 1866: 144	-	-	1	Ci,C	+	NA	C	+, -	+
Sessiles Walz 1866: 144	-	-	1	Ci,C	-	NA	C	NA	+
Tubuligeriae Walz 1866: 144	-	-	1	C	-	+	-	NA	+
Vaucheria (syn. Anomalae Hansgirg 1888: 234)	-	-	2-4	D	+	NA	S,C	-	+
Woroninia Solms-Laubach 1867: 366	-	-	1	O	-	-	-	NA	+

NA = Not applicable, ¹Wall disintegrates to release sperm.

Table 5.3 Diagnostic features of the sections recognised as a result of the current study. Data from plants collected in this study, protologues, Blum (1972) and Rieth (1980b).

Table 5.3.

Section	Antheridia subtended by wall-bound cavity	Androphore (L)ateral, (I)ntercalary, (T)erminal or absent (-)	Number of antheridial pores	Antheridial shape - (C)ylindrical, (D)eltoid-pulvinate, (F)usiform, (Cl)avate, (O)void to ellipsoid	Gametophores	Antheridia directed towards adjacent oogonium	Antheridia pedicellate	Distinct oogonial fertilisation pore
Acrandrae Ott & Hommersand	-	I,T	1	C	-	-	+	+
Androphorae Nordstedt	-	L	1	C	-	-	+	+
Corniculatae (Walz) Heering sens. nov.	-	-	1	C	-	NA	+	+
Hercynianae Rieth	-	-	0 ¹	Cl	+	NA	-	-
Piloboloideae (Walz) Heering	+	-	1-7	C,F	+, -	NA	NA	+, -
Racemosae (Walz) sect. nov.	-	-	1	C	+	NA	+	+, -
Tubuligeriae (Walz) Heering sens. nov.	-	-	1	O,C	-	+	-	+
Vaucheria	-	-	2-4	D	+	NA	+	+
Woroninia (Solms-Laubach) Heering	-	-	1	O,F	-	-	-	+

NA = Not applicable, ¹Wall disintegrates to release sperm.

Note that the status of Pseudoanomalaе Dangeard is uncertain and requires further study.

Table 5.4 Comparison of features in Vaucheria gyrogyana
sp. nov. and similar species in the section
Racemosae. Data from plants collected in this
study except: ¹ Blum (1972), and ² Jao (1939).

Table 5.4.

Species	Oogonial orientation	Oogonial length (μm)	Siphon diameter (μm)	Oogonial cavity length (μm)	Oogonial cavity shape	Septum in peduncle
<u>V. gyrogyna</u> sp. nov.	transverse to peduncle	89-120	43-79(-96)	14-32	oblique conical	-
<u>V. pseudogeminata</u> Dangeard	erect	53-79	22-77(-93)	9-25	oblique conical	-
<u>V. alaskana</u> Blum ¹	erect	83-120	42-71	5-16	reflexed tubular	-
<u>V. lii</u> Rieth	erect	(45-)55-67	21-29	15-25	circinate conical	+
<u>V. adunca</u> Jao ²	erect	62-70	17-27	≈ 30	subcircinate conical	-
<u>V. erythrospora</u> Christensen	pendent	72-94	28-64	(5-)10-23	oblique conical	-

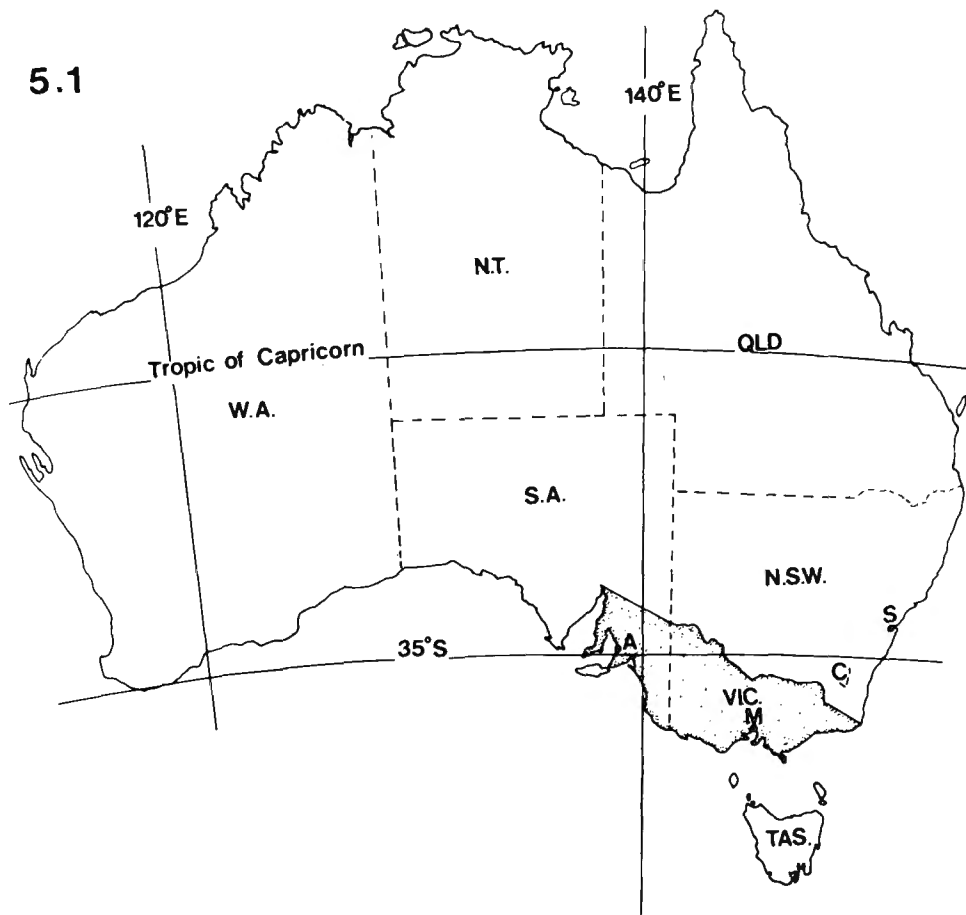
Table 5.5 Comparison of features in Vaucheria bicornigera sp. nov. and similar species in the section Tubuligerae. Data from plants collected in this study except: ¹ Rieth (1980b, V. fontinalis as V. ornithocephala), ² Blum (1972), ³ West & West (1907), and ⁴ Jao (1936).

Table 5.5.

Taxon	Gametangia (B)ilateral or (U)nilateral	Antheridia produced at apex of siphon	Oogonial long-axis parallel to siphon	Antheridial shape - (O)void, (C)ylindrical, (F)usiform, (Cu)rved, (S)accate, (St)raight, (Cl)rcinate	Antheridial length (µm)	Antheridial L/D	Oogonial length (µm)	Oospore L/D	Antheridial diameter (µm)
<u>V. bicornigera</u> sp. nov.	B	+	+	O, C, F, Cu	29-50	2.1-2.7	68-98	1.5-2.5	12-23
<u>V. prolifera</u> var. <u>prolifera</u> f. <u>prolifera</u> Dangeard	U	+	+	O, S, Cu	27-35	1.2-1.8	48-72	1.2-1.5	15-29
<u>V. prolifera</u> var. <u>prolifera</u> f. <u>corniculata</u> Rieth ¹	U	+	+	C, Ci	29-44	1.5-2.7	55-83	1.1-1.4	13-26
<u>V. fontinalis</u> (Linnaeus) Christensen ¹	B, U	-	-(+)	C, St	(39-) 52-104	(1.8-) 2.3-4.0 (-4.5)	(57-) 63-99	1.1-1.4 (-1.7)	13-34
<u>V. jonesii</u> Prescott ²	B	-	+, -	C, St	57-115	?	161-165	?	15-31
<u>V. globifera</u> West & West ³	B	-	+	C, St	?	?	90-100	?	23-30
<u>V. bilateralis</u> Jao ⁴	B	-	-	C	80-125	?	64-93	?	19-29

Fig. 5.1. Map of Australia showing study area (stippled).
A = Adelaide, C = Australian Capital Territory,
M = Melbourne, N.S.W. = New South Wales, N.T. =
Northern Territory, QLD = Queensland, S = Sydney,
S.A. = South Australia, TAS. = Tasmania, VIC. =
Victoria. W.A. = Western Australia.

5.1



Figs 5.2-5.7

Figs 5.2-5.5 Vaucheria arcassonensis Dangeard. MEL
1049096.

Fig. 5.2 Contorted antheridium (arrow indicates
distal end) next to oogonium reflexed towards
the siphon.

Fig. 5.3 Antheridium. Note that it is almost straight.

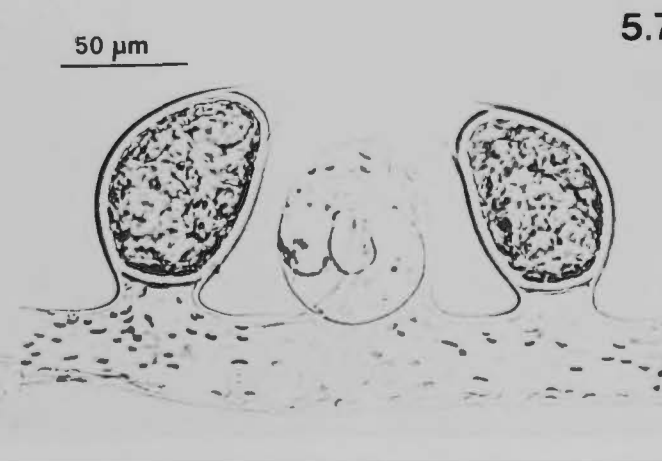
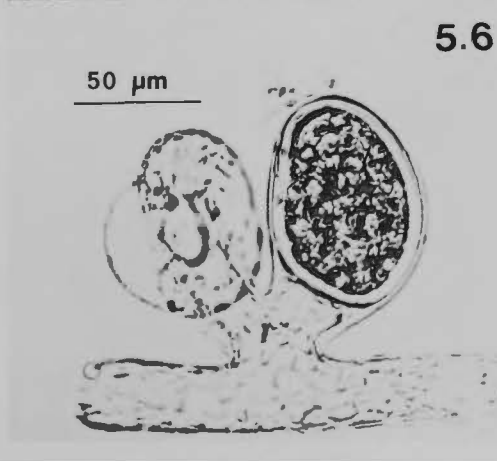
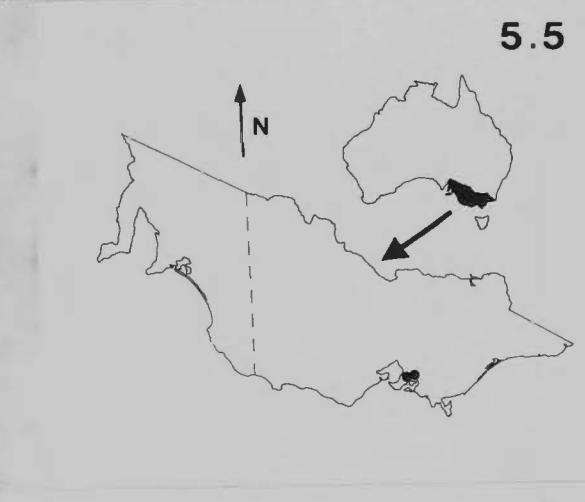
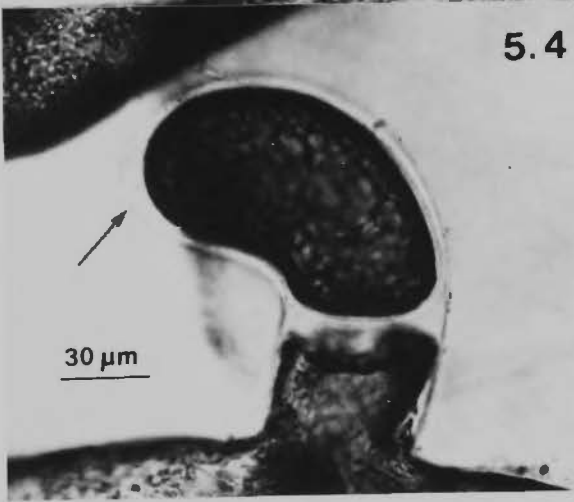
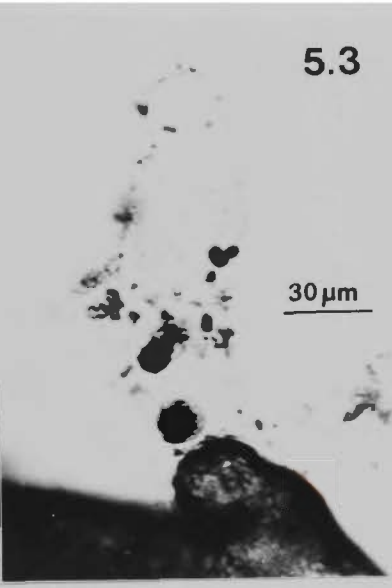
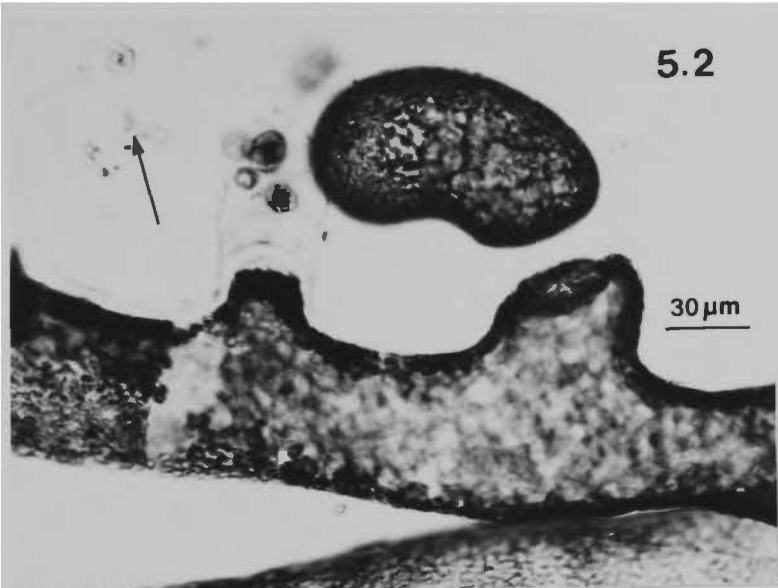
Fig. 5.4 Pedicellate oogonium, rounded near fertilisation
pore (arrow) and containing a curved-rectangular
oospore.

Fig. 5.5 Known distribution of V. arcassonensis in
south-eastern Australia.

