TAXONOMY OF *ULVA* SPECIES (CHLOROPHYTA) IN THE SOUTH WESTERN CAPE, SOUTH AFRICA.

M.A.P. Joska
Botany Department
University of Cape Town
Rondebosch 7700.

TABLE OF CONTENTS

ABSTRACT

Six species of Ulva, U. atroviridis Levring, U. capensis Areschoug, U. fasciata Delile, U. lactuca L., U. rigida C.Agardh and U. uncialis Kützing, have been reported to occur in the south western Cape Province. As a result of herbarium, field and culture studies it was found that five of these species do occur, but U. uncialis is a synonym of U. rigida (Agardh, 1883). Furthermore, U. atroviridis has correctly been reassigned to the genus Enteromorpha (Wynne, 1986). U. rhacodes (Holmes) Papenfuss, which has hitherto only been reported from the eastern Cape Province, was also found, giving a total of five species of Ulva in the region, which are described in detail.

Chloropelta caespitosa Tanner, a new genus and species, previously only recorded from the north east Pacific, was also found in False Bay and at Cape Hangklip during the course of this study. This genus has a germling which, during the initial phase of its growth resembles the germlings of both Ulva and Enteromorpha. Its further development differs however in that its monostromatic thallus becomes distromatic through cell division and not joining together of the monostromatic layers. A published note on the occurrence of this species in the south western Cape is included as Appendix I.

The genus Ulva displays a range of morphologies within species which leads to difficulty with clear species definition. In this study general thallus morphology

(including shape, thickness and presence or not of marginal dentation), cell shape in transverse sections of the thallus and ecological observations were used to construct a key for their identification.

INTRODUCTION

Perhaps one of the commonest components of the littoral zone algae worldwide are species in the Chlorophytan genus Ulva or "sea lettuce" as they are commonly known. The genus Ulva, together with the genera Fucus, Conferva and Chara, was one of the original four algal genera described by Linnaeus in his Species Plantarum (1753).

The Chlorophyta have most recently been reviewed by Round (1984), Bold and Wynne (1985) and Hoek, Stam & Olsen (1988). Until recently many taxonomists considered that genus Ulva belonged in the family Ulvaceae which was contained in the order Ulvales in the phylum Chlorophyta (Bliding,1968; Bold & Wynne,1985). Recent developments in algal ultrastructural research have brought considerable changes in thinking with regard to systematics of the Chlorophyta. It has recently been proposed to place the order Ulvales within the class Ulvophyceae in the phylum Chlorophyta (Hoek, Stam & Olsen,1988). This change is to a great extent due to the work of Kornmann (1973) who observed that morphologically divergent green algae shared a similar life history. This classification is based on zoid flagellar apparatus, mitosis, life history, thallus

chloroplast type. The class Ulvophyceae contains not only the Ulvales but the orders Codiolales, Cladophorales, Bryopsidales and Dasycladales. Separate classes Chlorophyceae, Zygnematophyceae, Trentepohliophyceae and Charophyceae contain both freshwater and terrestrial orders. The previous systems of subdivision were based on organisational levels and the family Ulvaceae has variously been placed in the order Ulvales, Ulotrichales and Chaetophorales which contain both freshwater and marine species (Round,1984). The order Ulvales, erected by Blackman and Tansley (1902), was not generally recognized until the alternation of isomorphic generations in species of Ulva and Enteromorpha was shown by researchers such as Foyn (1934) and Bliding (1963; 1968). Previously the Ulvaceae were placed in the order Ulotrichales by Borzi (1895). Absolute definition of families retained within these three orders remains arguable amongst taxonomists since some genera have characters which allow them to be attributable to more than one order. As stated by Bold and Wynne (1985) "the classification of green algae, as is the case with most other algal divisions, differs with the classifier". Bold and Wynne (1985) consider the single division Chlorophyta to contain fifteen orders which includes the order Ulvales. They further define five families within the order Ulvales, one of which is the Ulvaceae. Not all

taxonomists agree on this designation. Papenfuss (1960), considered that both Ulva and Enteromorpha, in their sporeling phase, "showed a striking resemblance to filaments of Ulothrix" thus he preferred their retention in the order Ulotrichales as proposed by Blackman and Tansley (1902). Mattox and Stewart (1980) consider the Ulvaceae as different from other Chlorophyta which they studied due to the fact that they have no transverse mictrotubules associated with the cytokinesis of vegetative cell division. However, the order Ulvales containing the family Ulvaceae has been generally accepted and is still recognized by some authors (Round,1984; Womersley,1984; Bold & Wynne,1985). Various classification schemes for genera within the family Ulvaceae (e.g.Tanner,1979; Phillips,1983; Womersley,1984) serve to underline the differences in opinion amongst taxonomists. Ulva and Enteromorpha are the only two genera which are constantly maintained within the family Ulvaceae in all the above mentioned schemes. Apart from Ulva and Enteromorpha the family Ulvaceae has, depending on the taxonomist, variously included the genera Percursaria, Ulvaria, Letterstedtia, Monostroma, Capsosiphon, Blidingia, Rhizenteron, Lobata, Gemina, Feldmannodora, Ulvopsis, Kornmannia and Chloropelta (Phillips,1983). Debate as to the validity of genera and their inclusion or not within the family will no doubt continue.

The genus Ulva has been separated from the other Ulvacean genera because of the presence of a continuously distromatic thallus (Womersley, 1984). It must be noted however that the genus Chloropelta, has also been compared to Ulva due to its initial growth being distromatic (Tanner, 1980). In Ulva the thallus is flat, distromatic (except at the initial germling stage) and attached at the base, or holdfast, with rhizoidal cells. The thallus may be simple, branched or ruffled and may have toothed or finger-like extensions on the margins. Vegetative cells have a single chloroplast and one or more pyrenoids. The Type species is Ulva lactuca, the type specimen of which is in the Linnaean Herbarium.

As has been previously stated the genus Ulva was one of the original four algal genera described by Linnaeus in his Species Plantarum in 1753. Linnaeus's typification of the genus stated that the fructifications were in a vesicular membrane, thus inferring hollow plants (Papenfuss, 1960). This very general description therefore allowed many algal species to be placed in the genus. To quote some species common in South Africa - Ulva dichotoma Hudson, 1762 [Dictyota dichotoma (Hudson) Lamouroux, 1809], Ulva rugosa Linnaeus, 1771 [Splachnidium rugosum (Linnaeus) Greville, 1830], Ulva

umbilicalis sensu Thunberg, 1807-1820 [Porphyra capensis Kuetzing, 1843].

C. Agardh (1822) assigned both distromatic and monostromatic species to the genus Ulva. Phycoseris, a genus erected by Kützing (1843), was defined as containing both completely and partially distromatic species from the order Ulvales. When Kützing published his Species Algarum in 1849 he placed both distromatic and monostromatic species in the genus Ulva, family Ulvaceae, and some distromatic species in the genus Phycoseris, family Enteromorpheae, because he maintained that the species in this genus had a hollow stipe. Monostromatic species were placed in the genus Enteromorpha also in the family Enteromorpheae (Kützing,1849). Kützing's definition of these genera did not gain acceptance and, in 1854, Thuret amended the description of the genus Ulva as stated by Linnaeus and also placed all Kützing's Phycoseris species within the genus Ulva. Thuret (1854) defined the genus Ulva as being composed of distromatic plants which had a parenchymatous, frond-like thallus. Le Jolis (1863) considered that many species previously defined and ascribed to the genus Ulva could not be truly described as distromatic and that interspecific differences were also not clear cut. Le Jolis regarded U. latissima and U. rigida as varieties of U. lactuca. It was only when

a Type of U. lactuca was found in the Linnean Herbarium and examined and was definitely shown to be distromatic that this controversy ceased (Papenfuss,1960). The original Type species of the genus Ulva was Ulva intestinalis, but this same plant was also designated as the Type for the genus Enteromorpha by Link (1820). Since the name Enteromorpha was conserved it could have been considered that all species presently assigned to the genus Ulva should be placed within the genus Enteromorpha. Silva (1952) reviewed the position of Ulva and Enteromorpha and the conservation of both names was upheld by the Stockholm International Botanical Congress of 1951.

Until more modern taxonomic approaches were undertaken by Dangeard (1951,1958), Gayral & Mazancourt (1959) and Bliding (1963, 1968), species placed in the genus Ulva were often described from preserved material, often from a single or very few specimens in poor condition. These original descriptions (See Appendix II) have led to a great deal of confusion when comparison of freshly collected specimens is made with Type material. Further, the loss or unavailability of a Type (as in the case of Ulva fasciata Delile and U. nematoidea Bory) allows only comparison with earlier written descriptions and drawings some of which lack the concise

information necessary for comparison with specimens collected.