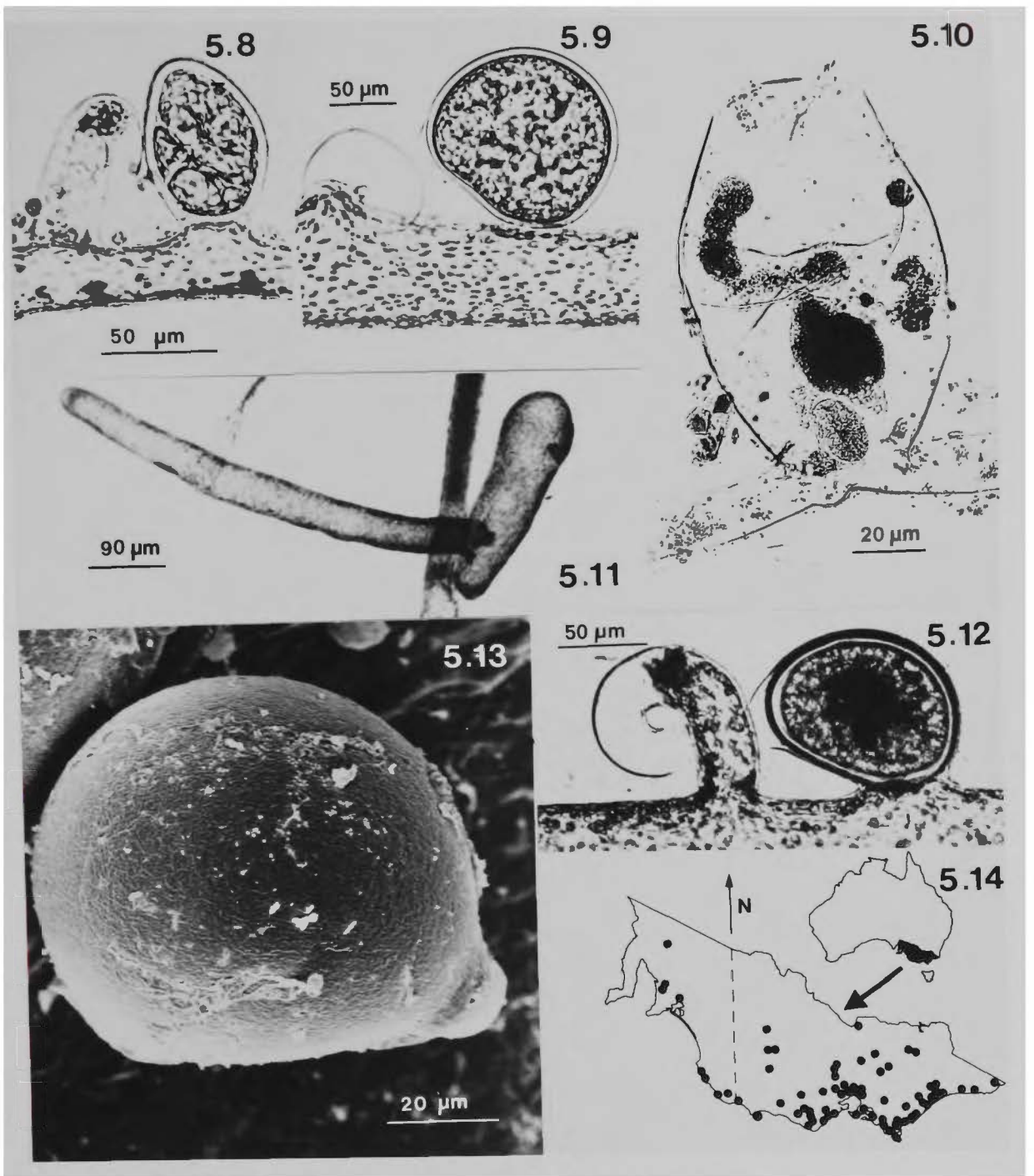
Figs 5.6-5.7 Vaucheria bursata (O.F.Müller)
C. Agardh. MEL 1049236.

Fig. 5.6 Oogonium with short pedicel arising from
antheridial pedicel.

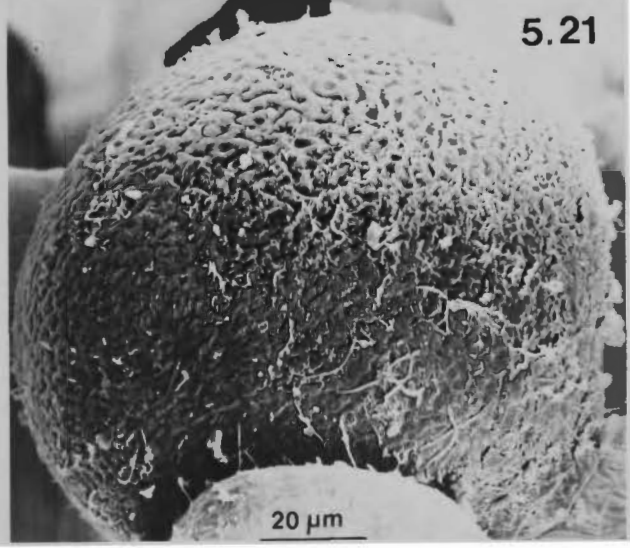
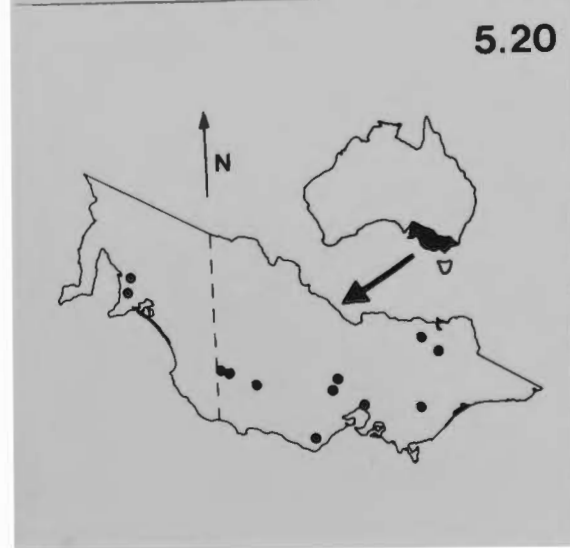
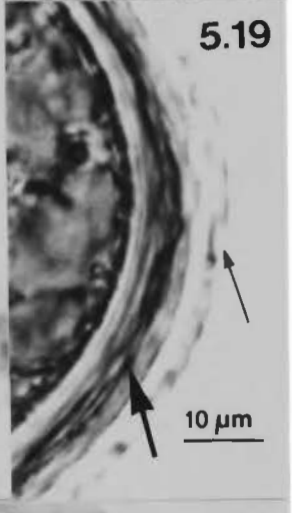
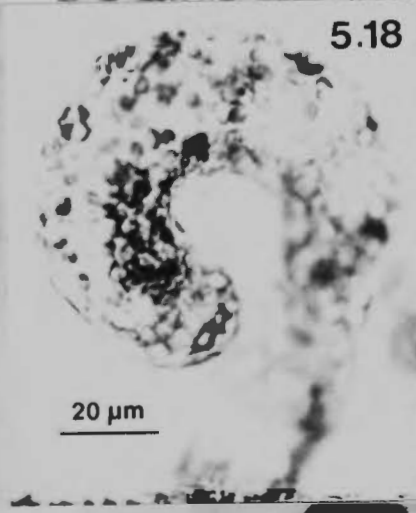
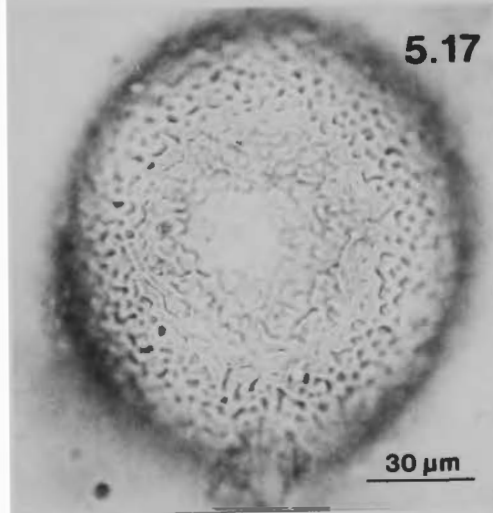
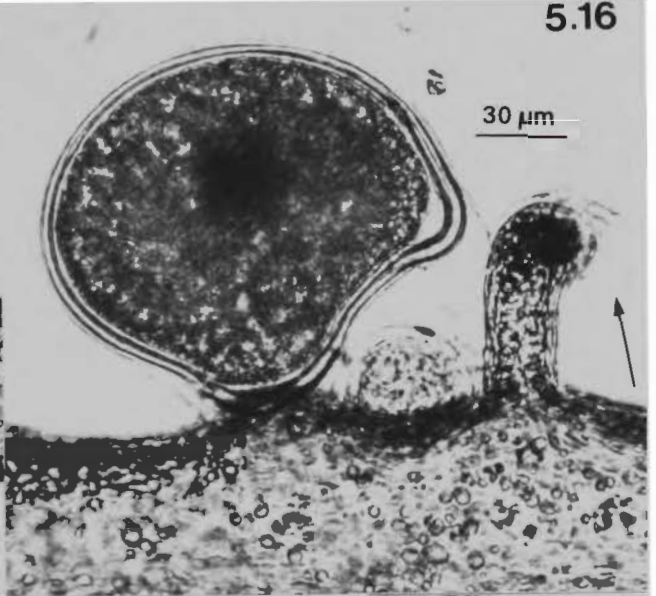
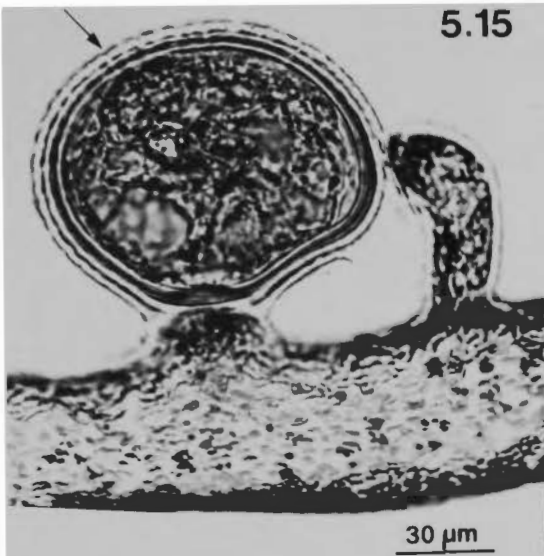
Fig. 5.7 Oogonia with pores directed away from siphon
and antheridium turning through less than a
full circle (entire antheridial system, however,
turns through more than a full circle).



- Figs 5.8-5.14 Vaucheria bursata (O.F.Müller)
C. Agardh.
- Fig. 5.8 Oogonium with long-axis almost perpendicular
to siphon, and nearly radially symmetric.
MEL 1049236.
- Fig. 5.9 Oogonium with pore directed towards siphon
and antheridium with very short pedicel.
MEL 1049237.
- Fig. 5.10 'Gall', probably formed by Proales werneckii
(Ehrenberg) Hudson & Gosse. MEL 1049150.
- Fig. 5.11 Germinating zoospore in agar. MEL 1049133.
- Fig. 5.12 Oogonium with pore directed towards siphon.
MEL 1049235.
- Fig. 5.13 Oogonium showing relatively smooth surface.
MEL 1049234.
- Fig. 5.14 Known distribution of V. bursata in
south-eastern Australia.



- Figs 5.15-5.21 Vaucheria dillwynii (Weber & Mohr)
C. Agardh. MEL 1049234 p.p.
- Fig. 5.15 Oogonium with undulate wall (arrow).
- Fig. 5.16 Oogonium and disintegrated antheridium
(arrow).
- Fig. 5.17 Oogonial wall showing rugose patterning.
- Fig. 5.18 Immature antheridium. Note cylindrical
shape.
- Fig. 5.19 Oospore with 'flaky' textured wall
(large arrow) inside and undulating oogonial
wall (small arrow).
- Fig. 5.20 Known distribution of V. dillwynii in
south-eastern Australia.
- Fig. 5.21 oogonium showing rugose oogonial wall.



Figs 5.22-5.28

Figs 5.22-5.24 Vaucheria dillwynii (Weber & Mohr)

C. Agardh. Germinating oospore in agar.

MEL 1049234 p.p.

Fig. 5.22 Oospore breaking through distal surface of oogonium. Note pigment spot entering siphon.

Fig. 5.23 Pigment spot migrating through siphon.

Fig. 5.24 Pigment spot beyond first branch of siphon.

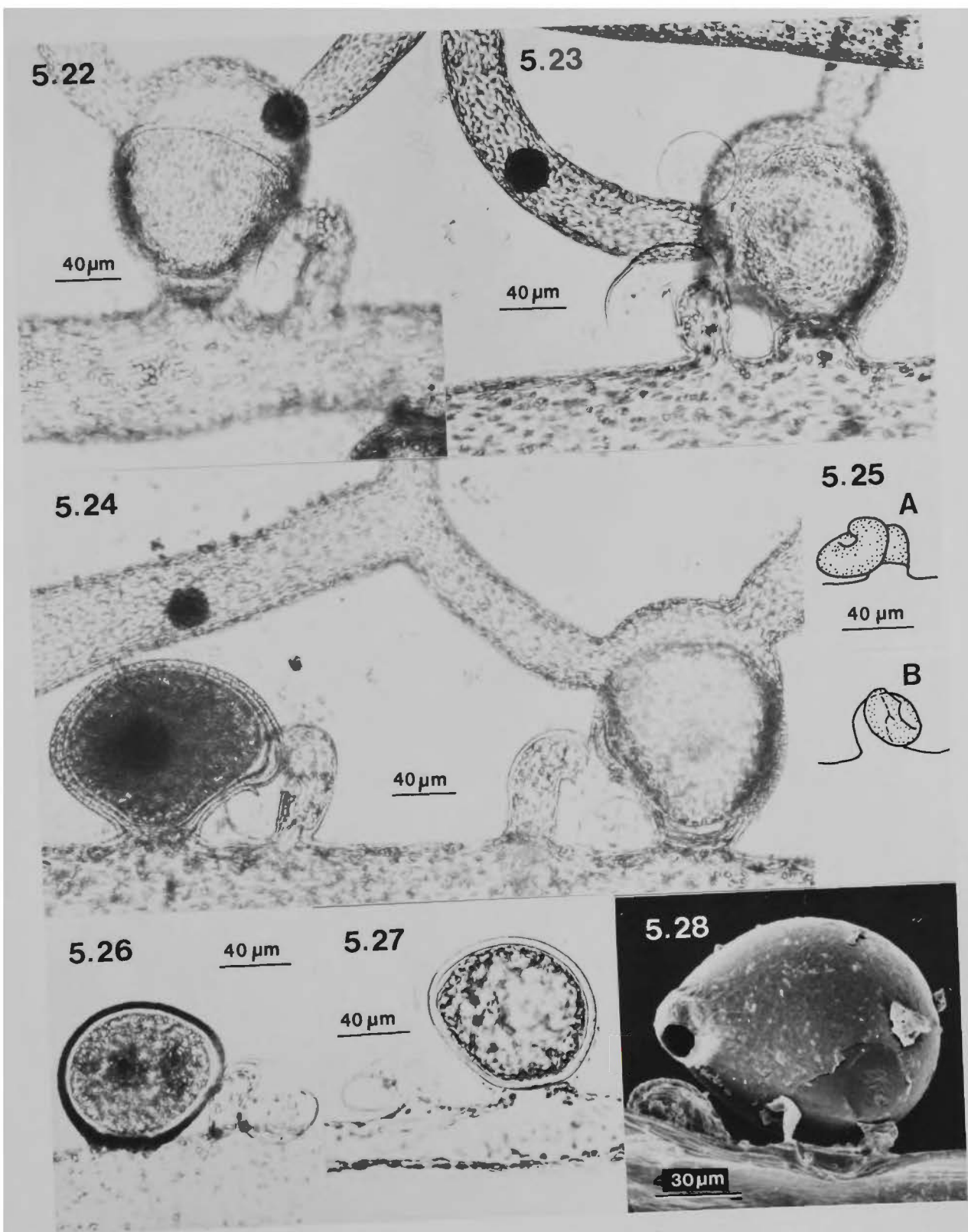
Figs 5.25-5.28 Vaucheria nanandra Christensen.

Fig. 5.25A,B Antheridia turning through more than a full circle. MEL 1049136.

Fig. 5.26 Oogonium with long axis and pore directed parallel with siphon. Note also contorted antheridium. MEL 1049102 p.p.

Fig. 5.27 Oogonium with long axis and pore directed parallel with siphon and contorted antheridium. MEL 1049137.

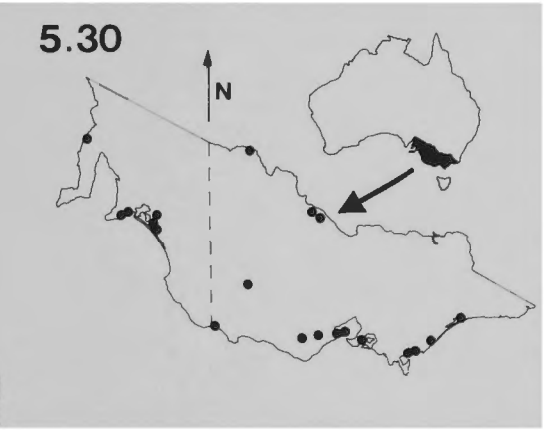
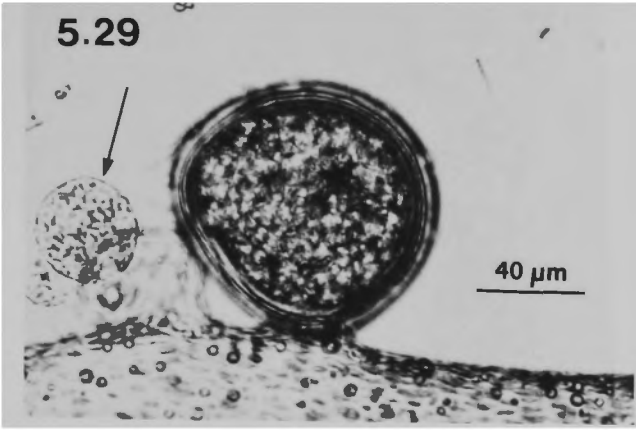
Fig. 5.28 Oogonium with relatively smooth wall. (fertilisation pore is deflexed more than usual). MEL 1049044 p.p.



Figs 5.29-5.30 Vaucheria nanandra Christensen.

Fig. 5.29 Oogonium with long axis and pore directed parallel with siphon and adjacent to a contorted antheridium. Note released mass of sperm (arrow). MEL 1049102 p.p.

Fig. 5.30 Known distribution of V. nanandra in south-eastern Australia.



Figs 5.31-5.38

Figs 5.31-5.34 Vaucheria glomerata Blum & Womersley.

A19102 (from herbarium slide material).

Fig. 5.31 Oogonium subtended by wall-bound cavity (arrow). Note oospore and proximal mass of cytoplasm.

Fig. 5.32 Antheridia in a monopodial cluster.

Fig. 5.33 Known distribution of V. glomerata in south-eastern Australia.

Fig. 5.34 Antheridium with cylindrical protuberances (large arrow). Note elongate wall-bound cavity (small arrow) subtending antheridium.

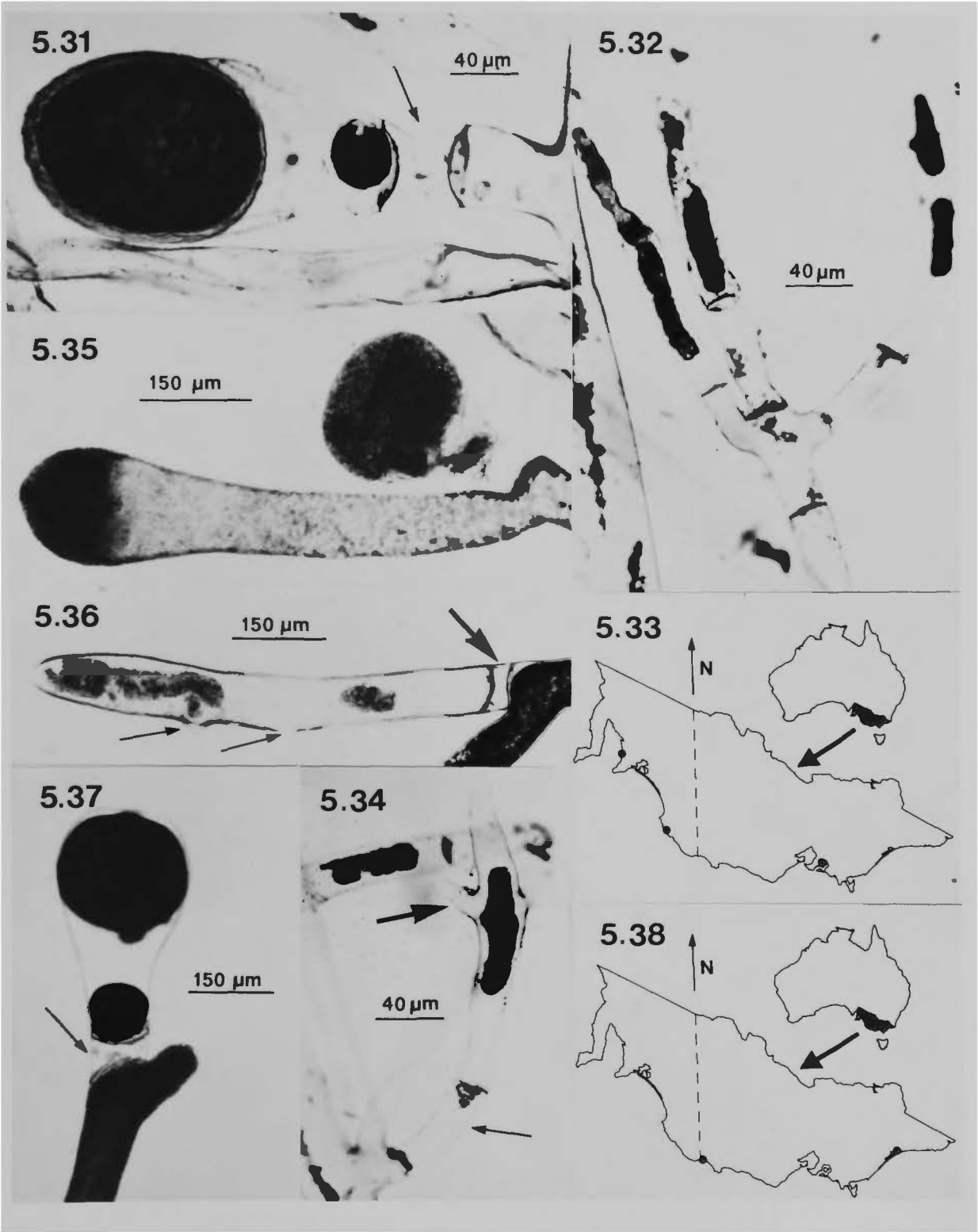
Figs 5.35-5.38 Vaucheria litorea Hofman & C. Agardh.

Fig. 5.35 Oogonium showing subsequent sympodial growth of siphon. MEL 1049199.

Fig. 5.36 Antheridium. Note relatively small lateral protuberances (small arrows) and subtending wall-bound cavity (large arrow). MEL 1049200.

Fig. 5.37 Oogonium with subtending wall-bound cavity (arrow) containing developing oospore and proximal mass of cytoplasm. MEL 1049199.

Fig. 5.38 Known distribution of V. litorea in south-eastern Australia.



Figs 5.39-5.46

Figs 5.39-5.40 Vaucheria litorea Hofman & C.Agardh.

Fig. 5.39 Oogonium. Note orientation. MEL 1049199.

Fig. 5.40 Sympodial cluster of antheridia. Note conical protuberance (arrow). MEL 1049200.

Figs 5.41-5.46 Vaucheria longicaulis Hoppaugh.

Fig. 5.41 Oospore in oogonium (lateral walls indistinct, proximal wall marked with arrow). Note absence of proximal mass of cytoplasm or subtending wall-bound cavity. (Siphon in background is not connected to the one supporting the oogonium.) MEL 1049204.

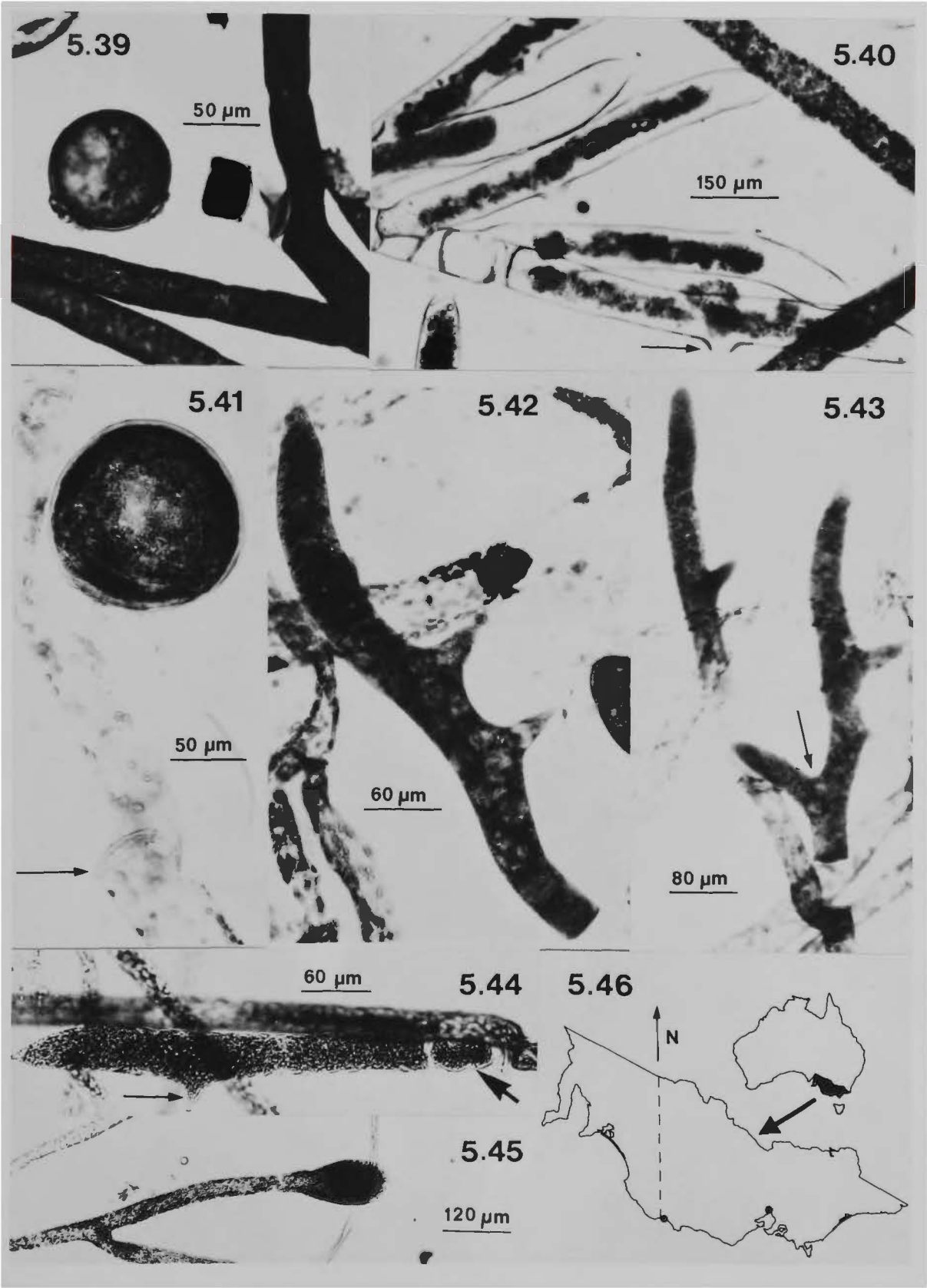
Fig. 5.42 Antheridium with large lateral protuberances. MEL 1049203.

Fig. 5.43 Antheridia. Note one is almost bifurcate (arrow). MEL 1049203.