Bliding's definitive description of the genus Ulva and the European species within this genus (1968) is considered a most important taxonomic work (Tanner, 1979; Koeman & v.d.Hoek, 1981; Hoeksema & v.d.Hoek, 1983). The true complexity of the taxonomic position of all species within the genus was gradually realised when plants were demonstrated to show great morphological plasticity within apparent species (Steffensen,1976; Bonneau,1977; Mshigeni & Kajumolo,1979; Tanner,1979; Phillips,1983). Cytological genetic studies within the genus have not reached a stage where taxonomic divisions may be drawn and, as stated by Mathieson et al.(1981), not only are special skills and equipment required for a simple identification but the plant is usually destroyed in the process. The most recent detailed studies are those of Tanner (1979), who studied the taxonomy and morphological variation of Ulva from the northeast Pacific; Koeman and v.d.Hoek (1981) and Hoeksema and v.d.Hoek (1983) on the European species of Ulva and Phillips (1983) undertook a full taxonomic study of southern Australian species of Ulva.

In this study comment on genera considered as being in the family Ulvaceae is restricted to taxonomic discussion of the species found in the south western Cape

Province, South Africa. Barton (1893) listed U. lactuca, U. lactuca var rigida, U. fasciata and U. uncialis as occurring at the "Cape of Good Hope" - this latter term was often used by collectors to describe any site which may have been in the then Cape Colony which reached as far east as Port Natal (now Durban). Delf & Michell (1921) noted these same species as being in the Tyson Collection held in the Bolus Herbarium at the University of Cape Town (BOL). Papenfuss (1940, 1960) investigated some South African species of Ulva, but did not undertake a full taxonomic study of all the then known species which were considered to occur there. Eight species of Ulva have been recorded as occurring on South African coasts (Seagrief, 1984) - U. atroviridis Levring, U. capensis Aresch., U. fasciata Delile, U. insignis (Aresch.) Papenfuss, U. lactuca Linnaeus, U. rhacodes Holmes, U. rigida C.Ag. and U. uncialis (Kützing) Montagne. Of these eight species, four have hitherto been considered endemic to the region, U. capensis, U. atroviridis, U. insignis and U. uncialis.

The aim of this study is to determine the correct name and distribution of those species occurring on the south western Cape coast. U. uncialis has been questioned as being a separate species (Areschoug, 1851) and although a Type collected by Drege exists, its actual position is uncertain. The Type was examined in this

study and comment will be made on its inclusion as a separate species within the genus. *U. atroviridis* has recently been reassigned to the genus *Enteromorpha* by Wynne (1986). However, the Type, described and collected by Levring (1938) was examined and its position within *Ulva* or *Enteromorpha* will be assessed. *U. capensis*, *U. fasciata*, *U. rigida*, *U. lactuca* and *U. rhacodes* are described in detail.

MATERIALS & METHODS

Ulva species were collected at various sites along the rocky intertidal coast of the south western Cape province, from Paternoster to Cape Aghulhas. This area is shown in Fig.1. The marine algal collection in the Bolus Herbarium was also studied, including plants from some sites outside the study area.

Material was brought back to the laboratory in seawater and where necessary, maintained in a 15°C aquarium until used. Herbarium specimens were preserved in 10% formalin in seawater for a few hours and then placed on sheets and dried. Permanent slides of sections were made using a 50% Corn Syrup solution with 1% Phenol added to inhibit fungal growth. Once dried these specimens were sealed with nail polish.
Fresh material was used for measurement of cells and thallus except where herbarium specimens were examined. Sections were handcut using a dissecting microscope. Cells were measured using a calibrated eyepiece on a compound microscope and photographs were made using a Zeiss Photomicroscope. Apical, mid and basal areas of the thallus were assessed according to Fig.2.
Measurement of thallus and cells were made according to

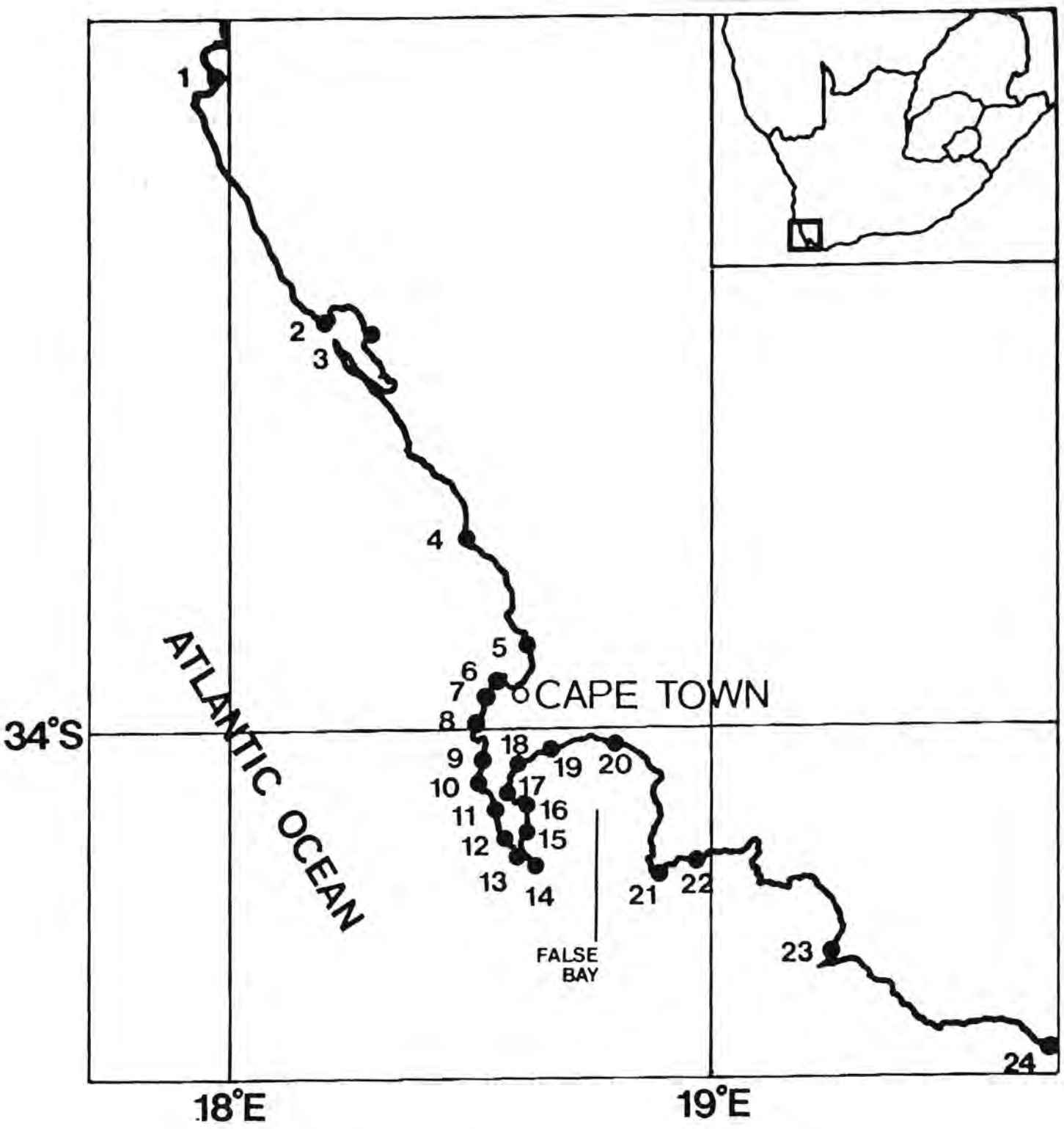


Fig.1. Map showing collection sites:

1. Paternoster
2. Saldanha
3. Langebaan
4. Melkbosstrand
5. Blouberg
6. Sea Point
7. Camps Bay
8. Oudekraal
9. Noordhoek
10. Kommetjie
11. Scarborough
12. Olifantsbos
13. Platboom
14. Cape of Good Hope
15. Buffelsbaai
16. Simonstown
17. Clovelly
18. Dalebrook
19. Muizenberg
20. Swartklip
21. Cape Hangklip
22. Betty's Bay
23. Gansbaai
24. Agulhas