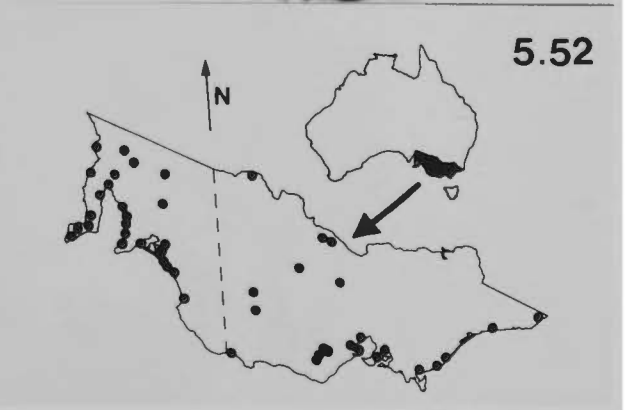
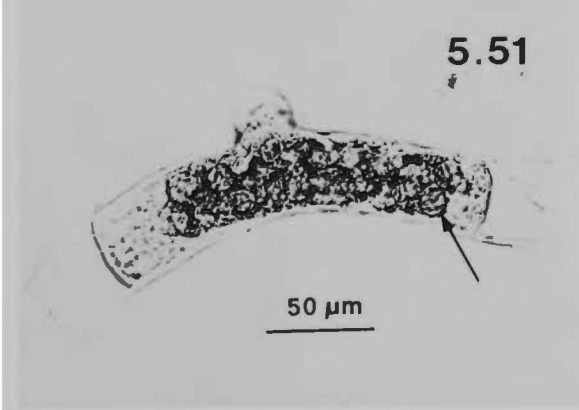
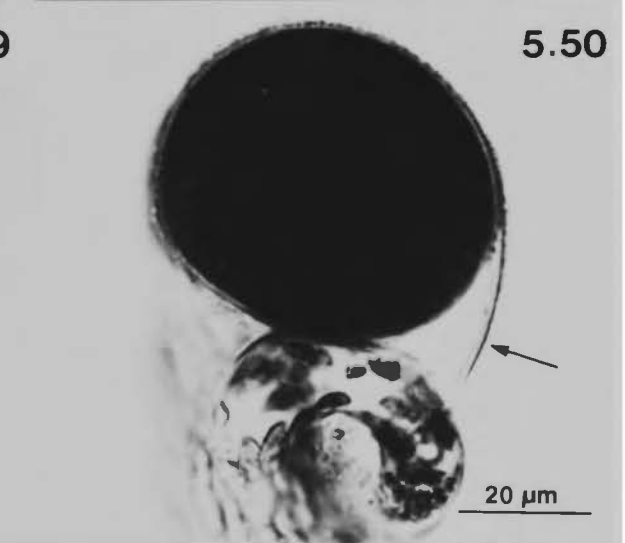
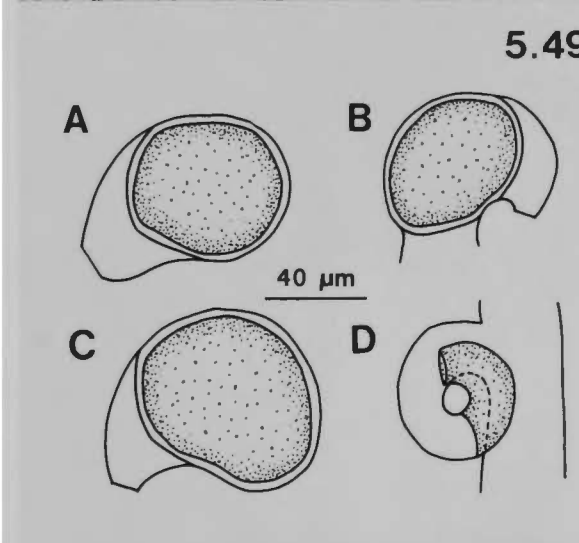
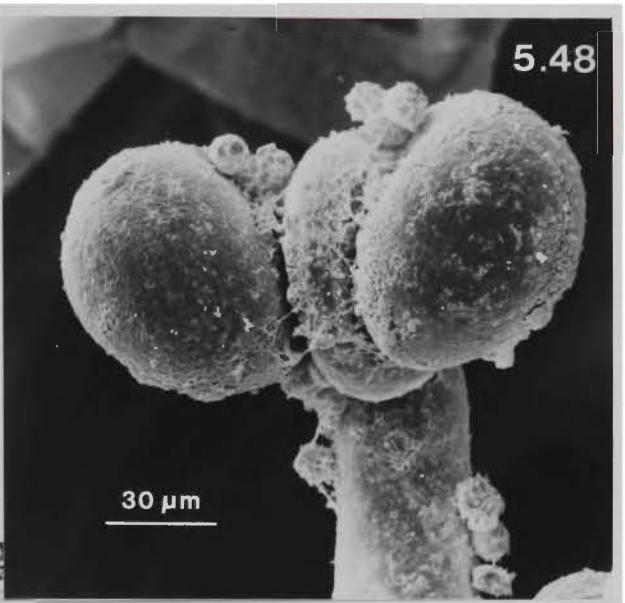
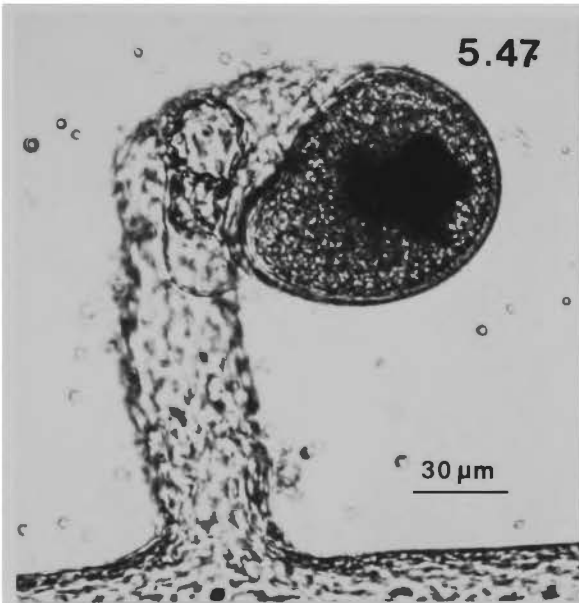
Fig. 5.44 Immature antheridium with relatively small lateral protuberance (small arrow). Note that subtending cell (large arrow) still contains cytoplasm. MEL 1049202.

Fig. 5.45 Developing oogonium. Note long oogonial pedicel. MEL 1049202.

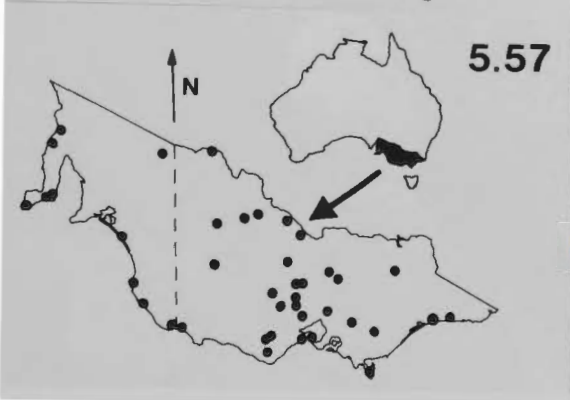
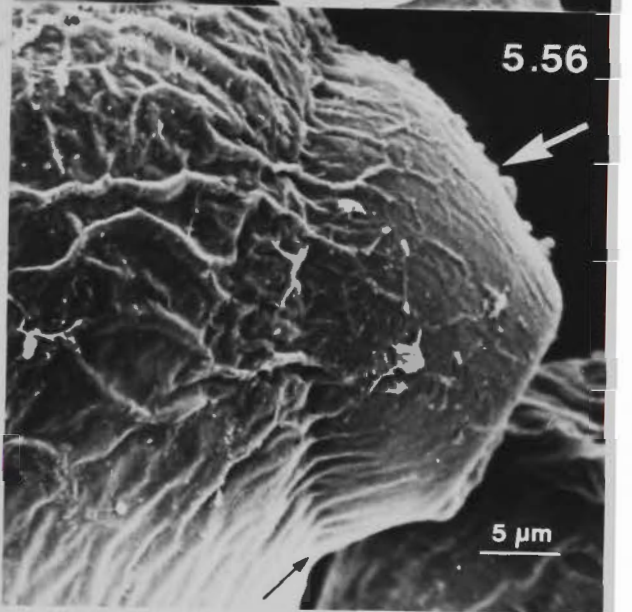
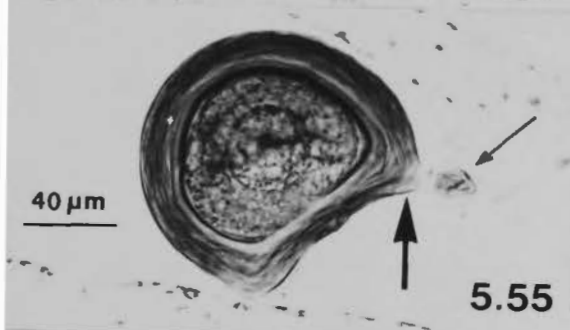
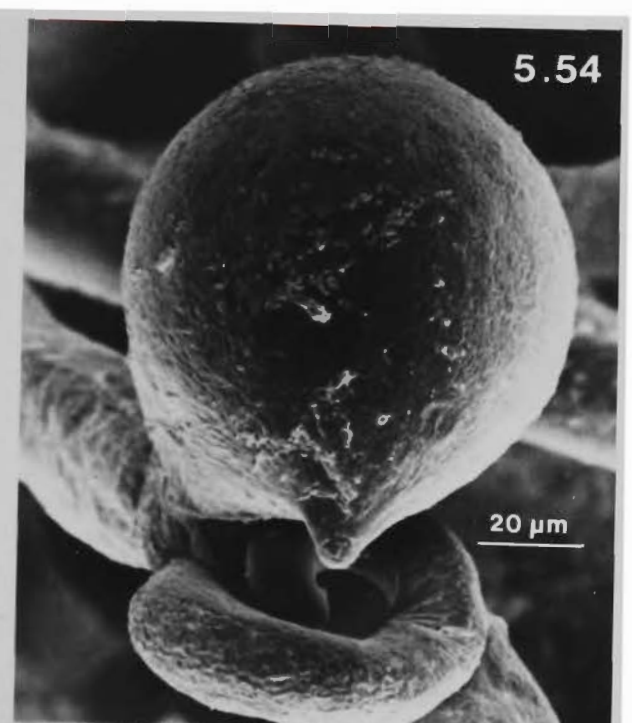
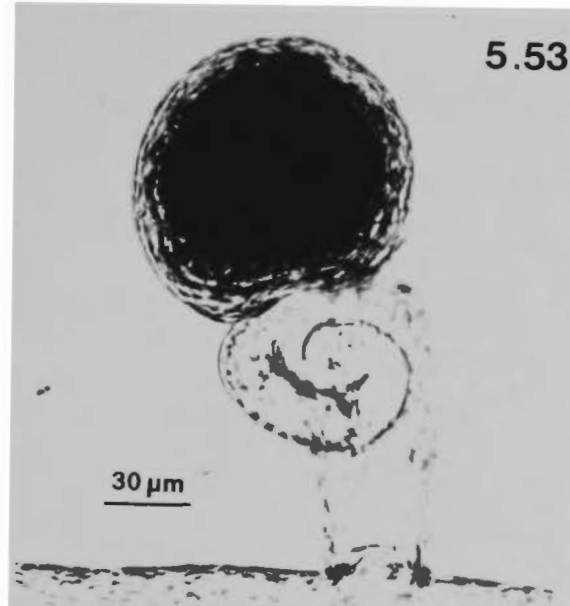
Fig. 5.46 Known distribution of V. longicaulis in south-eastern Australia.



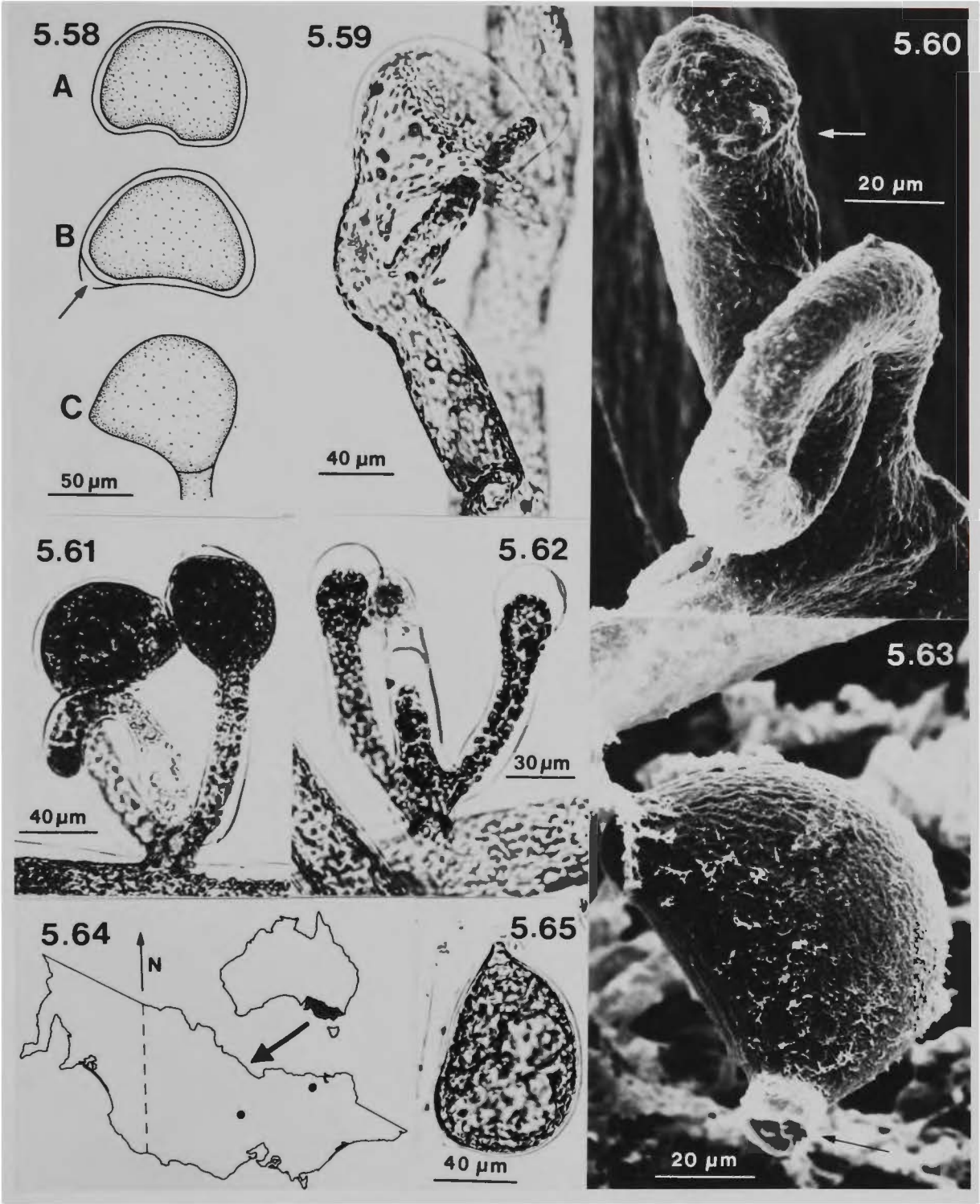
- Figs 5.47-5.52 Vaucheria erythrospora Christensen.
- Fig. 5.47 Gametophore with pendent oogonium (no distal cavity evident) and antheridium. MEL 1049065.
- Fig. 5.48 Gametophore with pendent oogonia and antheridium (some debris attached). MEL 1049062.
- Fig. 5.49A-C Oogonia showing variation in shape of distal oogonial cavity. A, MEL 1049068; B, MEL 1049070; C, MEL 1049068.
- Fig. 5.49D Antheridium. Note that it is relatively 'tightly' coiled. MEL 1049135 p.p.
- Fig. 5.50 Gametophore with oogonium. Note distal oogonial cavity (arrow). MEL 1049112.
- Fig. 5.51 ^{wall formation resembling} ~~A~~kinete in vegetative siphon. Note spherical (?fungal) inclusions (arrow). MEL 1049409.
- Fig. 5.52 Known distribution of V. erythrospora in south-eastern Australia.



- Figs 5.53-5.57 Vaucheria frigida (Roth) C. Agardh.
- Fig. 5.53 Gametophore with oogonium borne distally
to antheridium. MEL 1049268.
- Fig. 5.54 Gametophore (with adventitious gametophore
behind oogonium) showing oospore with distal
protuberance directed through antheridium.
MEL 1049268.
- Fig. 5.55 Oospore with thick, flaky wall and distal
protuberance (large arrow). Note oospore
wall material extruded through fertilisation
pore (small arrow). MEL 1049888.
- Fig. 5.56 Distal protuberance of oospore (large arrow).
Note the probable edge of oogonial wall
(small arrow). MEL 1049268.
- Fig. 5.57 Known distribution of V. frigida in
south-eastern Australia.



- Figs 5.58-5.65 Vaucheria gardneri Collins.
- Fig. 5.58A-C Oogonia showing variation in shape and presence (arrow) or absence of distal oogonial cavity. A, MEL 1049084; B, MEL 1049083; C, MEL 1049082.
- Fig. 5.59 Gametophore with long peduncle. Note erect antheridial pedicel and erect, proximally curved oogonial pedicel. MEL 1049083.
- Fig. 5.60 Gametophore with short peduncle. Note erect oogonial pedicel (arrow) with oogonia missing. (Antheridial pedicel is more curved than usual, probably contracting during preparation of mount.) MEL 1049183 p.p.
- Fig. 5.61 Gametophore with short peduncle . Note erect antheridial pedicel and long oogonial pedicels. MEL 1049082.
- Fig. 5.62 Gametophore with short peduncle. Note oogonial pedicel curved proximally and almost parallel with antheridial pedicel. MEL 1049082.
- Fig. 5.63 Detached oogonium with small part of pedicel (arrow). MEL 1049183 p.p.
- Fig. 5.64 Known distribution of V. gardneri in south-eastern Australia.
- Fig. 5.65 Oogonium. Note shape and distal prominence. MEL 1049083.



Figs 5.66-5.71 Vaucheria geminata (Vaucher) de Candolle.

Fig. 5.66 Gametophore showing erect oogonium borne on straight pedicel, and proximally erect antheridial pedicel (antheridial pedicel is more curved than usual). MEL 1049093 p.p.

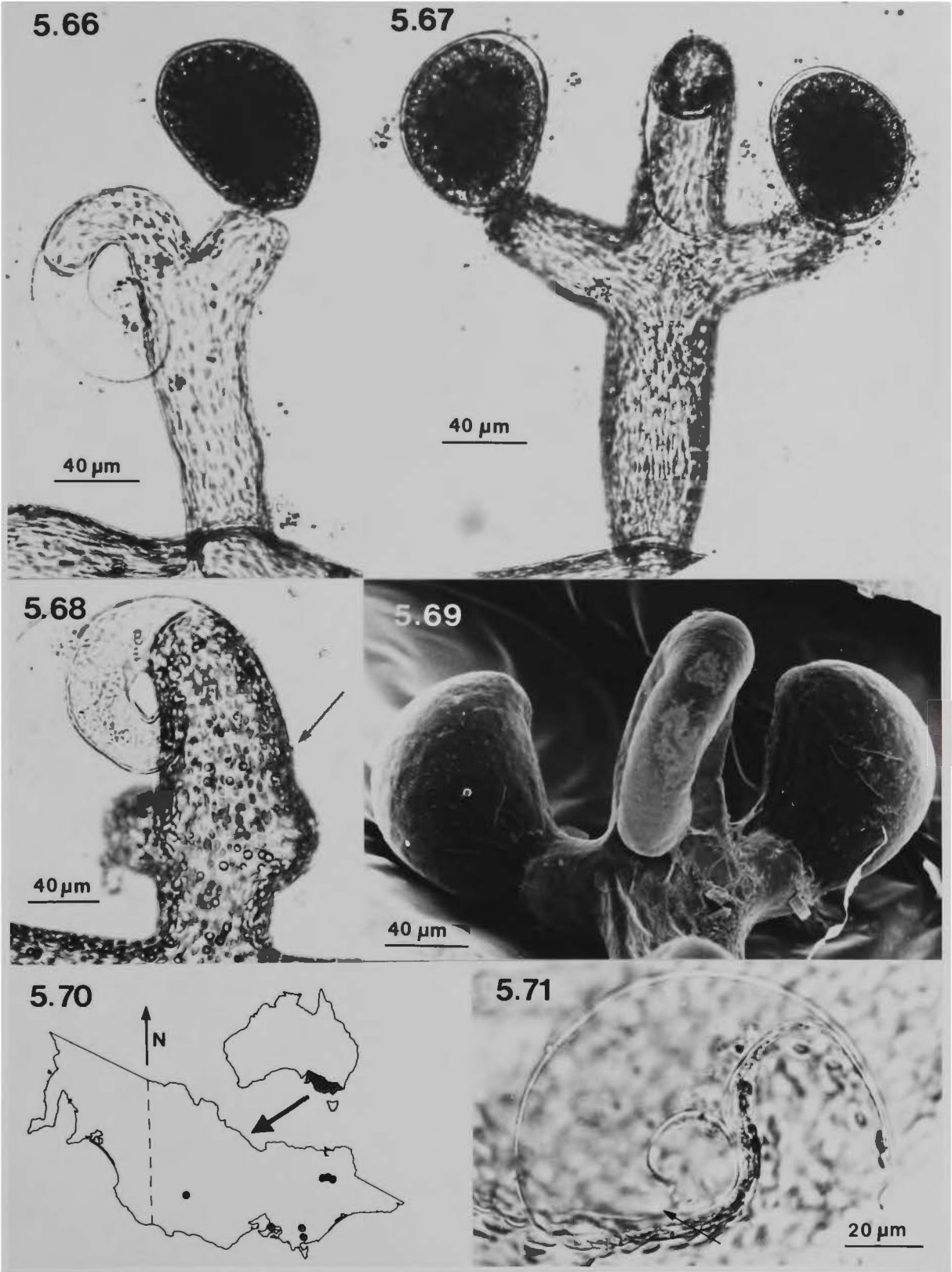
Fig. 5.67 Gametophore showing erect oogonia (somewhat flattened adaxially) and antheridial pedicel, and straight oogonial pedicel. MEL 1049093 p.p.

Fig. 5.68 Gametophore showing swollen peduncle at insertion of oogonial pedicels (arrow). MEL 1049089.

Fig. 5.69 Gametophore showing erect oogonia and antheridial pedicel, and circinate-cylindrical antheridium. MEL 1049093 p.p.

Fig. 5.70 Known distribution of V. geminata in south-eastern Australia.

Fig. 5.71 Antheridium showing single terminal antheridial pore (arrow). MEL 1049089.



Figs 5.72-5.77 Vaucheria gyrogyyna sp. nov.

Fig. 5.72 Gametophore in plane transverse to the peduncle. Note that the oogonial axis of symmetry is in the plane of the picture, and that the antheridium arises out of it. MEL 1049160.

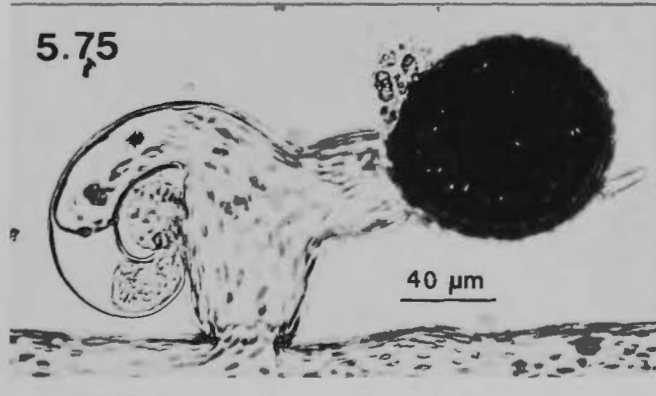
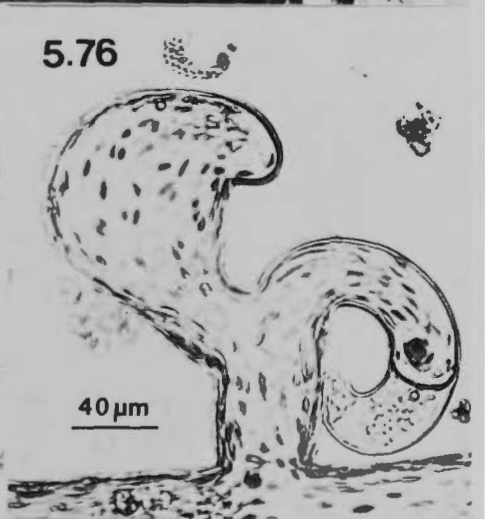
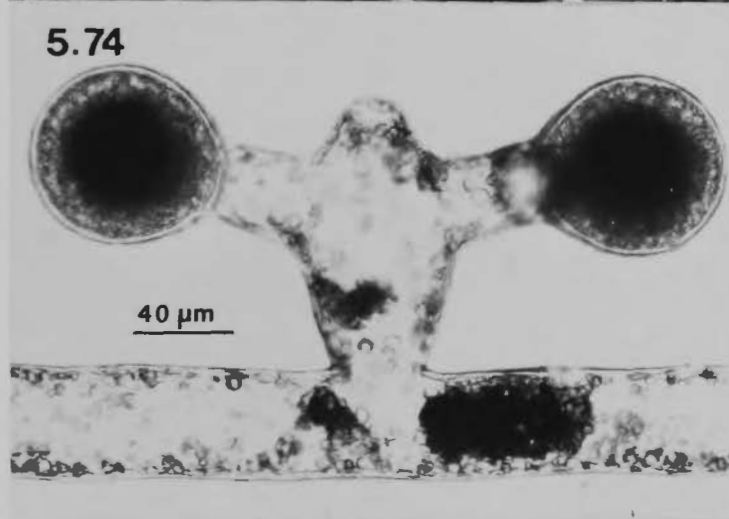
Fig. 5.73 Gametophore showing oogonium nearly perpendicular to the plane of the antheridium. MEL 1049160.

Fig. 5.74 Gametophore showing two oogonia with pore (not in field of view) directed out from the picture. Note that the oogonium and oogonial pedicels are in a plane transverse to the peduncle. MEL 1049160.

Fig. 5.75 Gametophore showing one oogonium with pore (not in field of view) directed out from the picture. MEL 1049160.

Fig. 5.76 Gametophore showing an erect oogonium with deflexed distal portion. MEL 1049160.

Fig. 5.77 Oogonium showing distal oogonial cavity (arrow). MEL 1049165.



Figs 5.78-5.84

Fig. 5.78 Vaucheria gyrogyyna sp. nov. Known
distribution in south-eastern Australia.

Figs 5.79-5.81 Vaucheria lii Rieth. MEL 1049169 p.p.
(little material of this species was
available for illustration).

Fig. 5.79 Detached oospore released by breakdown of
oogonial pedicel wall near peduncle (large
arrow). Note circinate distal oogonial
cavity (small arrow).

Fig. 5.80 Gametophore showing erect oogonia and
septum in peduncle (arrow). Note that
there is no cytoplasm distal to the septum.

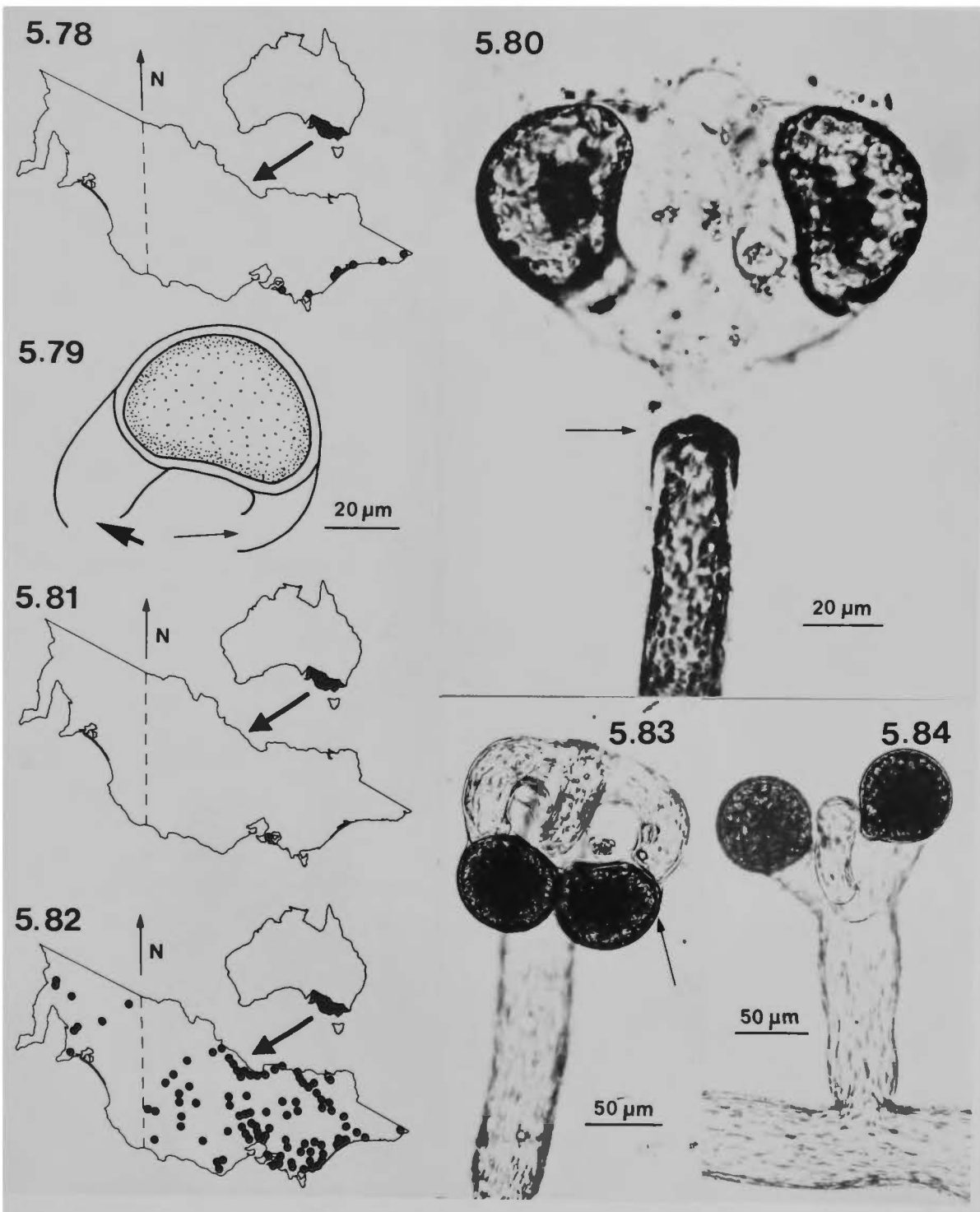
Fig. 5.81 Known distribution of V. lii in
south-eastern Australia.

Figs 5.82-5.84 Vaucheria prona Christensen.