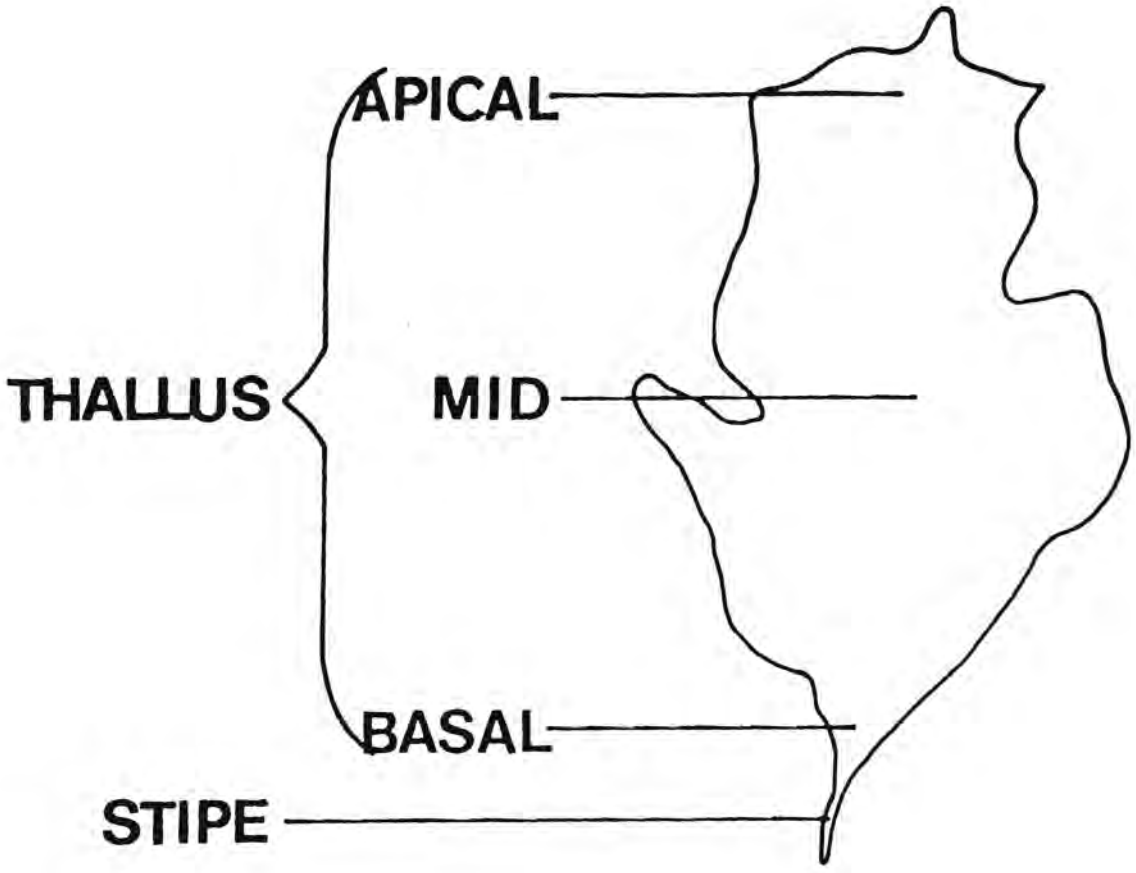


Fig.2. Schematic drawing of Ulva plant showing regions of thallus as described in text.

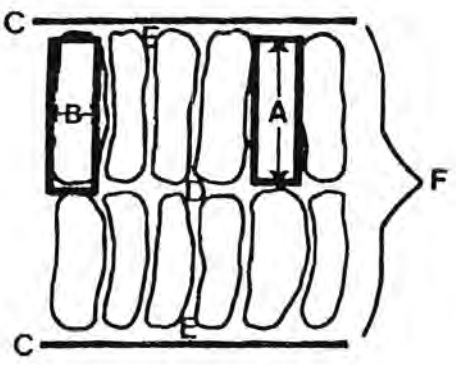


Fig.3. Schematic T/S of Ulva thallus:
A = cell height B = cell width
C = outer thallus wall
D = mid interstitial
E = outer interstitial
F = thallus thickness

Fig.3. Phycological terms for thallus description and cell shape are used according to Hine (1977).

Fertile material for culture experiments was kept damp, but not submerged and covered to exclude light until used. Marginal sections of thallus were immersed in filtered seawater in petri dishes. Gamete and zoospore release appeared to be enhanced by this method. Released spores were pipetted onto a microscope slide and one drop of iodine was added. This allowed the observation of flagella and measurement of zoids.

In order to determine whether sporelings of different species developed distinctive features, zoids from *U. capensis*, *U. fasciata*, *U. rhacodes* and *U. rigida* were placed in culture. *U. lactuca* was not cultured as it was obtained fresh on two occasions only. Zoids used for sporeling culture were pipetted onto sterilised microscope slides which had been placed in culture dishes containing 100 ml of 50% Provasoli ES medium (Provasoli, 1968). Sporelings were maintained in culture dishes at 15°C with a light intensity of ± 50 $\mu E\ cm^{-2}\ s^{-1}$ with a 16:8 hour day:night photoperiod. The medium was renewed once a week and sporelings were grown for two months.

Sporelings of *U. capensis* from Sea Point, *U. fasciata* from Simonstown and *U. rhacodes* from Sea Point

and the Kowie Estuary in the eastern Cape province were also cultured using the same methods as above, but in temperature controlled water baths at 4, 8, 12, 15, 19, 22, 26 and 30°C, respectively. The results of this last experiment are not presented in detail here and comments related to the results thereof are included in this study where applicable.

EVALUATION OF TAXONOMIC CRITERIA USED FOR DEFINITION OF *ULVA* SPECIES.

---

1. Thallus Morphology.

Original descriptions of Ulva were almost entirely based on external thallus morphology. Modern revisions carried out in Europe (Bliding, 1968; Koeman, 1985), the north east Pacific (Tanner, 1979) and southern Australia (Phillips, 1983) have shown that species exhibit a "plastic" morphology. This has also been found in culture and ecological experiments using Ulva species (Steffenson, 1976; Bonneau, 1977; Kapraun, 1970; Mshigeni & Kajumolo, 1979). Twelve Ulva species described as occurring on the north western coast of America (Setchell & Gardner, 1920 a,b) were reduced to six species by Tanner (1979).

Texture of the thallus depends upon thickness (Koeman, 1985). Position on the shore, age of the plant, amount of wave exposure and grazing pressure may affect thallus thickness among members of a population (Tanner, 1979). Phillips (1984) found mean thallus thickness to be an extremely variable character among three southern Australian species of Ulva - U. rigida, U. laetivirens Areschoug and U. stenophylla Setchell & Gardner.

Dentation of the thallus, microscopic and macroscopic, has been used as a definitive taxonomic feature by Bliding (1968), Hoeksema & v.d. Hoek (1983), Koeman (1985) and Tanner (1979). However, dentation may not be found where thallus edges are sloughed off after release of reproductive cells, where sand abrasion and probably where grazing has taken place. Watson & Norton (1985) found that the tips of thalli were more readily consumed by grazers since they had less "puncture resistance". Tanner (1979) found that in U. taeniata the number and length of teeth (dentation) decreased with increasing water temperature. Womersley (1984) found that dentation was present only on certain parts of the thallus in U. taeniata, U. rigida and U. fasciata, especially in older specimens from southern Australia. Dentation was found to be common in young thalli but scarce in adult thalli in specimens of U. fasciata collected from western Kyushu in Japan (Migita & Fujita, 1987). Original descriptions of Ulva species are often confusing. In his original description of U. rigida, C.Agardh (1822)(see Appendix II, page iii) stated that the thallus is "often crenate" (dentate). J. Agardh (1883) (see Appendix II, page xiv) described five forms of U. rigida, only one form described as having dentation. However, in his drawing of the species (Tab. IV) he clearly illustrated marginal teeth (No.119). Dentation is a feature of all forms of the species U.

rigida according to Bliding (1968) & Koeman (1985). Phillips (1983) considered U. rigida sensu Bliding (having marginal dentation) which occurs in southern Australia, to be a form of U. laetevirens. She upheld U. rigida sensu C. Agardh as a separately defined species which did not have marginal teeth (Phillips, 1990).

Although thallus shape and thickness cannot be accepted as a completely definitive taxonomic feature in all species, keys making major use of thallus morphology have been drawn up for Ulva species on the north eastern Pacific coast of America (Tanner, 1979) and southern Australia (Womersley, 1984).

2. Thallus colour.

Although this feature was commonly used as a diagnostic feature in older descriptions of Ulva species it has been noticeably omitted from recent studies by Bliding (1968), Tanner (1979), Phillips (1983) and Koeman (1985), but included by Womersley (1984). Colour definition could be construed as a subjective observation but colour/colour ranges can and are being used by modern taxonomists as part of species descriptions using fresh material (e.g. with crustose corallinaceae, Chamberlain, 1990). Colour of the thallus in the living Ulva plant may be affected by chloroplast position and size (Koeman,

1985). Drift specimens may be paler, due to fading and herbarium specimens may only partially retain colour or become darker, depending on collection and preservation methods.

3. Form, size and arrangement of cells in surface view and transverse section.

Original and early descriptions of cell arrangement and shape often did not state in which region of the thallus the described cells occurred. The taxonomic importance of the differing cell shape and size in the apical, mid and basal regions of the thallus was stressed by Bliding (1968), Hoeksema & v.d. Hoek (1983) and Koeman (1985) when describing European species of Ulva. However, Tanner (1979) and Phillips (1984) found that cell size in surface view and transverse section of the apical and mid regions of the thallus were too variable as characteristics for absolute species definition. They found that only the cells in the basal region showed stable characteristics. Ardrè (1967) described a new species, Ulva bifrons Ardrè, which had different cell shapes on each side of the thallus. Steffenson (1976) reporting on Ulva lactuca and U. lactuca var rigida from New Zealand found that cell size was not a definitive characteristic. Koeman and Hoek v.d.(1981) used the anatomy of the lower basal region of the blade in Ulva

species in the Netherlands as one of the major characteristics. Such features included central cavity or not, microscopically visible longitudinal ribs, narrow wings of smaller cells and rhizoidal cells being distinctly larger or not. U. lactuca and U. rigida are the only two species which apparently occur both in the Netherlands and the south western Cape. U. fenestrata from the northwest Pacific showed changes in cell shape, in surface view, dependant on locality and time of year (Tanner, 1979).

4. Number of Pyrenoids.

In members of the Chlorophyceae the pyrenoid is found embedded in the chloroplast usually surrounded by a starch sheath. The central matrix is composed of proteinaceous material which is considered to act as an enzyme reserve of RuDP carboxylase (Griffiths, 1980; Staehelin, 1988). Bold & Wynne (1985) state that the pyrenoid is the site of starch formation and acts possibly as a temporary storage area for photosynthetic products but Staehelin (1988) considered that "the functional significance of pyrenoids is still an enigma". Pyrenoid division has been shown to occur prior to or at the same time as, the division of the chloroplast. In Spirogyra, the number of pyrenoids increases with the increasing size of the chloroplast, and some algae when

cultured in the dark, lose all their pyrenoids (Griffiths, 1970). Thus it appears that the number of pyrenoids present may be dependant on (a) the photosynthetic "state" or (b) the mitotic/meiotic division stage of the cell. According to Griffiths (1980) algae which contain pyrenoids "occupy a rather special position in the evolution of the process of photosynthesis". He further states that the usefulness of the pyrenoid as a criterion in the classification of algae appears to be rather limited. This last statement would seemingly be meant to apply to genus and family classification however.

The number of pyrenoids in cells in the apical, mid and basal region of the thallus is given as a major taxonomic feature for European species of Ulva by Bliding (1968), Hoeksma & v.d.Hoek (1983) and Koeman (1985). Tanner (1979) and Phillips (1983) consider pyrenoid number as a variable and non-definitive taxonomic feature for Ulva species from the north east Pacific and southern Australia, respectively. It is not understood why the pyrenoid number should vary among cells in different regions of the thallus in Ulva species.

5. Chloroplast.

Ulva species have parietal chloroplasts usually seen on

the outer cell wall (Koeman, 1985). Often the chloroplast may be tilted to one side of the outer wall especially in the apical and mid regions of the thallus (Bliding, 1968; Phillips, 1983; Koemann, 1985) and occasionally the chloroplast may lie in the basal region of the cell (Bliding, 1968). Phillips (1983) found that chloroplast position in the cells of the basal region of the thallus was a non-variable character in three of the southern Australian Ulva species. However, Britz and Briggs (1976) found that U. lactuca var. latissima, U. lactuca var rigida (U. rigida) and U. mutabilis showed a "rhythm of spontaneous, non-light induced chloroplast translational movement". Their findings indicate that chloroplast position in the cell varies according to light intensity, moving towards the light from the side of the cell to the outer wall after an 8 hour period of darkness and away from the outer wall in the last third of a 16 hour light period.

6. Method of reproduction.

In Ulva, reproduction, whether sexual (gametes) or asexual (zoospores), is effected by internal division of the ordinary vegetative cells of the thallus, usually by those cells on the margins of the blade. No sporangia or specialised regions of reproduction have been noted but

the general tendency is for spores to be formed in cells at the thallus margins.

Bliding (1968), Tanner (1979), Phillips (1983) and Koeman (1985) found that all species investigated showed alternation of isomorphic generations. Zoospores tended to be larger than gametes but size variation of both types of reproductive body within species was such that it was not considered to be a reliable taxonomic feature (Dangeard, 1958; Tanner, 1979; Phillips, 1983).

Zoospores produced by sporophyte plants are generally quadriflagellate but many researchers have found that sporophyte plants may also produce some or only biflagellate zoospores. These zooids are asexual and produce sporophytes. Gametes are biflagellate and although fusion of two gametes usually occurs single gametes may also produce adult plants by parthenogenesis without fusion occurring (Bonneau, 1978). Phillips (1983) observed that these parthenogenic plants produced both biflagellate zooids and quadriflagellate zoospores. Although crossing experiments between species has been proposed as a method of taxonomic definition (Føyn, 1955; Dangeard, 1958; Bliding, 1968; Kapraun, 1970) no definitive studies in this regard appear to have been undertaken.

7. Growth and morphology of sporelings.

Species in the genus Ulva develop directly by cell division from a single settled spore or zygote. After division of the initial cell a uniseriate filament develops from the upper cell whilst the lower cell divides to form the basal rhizoidal disc. The upright uniseriate filament later undergoes longitudinal division to form a hollow tubular sporeling. This finally flattens to become an upright distromatic plant. Cells in the thallus have one nucleus but rhizoidal cells are multinucleate (Bliding, 1968). Complete flattening of the thallus viz. distromatic from edge to edge may not always take place as was found in U. atroviridis (Levring, 1938). This latter species has recently been placed in the genus Enteromorpha (Wynne, 1986). Agardh (1883) noted that U. fasciata had, "at the margins a minute canal around which the cells formed a semicircle" (See Appendix II, page xxiv). None of the early descriptions of Ulva species describe the growth and morphology of germlings. Bliding's study of European species of Ulva (1968) was apparently the first which used culture methods to differentiate between species. Early development of the settled zoospore, zygote or parthenogenic gamete may show marked differences between species. In his culture studies of north east Pacific species of Ulva, Tanner (1979) found that U. fenestrata,

U. stenophylla and U. taeniata developed from the original division of the zygote or zoospore into two cells. The lower cell became the rhizoidal section of the plant and the upper cell developed into the thallus. However, U. californica and U. scagelii developed a germination tube through which the entire original cell passed prior to cell division. None of the European species cultured by Koeman (1985) or southern Australian species cultured by Phillips (1983) developed a germination tube prior to cell division. Phillips (1983) and Koeman (1985) found that the developmental pattern of the thallus was generally characteristic for described species.

8. Ecological factors.

It became apparent during this study that certain species were often only found in specific areas of the shore, in a particular geographic region and at certain times of the year. The study area, from Saldanha Bay to Cape Agulhas (Fig.1), encompasses 400 km of coastline. Very rough wave conditions pertain in the major part this area, especially in winter. Few quiet water areas are found except for Langebaan Lagoon. False Bay is more protected than Table Bay and water temperatures are considerably warmer (Bolton & Anderson, 1990). Three major substrate types occur, Malmesbury shale, granite

and Table Mountain sandstone. The latter substrate is generally eroded to provide many rockpools and fissures.

Bennett *et al* (1983) and Gerking (1984) found that two species of rocky intertidal fish, *Caffrogobius caffer* (Günter) Smith and *Sarpa salpa* (Linn.), had gut contents indicating that *Ulva spp.* constituted a major portion of their diets. *C. caffer* occurs mainly in high-shore rock pools east of Cape Point whilst *S. salpa* feeds with tidal inflow. These selective grazers may possibly influence the distribution and morphology of certain *Ulva spp.* on the rocky intertidal. Predictable habitats for different species are described by most recent workers.

DESCRIPTION OF ULVA SPECIES IN THE SOUTH WESTERN CAPE.

ULVA CAPENSIS Areschoug, 1851. Phyceae Capensis, Uppsala (Plates 1 - 3)

Agardh, J. 1883.

De-Toni, J.B. 1889.

Papenfuss, G.F. 1940.

Holotype: Whereabouts unknown.

Lectotype: S 86 007! Designated by G.F. Papenfuss.