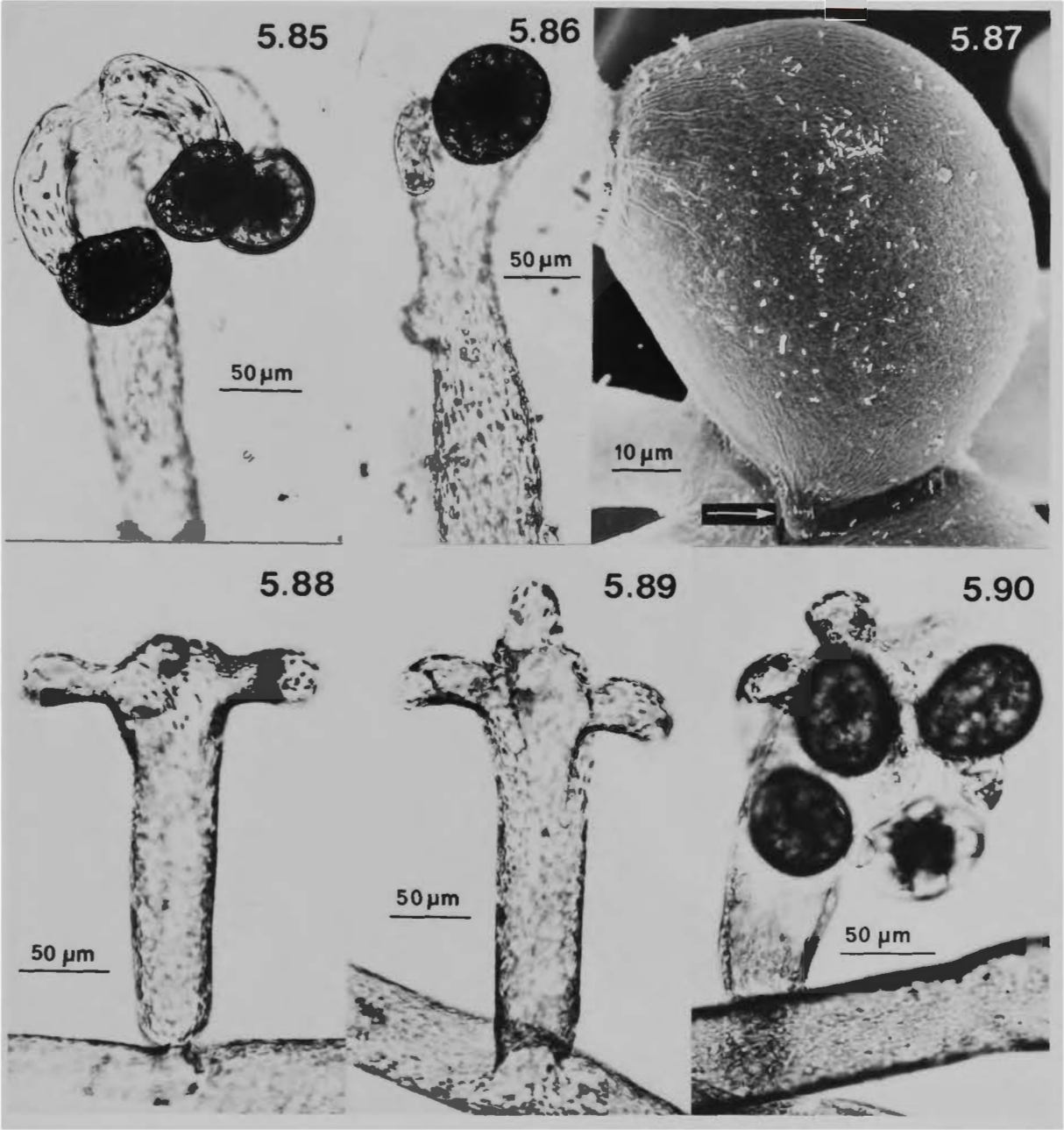
Fig. 5.82 Known distribution of Vaucheria prona
in south-eastern Australia.

Fig. 5.83 Gametophore showing orientation of oogonia
and oogonial pedicels. Note oospore wall
(arrow) indistinct. MEL 1049269.

Fig. 5.84 Gametophore showing orientation of oogonia
and oogonial pedicels. MEL 1049233 p.p.



- Figs 5.85-5.90 Vaucheria prona Christensen.
- Fig. 5.85 Gametophore showing orientation of oogonia
and oogonial pedicels. MEL 1049269.
- Fig. 5.86 Gametophore showing orientation of oogonia
and oogonial pedicels. MEL 1049233 p.p.
- Fig. 5.87 Oogonium with small distal prominence
(arrow). MEL 1049269.
- Fig. 5.88 Gametophore without oogonia showing
orientation of two oogonial pedicels
(antheridium not in focal plane).
MEL 1049269.
- Fig. 5.89 Gametophore without oogonia showing
orientation of three oogonial pedicels
(antheridium not in focal plane).
MEL 1049269.
- Fig. 5.90 Gametophore showing oogonia clustered
near antheridium. MEL 1049269.



Figs 5.91-5.97

Figs 5.91-5.95 Vaucheria pseudogeminata Dangeard.

Fig. 5.91 Gametophore showing erect oogonium with a slightly reflexed distal portion.
MEL 1049190.

Fig. 5.92 Gametophore showing erect oogonia and conical distal oogonial cavity. MEL 1049191.

Fig. 5.93A,B Oogonia with oospores showing variation in shape of oogonium and oogonial cavity.
MEL 1049358.

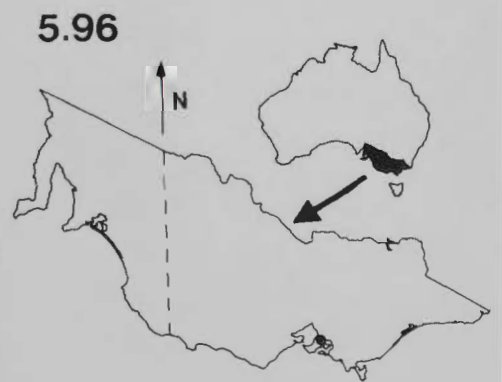
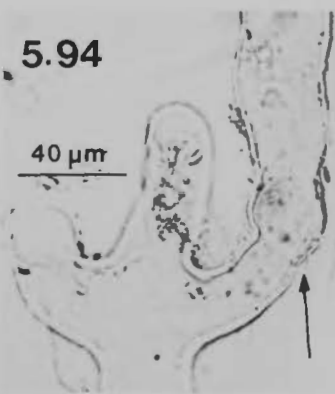
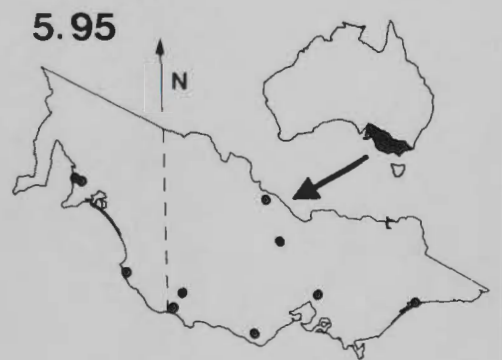
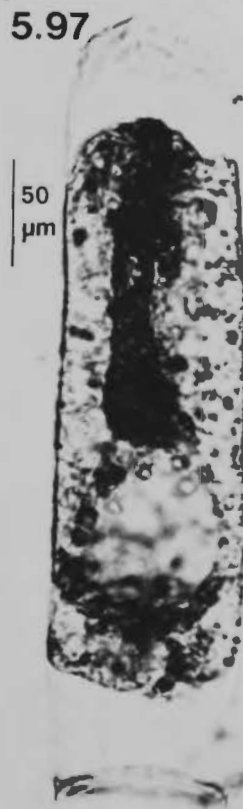
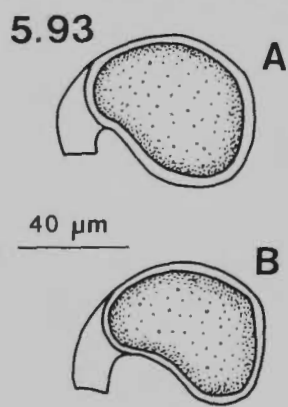
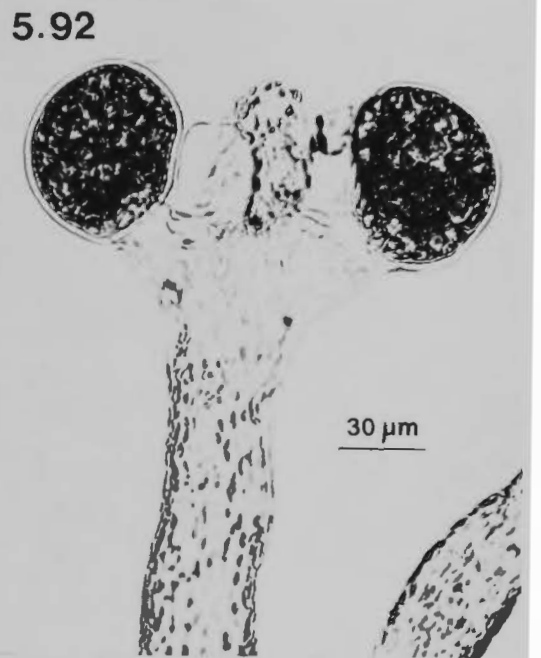
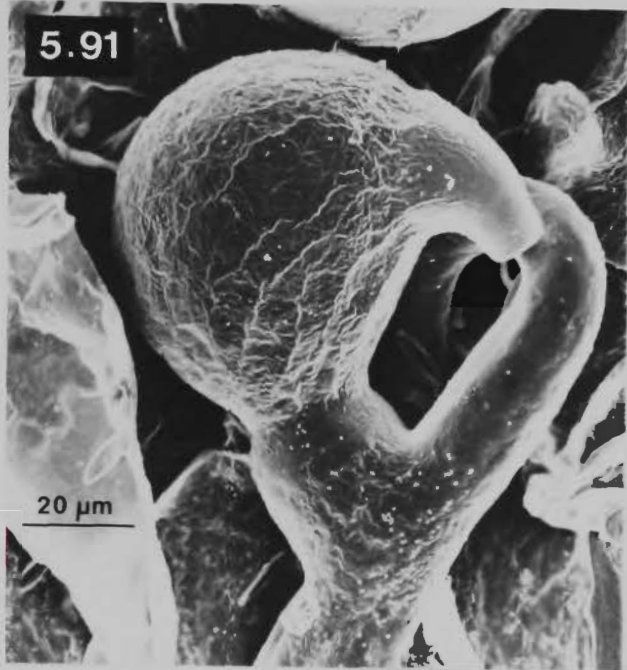
Fig. 5.94 Adventitious gametophores (arrow) arising from oogonial pedicel. MEL 1049187 p.p.

Fig. 5.95 Known distribution of V. pseudogeminata in south-eastern Australia.

Figs 5.96-5.97 Vaucheria subarechavaletae Borge.
MEL 1049192.

Fig. 5.96 Known distribution of V. subarechavaletae in south-eastern Australia.

Fig. 5.97 Straight-cylindrical antheridium.



Figs 5.98-5.104

Figs 5.98-5.100 Vaucheria subarechavaletae Borge.

MEL 1049192.

Fig. 5.98 Immature gametophore.

Fig. 5.99 Gametophore with mature antheridium and developing oogonium.

Fig. 5.100 Gametophore with mature antheridium and developing oogonium. Note that oogonium is erect and radially symmetrical.

Figs 5.101-5.104 Vaucheria uncinata Kützing.

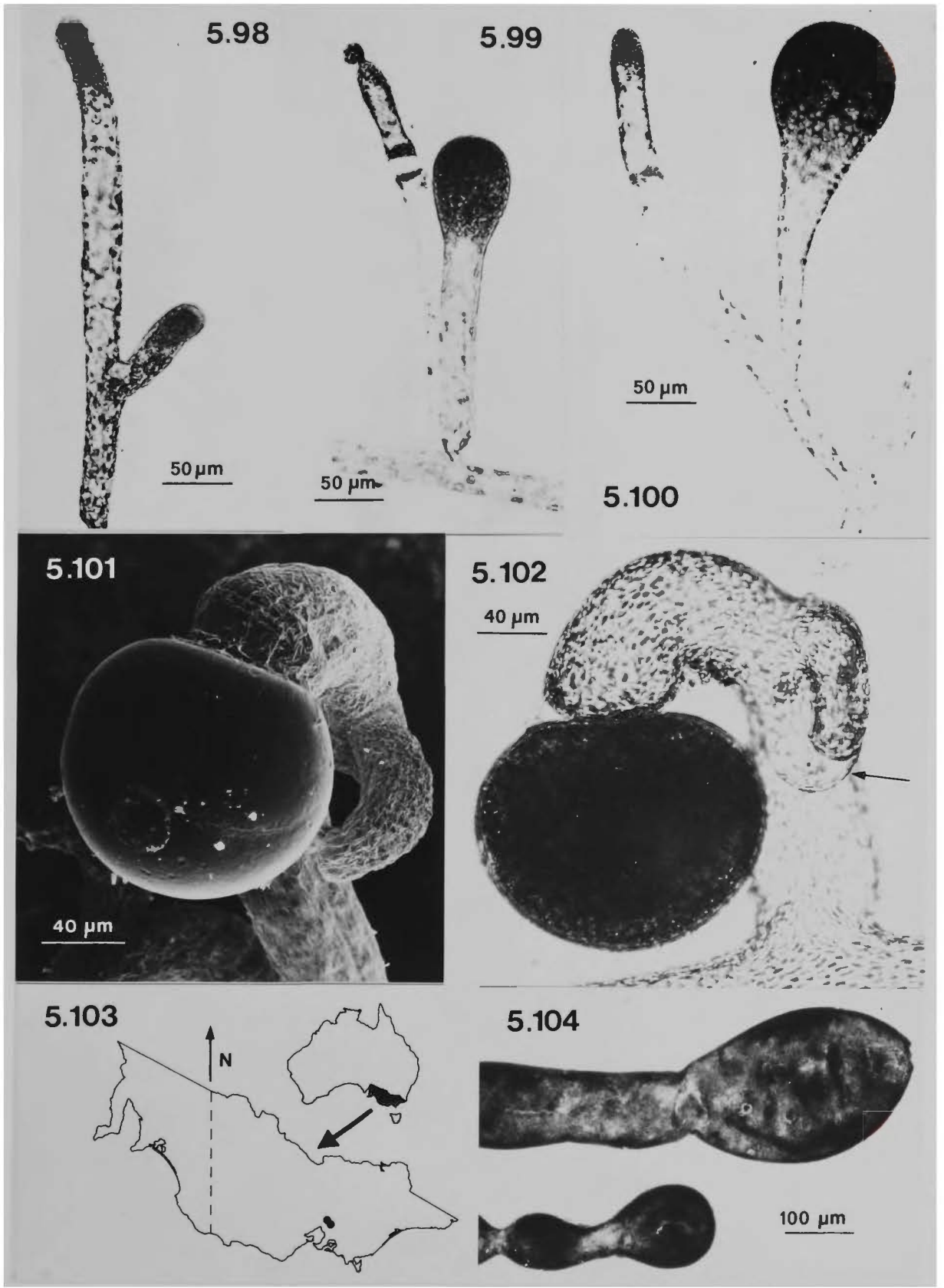
MEL 1049195.

Fig. 5.101 Gametophore with radially symmetrical oogonium and no distal prominence (siphons became wrinkled during preparation of mount).

Fig. 5.102 Gametophore showing radially symmetrical oogonium with no distal prominence and short cylindrical antheridium (arrow).

Fig. 5.103 Known distribution of V. uncinata in south-eastern Australia.

Fig. 5.104 Constrictions in siphon produced when plants grown in media with high salinity and pH.



Figs 5.105-5.111

Figs 5.105-5.108 Vaucheria aversa Hassall.

Fig. 5.105 Oogonium with reflexed distal portion and developing oospore. MEL 1049106.

Fig. 5.106 Oogonium with oospore leaving a peripheral cavity. Note reflexed distal portion of oogonium and antheridium (arrow) directed towards it. MEL 1049105.

Fig. 5.107 Antheridium directed towards oogonium (both immature). MEL 1049090 p.p.