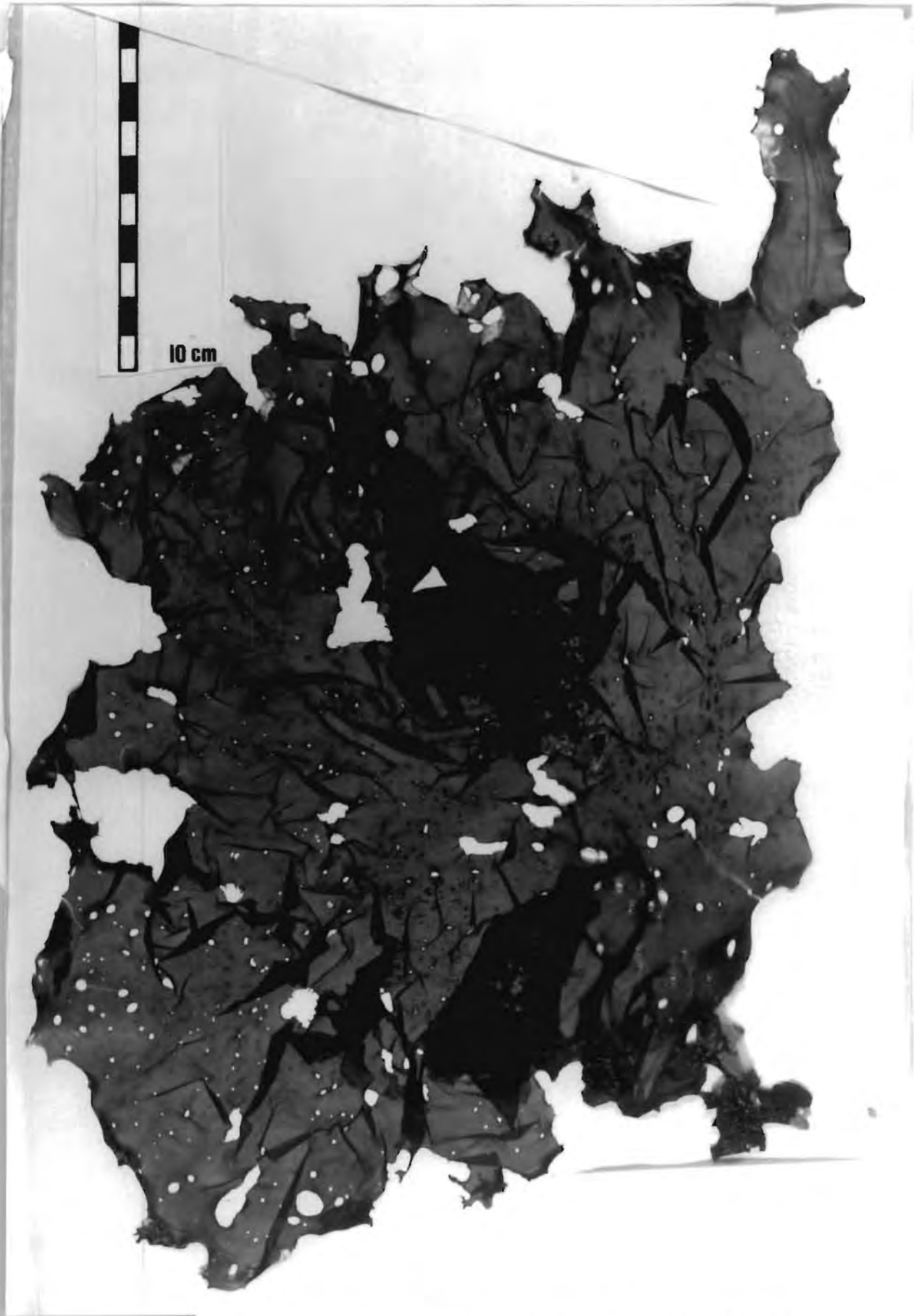
Synonyms: Phycoseris lobata β africana Kützing, J., 1849.

Phycoseris capensis Grunow, A. 1867.

Gemina linzoidea Chapman, 1952.

Ulva laetevirens (pro parte) sensu Phillips, 1983.

Description: In mature plants the thallus is usually a bright grass green but often dark green, with little or no colour difference between the base and apex. Herbarium specimens olive to dark blackish green. The thallus is usually thick and tough to the touch always with macroscopically visible single or double dentation on the margin. The thallus may be simple, lanceolate, linear, cuneate or oblanceolate, often deeply torn and with numerous



ate 1. Ulva capensis collected at Oudekraal.

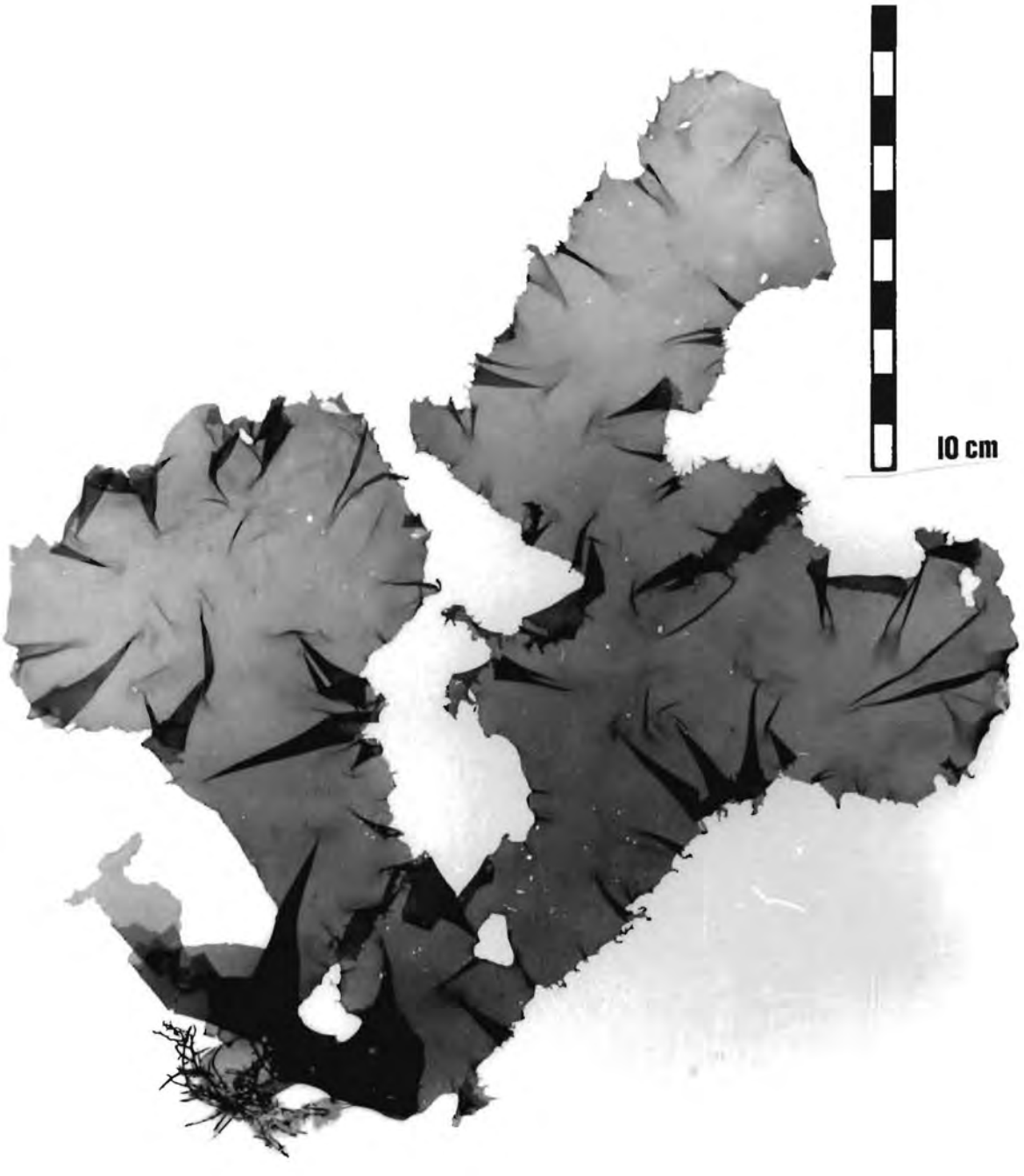
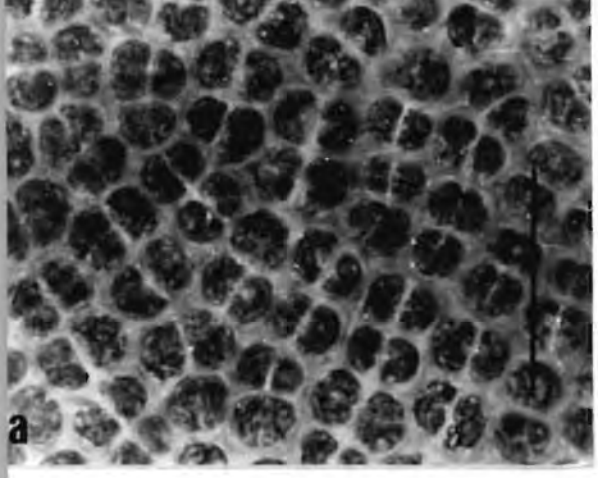
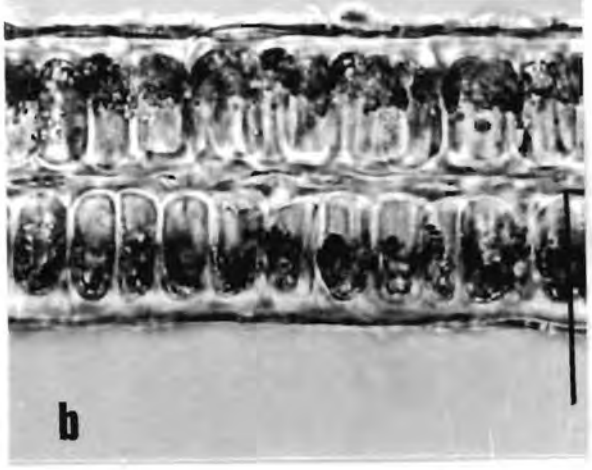
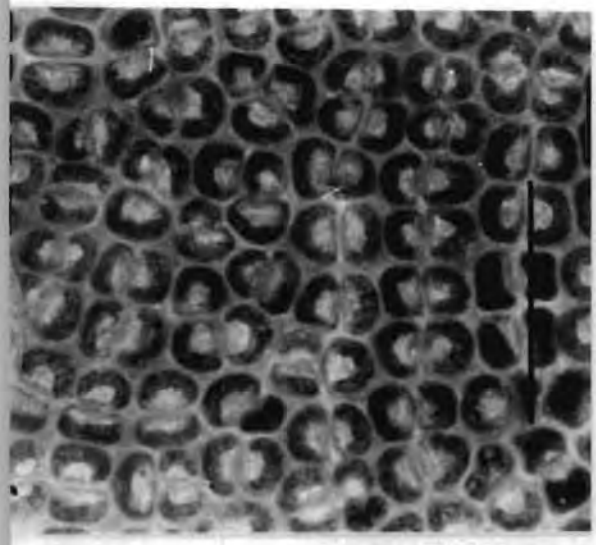
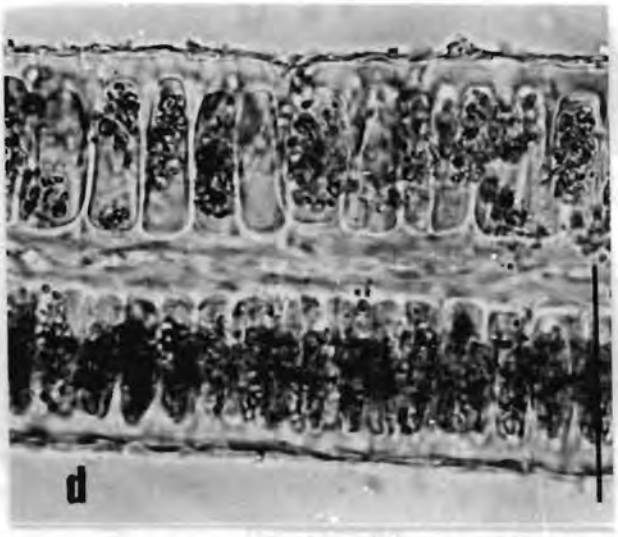


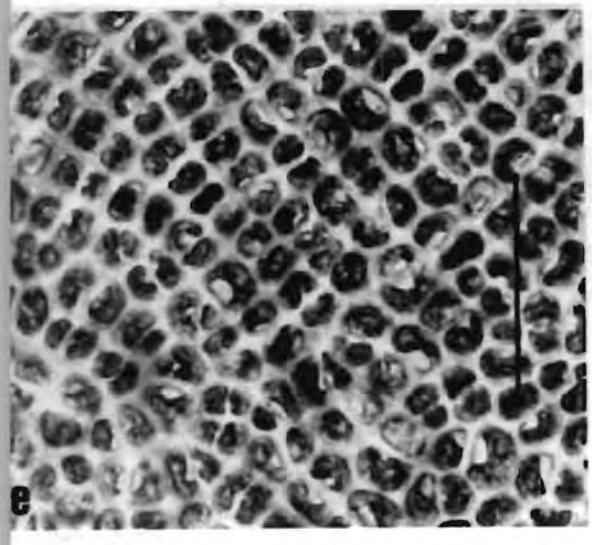
Plate 2. Ulva capensis collected at Kraalbaai near Langebaan











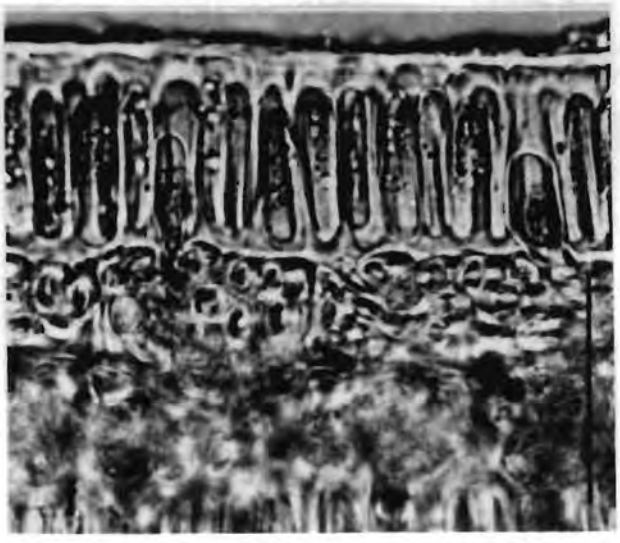


Plate 3. Ulva capensis **a:** surface of apical thallus **b:** transverse section of apical thallus **c:** surface of mid thallus **d:** transverse section of mid thallus **e:** surface of basal thallus **f:** transverse section of basal thallus. (bar = 50 µm)

Basal thallus: 135 to 265 µm thick. In surface view rounded, not paired and with many darkened rhizoidal cells (Plate 3e). In transverse section the cells are commonly spindle shaped sometimes ovate elongate, narrowly rounded at both ends or more so at the outer edge of the blade, with a L/B ratio 7:2 (Plate 3f). Mid interstitial space often wider than cell row height. Marginal "wings" - where cells at the basal thallus margins appear paler than the rest of the thallus - were only seen on a few specimens.
In the apical and mid thallus the chloroplast usually lie at the top of the cells, occasionally lying laterally. In the cells of the basal thallus the chloroplast commonly appeared granular, and often spread throughout the cell length. Quadriflagellate zoospores and biflagellate gametes were seen to be released from different plants. Zoospores were rounded elliptical and gametes were narrow elliptical. Sporelings germinating from zoospores or fused gametes were identical in development. After one month in culture, sporelings were dark green, lanceolate with developing dentation at the upper margin. Sporelings were also cultured in a range of temperatures, 4, 8, 12, 15, 19, 22, 26, 30°C, for 15 days at a L:D of 16:8. After 15 days only the 8 - 26°C sporelings had survived, with those cultured at 19°C having the greatest average length.

Ecology: This is a common species, occurring throughout the year, epilithically, usually in the lower littoral to

holes which may also show dentation around their margins . Mature plants are commonly 15-30 cm. in length and vary in width from 5-20 cm. Some specimens from Kommetjie exceeded 1 m. in length. Stipe, if present, short and the holdfast well developed.

Apical thallus: 60-95 µm thick. In surface view (Plate 3a), cells often arranged in pairs, kidney shaped or almost spherical, and forming short curved rows of three to five cell pairs. There is often a wide interstitial space between the paired cells but some specimens have narrow intercellular matrices. The cells are rounded and usually arranged in short rows (Plate 3a). In transverse section the apical cells narrowly ovate, or ellipsoidal, occasionally rounded rectangular, always with a length to breadth ratio (L/B) 2.5-3:1 (Plate 3b). Average cell length in the apical region is 25-40 µm and average cell width is 8-12 µm. Usually one, sometimes two pyrenoids.

Mid thallus: 95 to 150 µm thick. In surface view the cells are rounded, often paired and sometimes forming rows of up to six cells (Plate 3c). In transverse section the cells are longer and often elongate commonly narower at the thallus surface edge or spindle shaped. Average cell length in the mid thallus is 30-60 µm and cell width is 10-20 µm (Plate 3d). One to two pyrenoids.

subtidal zone and always where tidal exposure was minimal. Plants were collected from nearly all sites on the entire south western Cape coast. No epiphytic plants were found. Specimens collected from Die Walle near Agulhas and Oudekraal on the Cape Peninsula had numerous holes in the thallus which had become markedly dentate. It is possible that this feature developed in these plants because of the strong sandwash conditions prevailing in these two areas.

Taxonomy: This species was originally described by Areschoug (1851) possibly from a collection made by Drege in Table Bay. The Holotype is no longer extant but Specimen No.86007 from Stockholm ex Herb J.E. Areschoug, collected in Table Bay, was designated as a Lectotype by Papenfuss in 1960. An even earlier description of a specimen collected by Thunberg (1794) from Table Bay in 1773 and named as U. lactuca was considered to be U. capensis when examined by Papenfuss (1940). Kützing (1849) described a specimen collected in Table Bay as Phycoseris lobata ß africana a form of a species originally decribed from Chile. Areschoug (1851) considered P. lobata ß africana to be a synonym of U. capensis. J. Drege, who collected algae from Table Bay in the early 19th century, apportioned and sold his collections to many herbaria in Europe (Gunn & Codd, 1981) and it is possible that Kützing and Areschoug described P. lobata ß africana and U. capensis, respectively, from a collection from the same source.

Kützing did not list P. lobata ß africana in his Tabulae Phycologicae (1856). Grunow (1867) documented P. capensis as being found at the Cape of Good Hope. Agardh (1883) maintained the form capensis within U. lactuca whilst De Toni (1889) upheld U. capensis as a separate species.

Chapman (1952) described a new genus, Gemina, in which cells in the base of the thallus produce zoids. Within this genus he described G. linzoidea which was found in New Zealand. Chapman also examined a specimen, No.L.939.23.232 in the Rijksherbarium,Leiden, which had been collected at the Cape and labelled as both U. fasciata and Phycoseris lobata ß africana, and annotated it as Gemina linzoidea. Accordingly, Chapman listed the Cape of Good Hope as a site for Gemina linzoidea. Specimen L.939.23.232 was examined in this study and its thallus morphology and sections made showed the cells to be the same as Ulva capensis. It was found in this study that when sections of adult Ulva thalli were stressed during culture experiments (Joska, unpublished) they often became reproductive. Similarly, specimens in the field often had groups of cells which appeared darker than the rest of the thallus - a feature of the genus Gemina. It is therefore considered, as a result of this study, that Gemina linzoidea should be considered as a synonym of U. capensis.