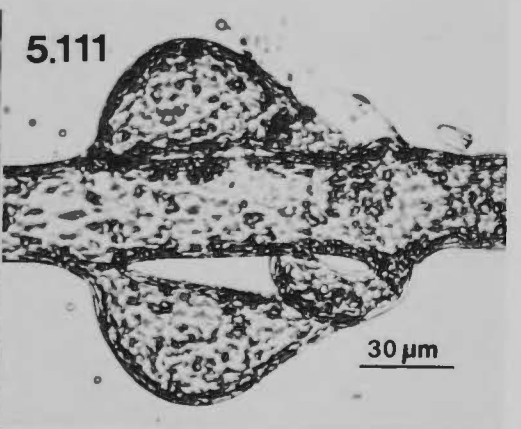
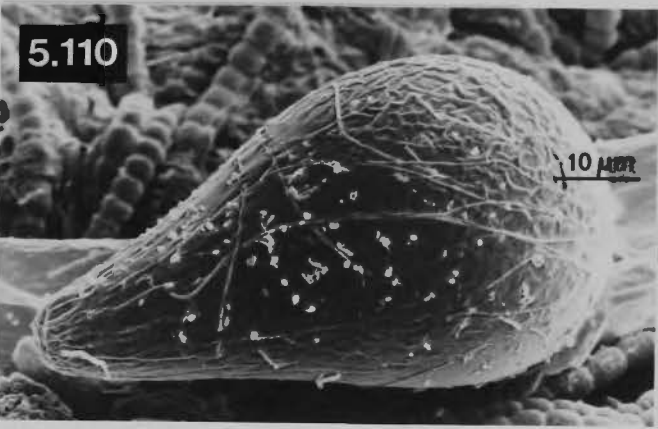
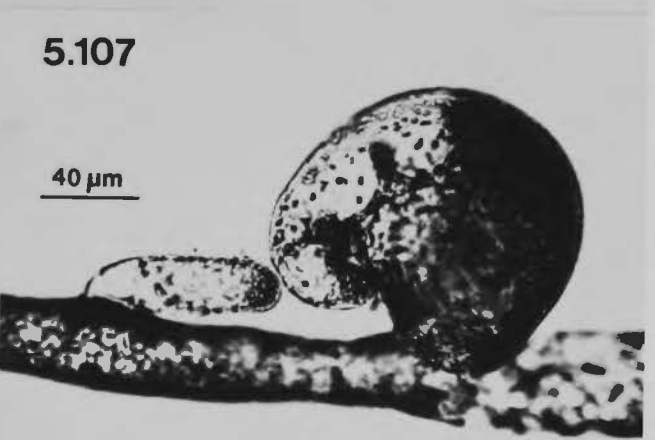
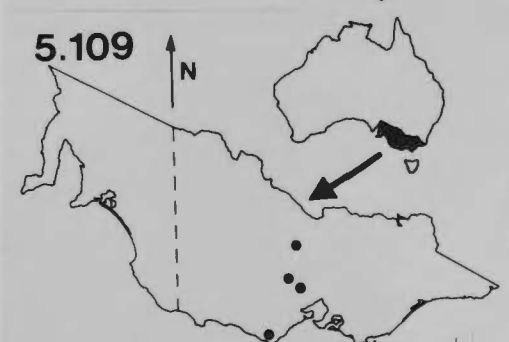
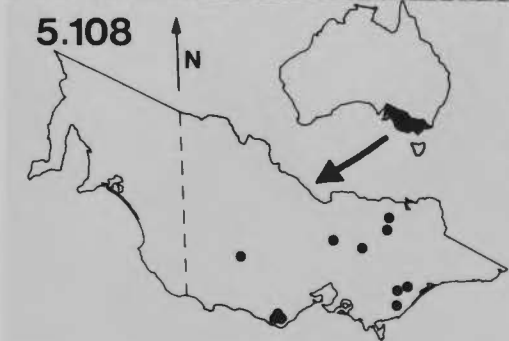
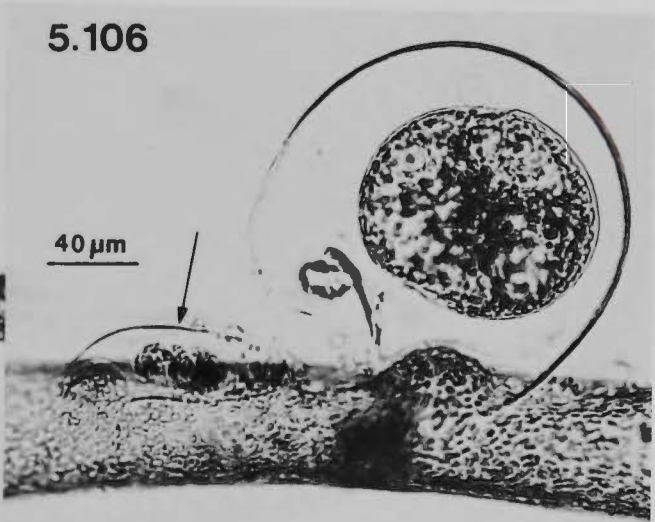
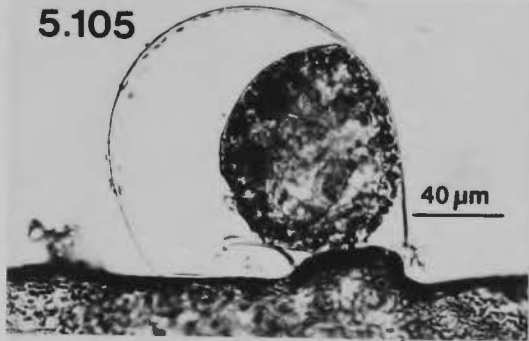
Fig. 5.108 Known distribution of V. aversa in south-eastern Australia.

Figs 5.109-5.111 Vaucheria bicornigera sp. nov.
MEL 1049113.

Fig. 5.109 Known distribution of V. bicornigera in south-eastern Australia.

Fig. 5.110 Oogonium. Note elongate-obovoid shape.

Fig. 5.111 Oogonium and antheridium (both immature) in opposite pairs and both parallel to the siphon. Note elongate antheridia directed towards oogonia.



Figs 5.112-5.119

Figs 5.112-5.115 Vaucheria bicornigera sp. nov. MEL 1049113.

Fig. 5.112 Oogonia and antheridia in opposite pairs.

Fig. 5.113 Group of oogonia near an opposite pair of antheridia.

Fig. 5.114 Single oogonium near opposite pair of antheridia.

Fig. 5.115 Antheridium produced at apex.

Figs 5.116-5.119 Vaucheria prolifera Dangeard. MEL 1049117
p.p.

Fig. 5.116 Oogonium near disintegrated antheridium at apex of siphon. Note unilateral arrangement of gametangia and short antheridial pedicel (arrow).

Fig. 5.117A,B Antheridia (arrows) and oogonia. Note little to no antheridial pedicel present and stout antheridia.

Fig. 5.118 Known distribution of V. prolifera in south-eastern Australia.

Fig. 5.119 Oogonium and disintegrated antheridium (arrow).

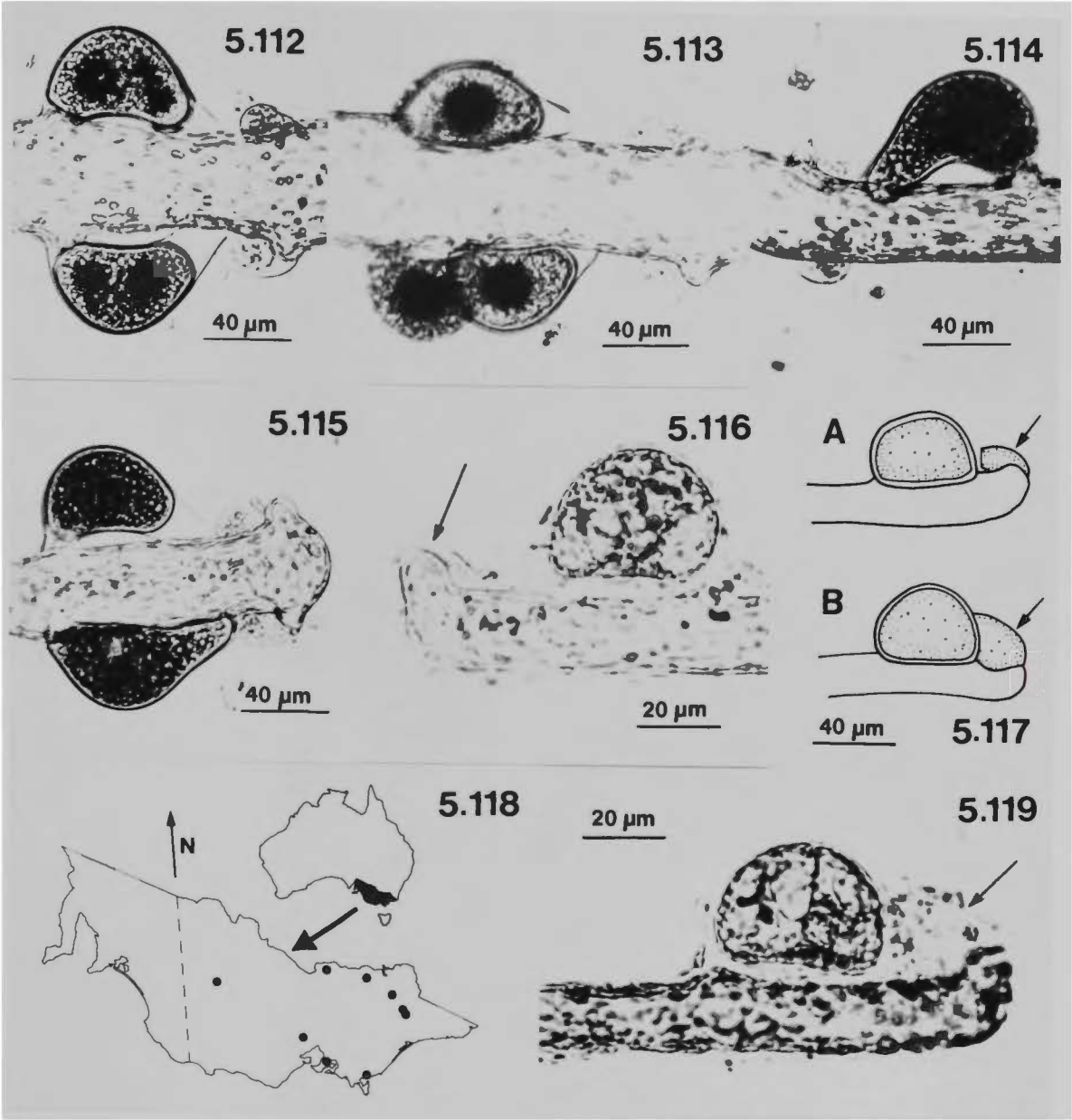
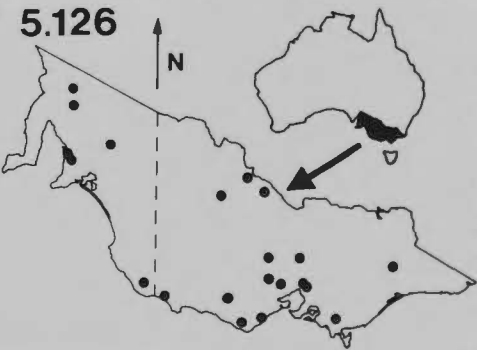
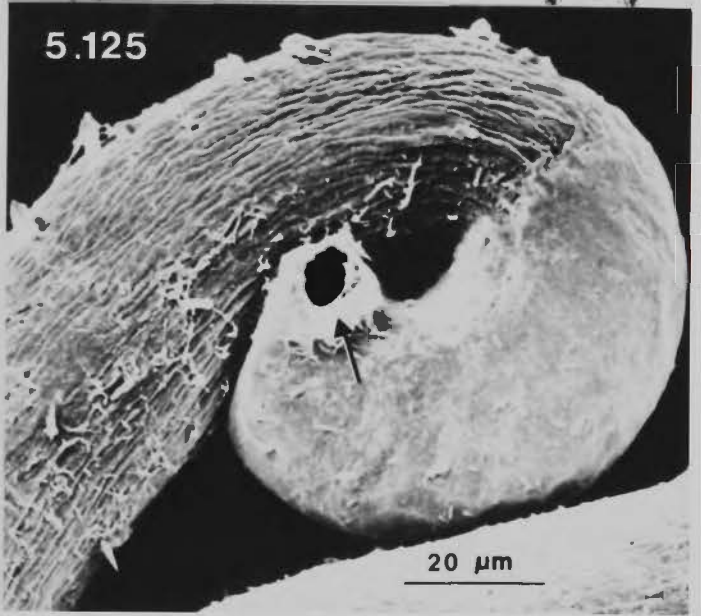
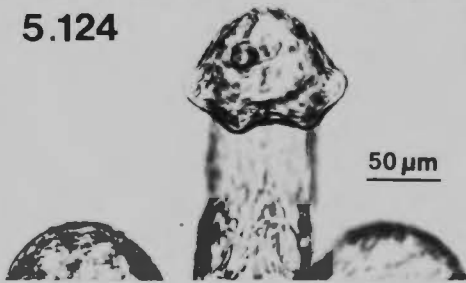
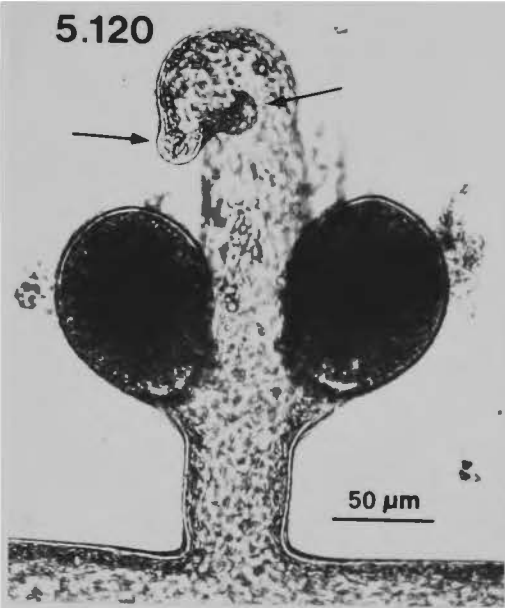


Fig. 5.120-5.126 Vaucheria canalicularis (Linnæus) Christensen.