Phillips (1983) examined subtidal and intertidal plants from Stewart Island, New Zealand, and considered them to be U. laetevirens, Areschoug. She further gives detailed cell dimensions from specimens of U. laetevirens collected at different sites in southern Australia. From these detailed cell dimensions and differing morphologies of specimens according to collection site it would appear that some populations of U. laetevirens, which had elongate cells in transverse section and which had macroscopically dentate thalli, specifically from St.Helens in Tasmania and Port Philip Bay in Sorrento in southern Australia are, pro parte U. capensis.

Distribution: Southern Australia, New Zealand, Namibia, entire coast, from Paternoster to Cape Agulhas, in the south western Cape, South Africa.

Collection Sites in Southwestern Cape and Bolus Herbarium Number where available.

Lamberts Bay (54029, 54014); Lagoon, Cape of Good Hope (54028,54027,54026); Platboom (54025); Sea Point; Table Bay (54024,54003); De Walle, Agulhas (54021); Oudekraal (54015,54012); Bakoven (54000); Oliphantsbos (54013); Buffels Bay (54011); Kommetjie (54009,53996); Kraalbaai; Langebaan; Noordhoek (54004).

ULVA FASCIATA Delile, 1813 Flore D'Egypte, Explication des Planches.

(Plates 4 & 5)

J.G. Agardh 1883, De Toni 1889, Barton 1893, Boergesen 1914, Hamel 1931, Chapman 1956, Dangeard 1958, Krishnamurthy & Josi 1969, Kapraun 1970, Jaasund 1976, Tanner 1979, Phillips 1983.

Holotype: Whereabouts unknown.
Type locality: Port of Alexandria, Egypt.
Lectotype: Not designated.

Synonyms: Phycoseris fasciata Kützing, J. 1849.
U. lactuca forma multifida Le Jolis, A. 1863.

Description: In mature plants the thallus may be single elongate, divided into two or more elongate thalli, or lanceolate thalli may arise from a short broad basal section. Grass green to pale green with a notably thicker, paler central portion. Lanceolate thalli not less than 1 cm or greater than 6 cm wide, extending from the base to the apex. The margins slightly or strongly ruffled often with dentate edges. Plants found ranged from 4 to 42 cm in length. The single lanceolate thalli from the Simonstown and Clovelly populations were never > 6 cm in width and the

Plate 4. Ulva fasciata collected at Swartklip in False Bay.

multilanceolate thalli from Kalk Bay and Dalebrook and Swartklip were never > 4 cm in width. The length of the mature plant is apparently dependant upon the amount of water cover. Plants highest on the shore and exposed for longer periods intertidally remained short but were reproductive.

Apical thallus: 40-60 µm thick. Cells in surface view polygonal, rounded to subquadrate, with minimal intercellular spaces, sometimes in short rows of three to four cells (Plate 5a). Cells in transverse section rectangular, markedly rounded with a L:B ratio 2-1.5:1, 20-40 µm in height and 10-24 µm in width (Plate 5b). Pyrenoids mostly 2 to 3, seldom 1.

Mid thallus: 45-60 µm thick at the edge, 70-130 µm thick in the paler centre of the mid thallus. Cells in surface view rounded, polygonal, sometimes in paired rows of up to ten cells (Plate 5 c,d). In transverse section the cells at the margins appeared the same as those in the apex but cells in the centre, paler thicker region were longer, and rounded with a L:B ratio 2-2.5:1, 30-50 µm in height and 12-26 µm in width. In this thicker region of the mid thallus there is a marked interstitial space between the two rows of cells and between the top of the cells and the surface of the thallus (Plate 5e). Pyrenoids 1 to 3.

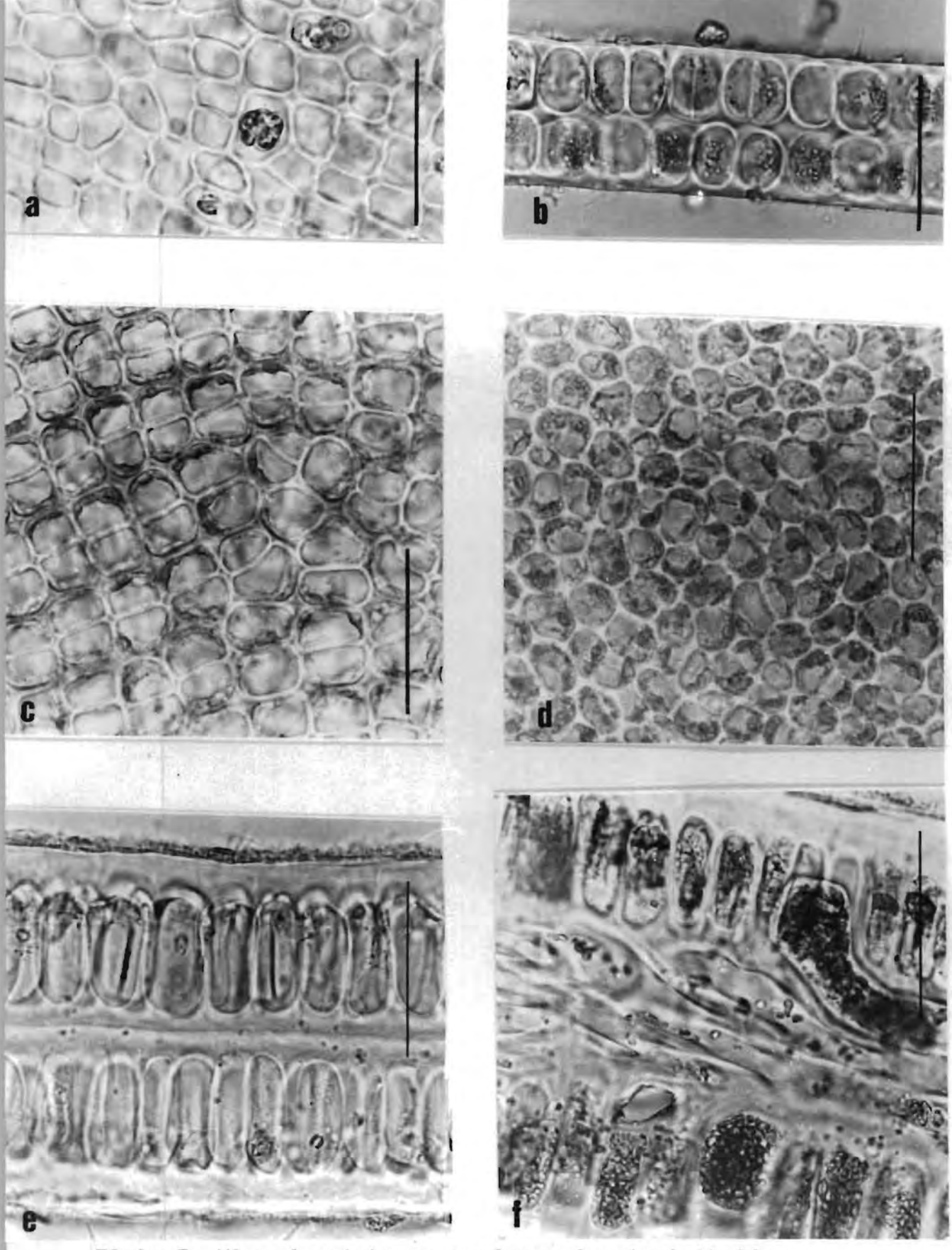


Plate 5. Ulva fasciata **a:** surface of apical thallus **b:** transverse section of apical thallus **c:** surface of mid thallus at edge **d:** surface of mid thallus at mid-rib **e:** transverse section of mid thallus at mid-rib **f:** transverse section of basal thallus. (bar = 50 µm)

Basal thallus: 120-180 µm thick. Cells at the surface of the basal thallus are similarly rounded and showed no order but were interspersed with darker rhizoidal cells.
In transverse section the cells are rectangular with rounded upper and lower ends. Cells 24-45 µm in height and 12-30 µm in width (Plate 5f). Short specimens from the more exposed intertidal zone at Simonstown had many spherical cells in the rhizoidal region. The rhizoidal cells were large and the central intercellular space was wider than the height of the individual cells (Plate 5f). Rhizoidal cells were found up to 4 cm above the holdfast; this feature was also noted by Papenfuss (1960).

Plants were observed to release biflagellate gametes or quadriflagallate zoospores from different plants. Migita & Fujita (1987) similarly found both biflagellate and quadriflagellate spores and also that there was an alternation of isomorphic generations. Zoospores from a plant from Simonstown were placed in culture and it was noted that after 15 days growth the sporelings were 2.5 x the length and .5 the width of U. capensis sporelings which were grown under the same conditions. At two months, the plants remained lanceolate, pale green and no dentation was apparent. This was also found by Tanner (1979) but Migita & Fujita (1987) reported that germlings of U. fasciata initially developed "dentate cells" which were later not apparent on adult thalli.