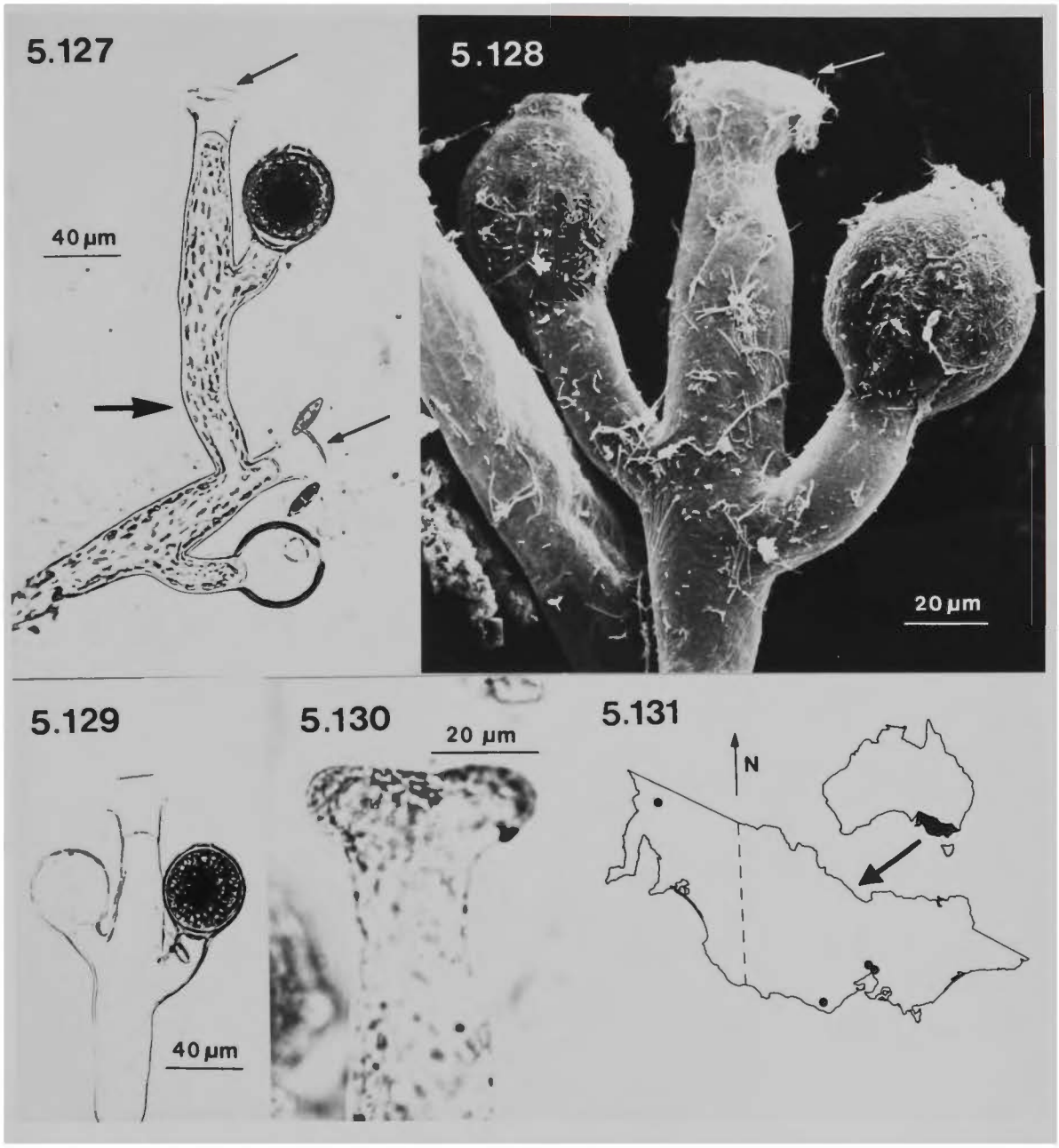
- Fig. 5.120 Gametophore showing immature circinate antheridium with two lateral swellings (arrows). MEL 1049051.
- Fig. 5.121 Gametophore showing dehiscent antheridium with two lateral pores (arrows). MEL 1049051.
- Fig. 5.122 Dehiscent antheridium which appears to have one terminal pore (arrow). MEL 1049054 p.p.
- Fig. 5.123 Aplanosporangium. MEL 1049134 p.p.
- Fig. 5.124 Immature antheridium with two lateral swellings. Note that in this case, each swelling has two lobes. MEL 1049051.
- Fig. 5.125 Antheridium with one lateral pore (arrow) in view. MEL 1049051.
- Fig. 5.126 Known distribution of V. canalicularis in south-eastern Australia.



Figs 5.127-5.131 Vaucheria cruciata (Vaucher) de Candolle.

MEL 1049058.

- Fig. 5.127 Adventitious gametophore (large arrow).
Note straight biporic antheridia on both
gametophores (small arrows).
- Fig. 5.128 Gametophore with deltoid-pulvinate
antheridium (arrow).
- Fig. 5.129 Gametophore with two erect oogonia.
- Fig. 5.130 Immature antheridium with two lateral lobes.
- Fig. 5.131 Known distribution of V. cruciata in
south-eastern Australia.

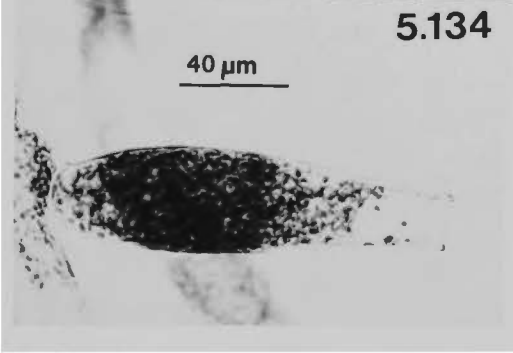
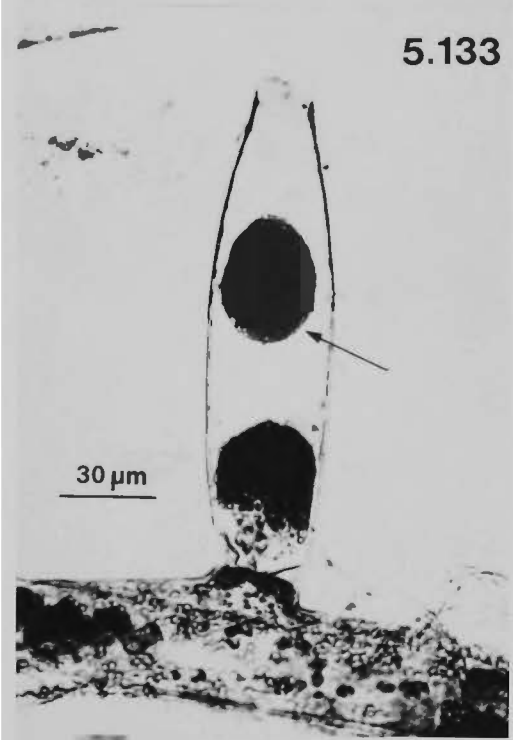
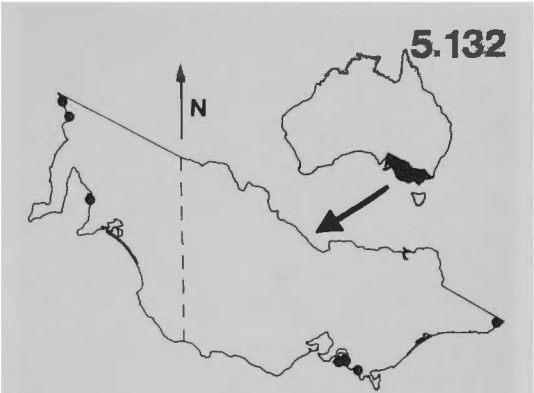


Figs 5.132-5.134 Vaucheria conifera Christensen.

Fig. 5.132 Known distribution of V. conifera
in south-eastern Australia.

Fig. 5.133 Antheridium with globular mass of sperm
(arrow) and relatively large terminal
opening. MEL 1049407.

Fig. 5.134 Antheridium. Note shape. MEL 1049408.



Figs 5.135-5.142

Figs 5.135-5.136 Vaucheria conifera Christensen.

MEL 1049408.

Fig. 5.135 Oogonium with globose oospore and obtuse base.

Fig. 5.136 Immature oogonium with obtuse base.

Figs 5.137-5.142 Vaucheria velutina C. Agardh.

Fig. 5.137 Immature oogonium with acute base.

MEL 1049128.

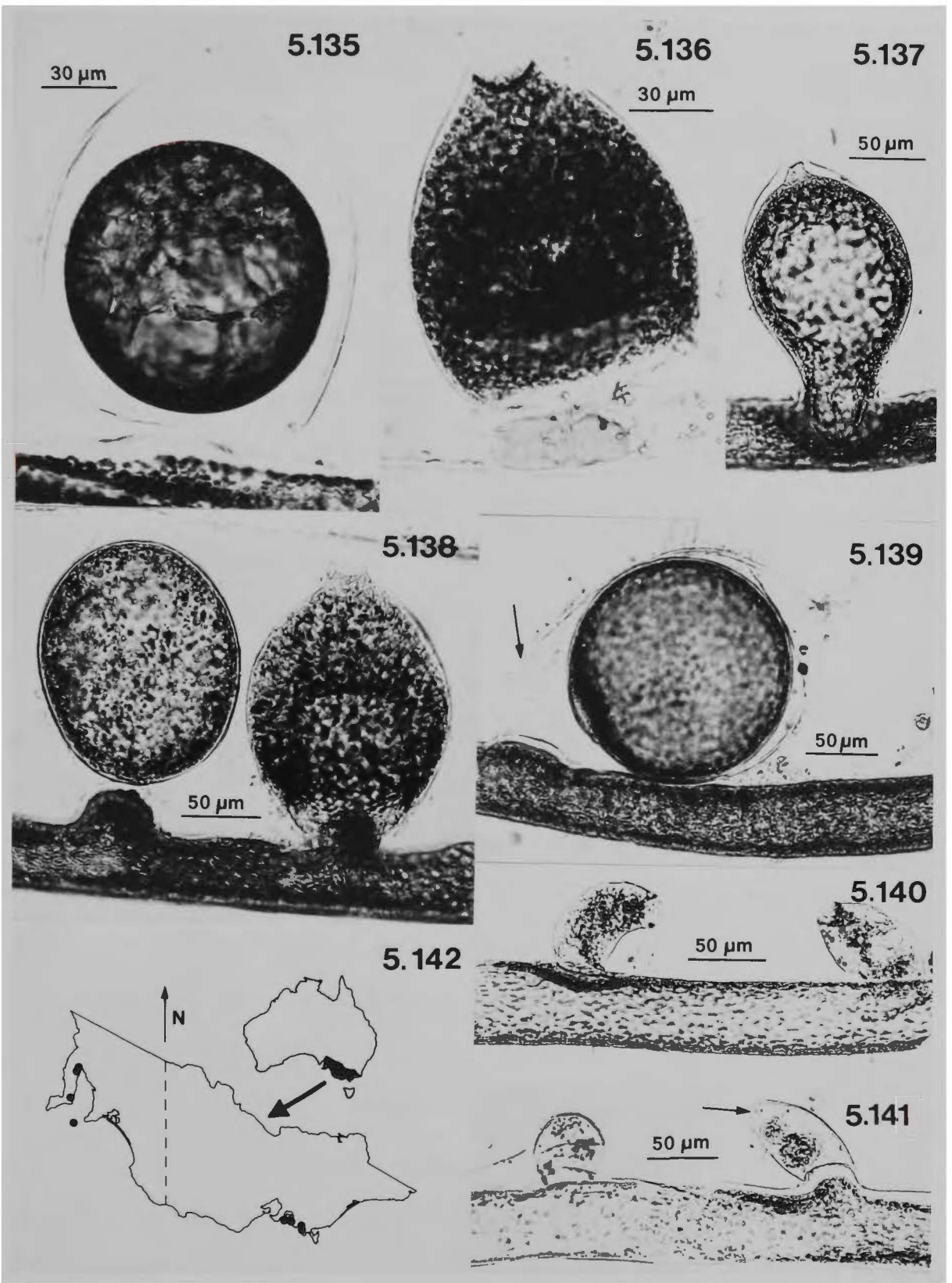
Fig. 5.138 Oogonium with oospore, next to unfertilised oogonium. MEL 1049128.

Fig. 5.139 Oogonium with oospore. Note that it is reflexed at base (arrow). MEL 1049128.

Fig. 5.140 Antheridia. Note variation in shape. MEL 1049129.

Fig. 5.141 Antheridia. Note variation in shape and relatively small terminal pore (arrow).

Fig. 5.142 Known distribution of V. velutina in south-eastern Australia.



CHAPTER SIX
CONCLUDING REMARKS

The south-eastern Australian algal flora includes 24 species of Vaucheria, representing six of the nine sections in the genus. This includes less than half of the species of Vaucheria worldwide, and consequently further research is needed to confirm the conclusions about sectional, and in some cases species, delineations within the genus.

Although intensive studies were carried out on the stability of taxonomic characters in species from the sections Corniculatae (Walz) Heering emend. Entwisle and Racemosae (Walz) Entwisle, some species concepts are still unclear. Limited material of V. borealis Hirn was available for study and its delineation and diagnostic features require further attention. The variation in antheridial shape following dehiscence in V. dillwynii (Weber & Mohr) C. Agardh (and also V. prolifera Dangeard) should be studied further. No material unequivocally referable to V. terrestris (Vaucher) de Candolle, V. terrestris var major (Wille) Rieth and V. racemosa (Vaucher) de Candolle was available, so culture and field studies are needed to evaluate taxonomic characters and formulate species concepts for these taxa.

From the monograph, a number of other taxonomic problems arose which require further study. The circumscription of V. geminata varies widely between authors (cf., Christensen 1969 and Jao 1936), encroaching on that of V. taylorii Blum, V. gardneri Collins and V. prona Christensen. Furthermore, although Christensen (1969) has attempted to characterise the plants which Vaucher (1803) called V. geminata, there seem to be some discrepancies between the descriptions of Vaucher (1803) and Christensen (1969) and thus both the identity of the plants described in the protologue and the circumscription of V. geminata needs

to be clarified.

The variation in size and shape of oogonial cavities also should be studied further. Species such as V. erythrospora and V. gyrogynea usually can be characterised by the presence of a distal oogonial cavity, but in some culture isolates, it is totally lacking. Vaucheria gardneri can have either a small distal oogonial cavity, or none at all. As most oogonia which regularly have distal cavities are attenuate at the distal end, oogonial shape should also be assessed as a taxonomic character. There are other characters in need of critical evaluation, and intensive studies of species in culture and in field populations are needed in most sections. The distinction between antheridia with lateral pores and those with a single terminal pore should be evaluated with respect to its use as a diagnostic character for the sections Vaucheria and Racemosae. All sectional characters should be assessed in those species not found in south-eastern Australia to confirm the conclusions of this study.

A number of species concepts have been modified following the studies on south-eastern Australian species. The intensive studies of taxonomic characters in the V. bursata (O.F. Müller) C. Agardh, V. dillwynii and V. prona Christensen complexes have resulted in the confirmation of some authors' concepts and the rejection of others. It was also found that the peduncles of V. gardneri produce relatively long peduncles in culture, rather than always short or nearly absent as has been recorded previously (Collins 1909, Blum 1972). In some populations of V. velutina the oogonia were all erect, rather than reflexed (cf., Christensen 1952, 1986a; Ott & Hommersand 1974). The three dimensional orientation of gametangia in many species has been more clearly illustrated using scanning electron micrographs, and where

possible, light or scanning electron micrographs have been provided rather than drawings. It is likely that new taxonomic characters will be found after more extensive use of scanning electron microscopy and that the suitability of some currently used characters, such as antheridial shape, could be better assessed.

These studies comprise the first detailed account of Vaucheria in Australia and the first major monograph of this genus in the southern hemisphere. As such, it is impossible to comment of the endemism of species and how they compare with the largely endemic marine flora (Womersley 1981b) and the apparently cosmopolitan freshwater flora (Entwistle & Kraft 1984). Furthermore, Vaucheria has a wide habitat range and further collecting is needed to fully represent the flora of south-eastern Australia.

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