Sporelings grown through a range of temperatures, 4, 8, 12, 15, 19, 22, 26, 30°C, for 15 days did not survive at temperatures > 26°C. Growth was very limited (less than 80 µm in length) after 15 days at 4 and 8°C and the greatest average growth was at 19°C. These sporelings showed a greater growth rate than U. capensis or U. rhacodes.

Ecology: This is not a common species in the south western Cape. Populations were found only at Simonstown near a freshwater outlet, Clovelly, Dalebrook, Kalk Bay, Swartklip, Cape Point Lagoon and De Walle. No subtidal specimens were found and plants occur most commonly in the low intertidal region, exposed only at the lowest tides. Plants were found throughout the year. U. fasciata has been described as a subtropical to tropical species (Agardh, 1883) but its occurence in southern Australia (Phillips, 1983;Womersley, 1984) and in the south western Cape would seem to indicate that it can also be considered as a warm temperate species. It is noticeable that it was found only in the warmer water regions of this study viz. in False Bay and near Agulhas but not in the western Cape coast region from Paternoster to Cape of Good Hope. It appears to share its distribution with many warmer water species of the Agulhas province (Bolton,1986; Bolton & Anderson, 1990). Arasaki (1984) reported that U. fasciata had become a common species in the Inland Sea of Japan and that it had probably been introduced

by foreign shipping and replaced U. pertusa in polluted waters.

Taxonomy: U. fasciata is readily distinguishable from U. capensis, U. lactuca, U. rigida and U. rhacodes by its external morphology. In general however it appears to fall within a group of species with linear thalli viz. U. costata (Howe, 1914), U. nematoidea (Bory, 1828), U. stenophylla (Setchell & Gardner, 1920) and U. taeniata (Setchell & Gardner, 1920). In this study specimens of U. nematoidea were obtained from Namibia (see Wynne, 1986). Although this species has a noticeably narrower (± .5 cm) center thickened section in the thallus and tended to be darker in colour some U. fasciata plants from Simonstown had very similar appearance. U. nematoidea was not found to have dentate margins, but some specimens of U. fasciata were also not dentate. J.Agardh (1883) considered U. nematoidea to be a synonym of U. fasciata. Similarly, specimens of U. stenophylla from Australia (Phillips, 1983) have an external and cell morphology similar to U. fasciata plants from the Simonstown population. Since no Type or Lectotype of U. fasciata exists it is difficult to absolutely define this species purely by means of the original description. Tanner (1979) found that U. stenophylla, U. taeniata, U. costata and U. fasciata had similarities in "habit, morphology, anatomy and development". Tanner further found that the presence or

absence of dentation could be related to water temperature and that position on the shore could be related to width and length of thallus. Arasaki (1984) found that two forms of U. fasciata occur on the Japanese coast. Form A - similar to U. rigida, U. lobata and U. expansa and Form B - similar to U. dactylifera, U. costata. Different populations of U. stenophylla also appeared to be seasonal or persistent at the same site in southern Australia (Phillips, 1983). Experiments conducted by Mshigeni and Kujumalo (1979) with U. fasciata in Tanzania showed that this species exhibited different morphology according to amount of water cover. Culture experiments involving a full range of these species with linear thalli are needed to test the validity of their definition.

Distribution: Cosmopolitan in warm temperate, sub-tropical and tropical seas. Reported from Tanzania (Jaasund, 1976) and probably also occurs on the Mozambique, Natal and Zululand coasts. Eastern Cape to Transkei (Bolton & Stegenga, 1987; Seagrief, 1988) and south western Cape coast from Cape Point to Agulhas in South Africa.

Collection Sites in the south western Cape and Bolus Herbarium Number where available.

Swartklip, False Bay (54054,54053), Dalebrook, False Bay (54059,54056), Kalk Bay, False Bay (54061), Clovelly, False Bay (54058,54057), Simonstown, False Bay (54052,54051,54047)

Lagoon, Cape Point (54045); De Walle, Aghulhas (54055);

Storms River mouth 23°54'E 34° 1'S (1645,1647).

ULVA LACTUCA Linnaeus 1753. Species Plantarum. Stockholm.

(Plates 6 & 7)

Thuret 1854, Kützing 1849, De Toni 1889, Setchell & Gardner 1920b, Papenfuss 1960, Bliding 1968, Krishnamurthy & Joshi 1969, Abbott & Hollenberg 1976, Kornmann & Sahling 1977, Koeman & van den Hoek 1981, Phillips 1983, Womersley 1984.

Type: Herbarium of the Linnaean Society, London.
Type locality: West Coast of Sweden.

Description: Thallus usually plain, without ruffled margins, occasionally lobed, ovate, ovoid sometimes shortly lanceolate. Thallus thin and often lubricous to the feel. Commonly arising from a small holdfast with an obvious stipe which is often V-shaped. However, specimens from the tug basin at Saldanha Bay had no obvious stipe or holdfast. Plants pale green to grass green. Margins entire and without dentation. Intertidal plants found were seldom > 30 cm in length or 15 cm in width. However, plants from Saldanha Bay at 2 - 5 m depth reached 1m in length.

Apical thallus: 45-63 µm thick. Cells in surface view closely packed, polygonal, occasionally in short rows of three to four cells (Plate 7a). Cells in transverse

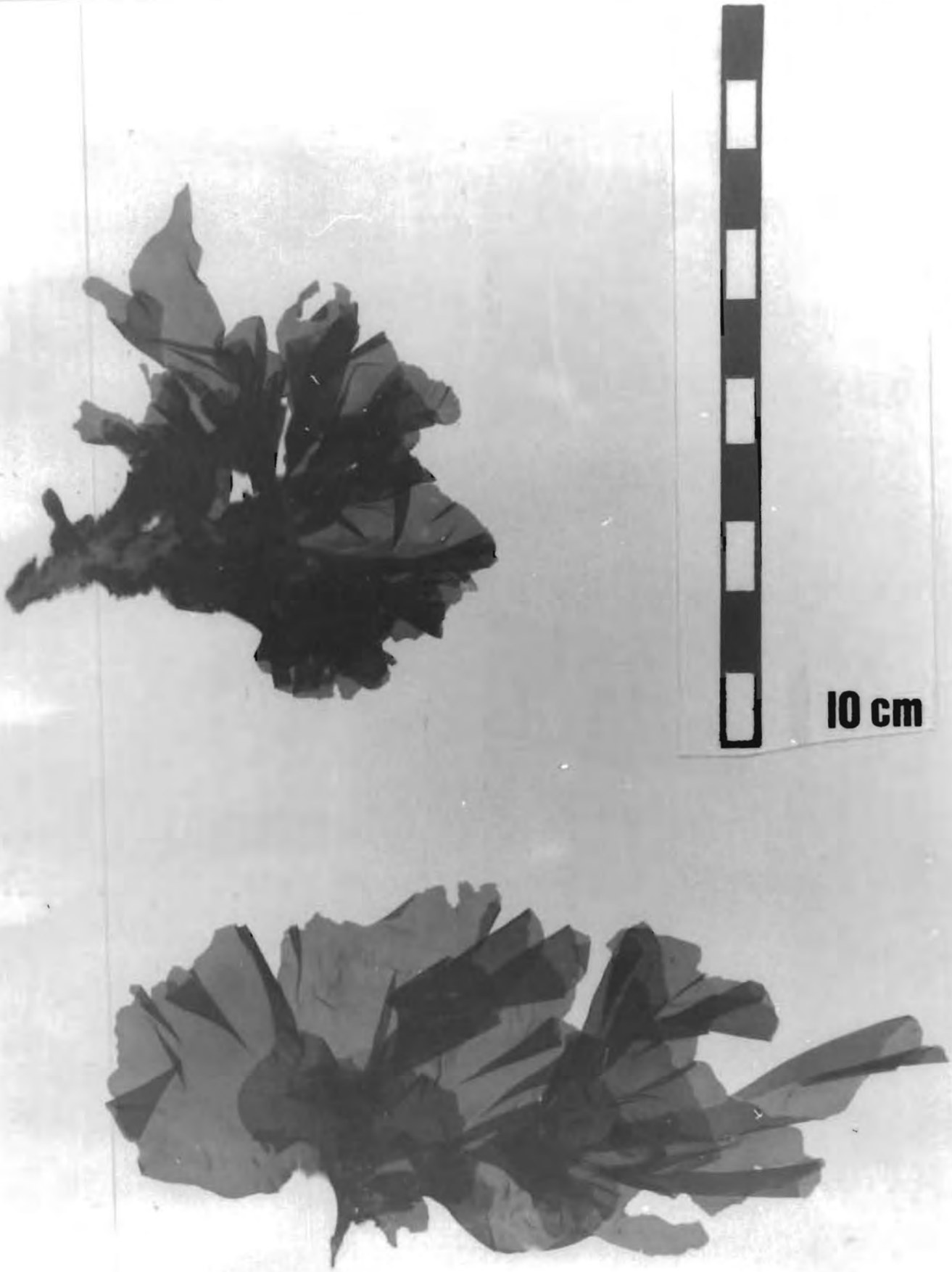


Plate 6. Ulva lactuca collected at Sea Point.

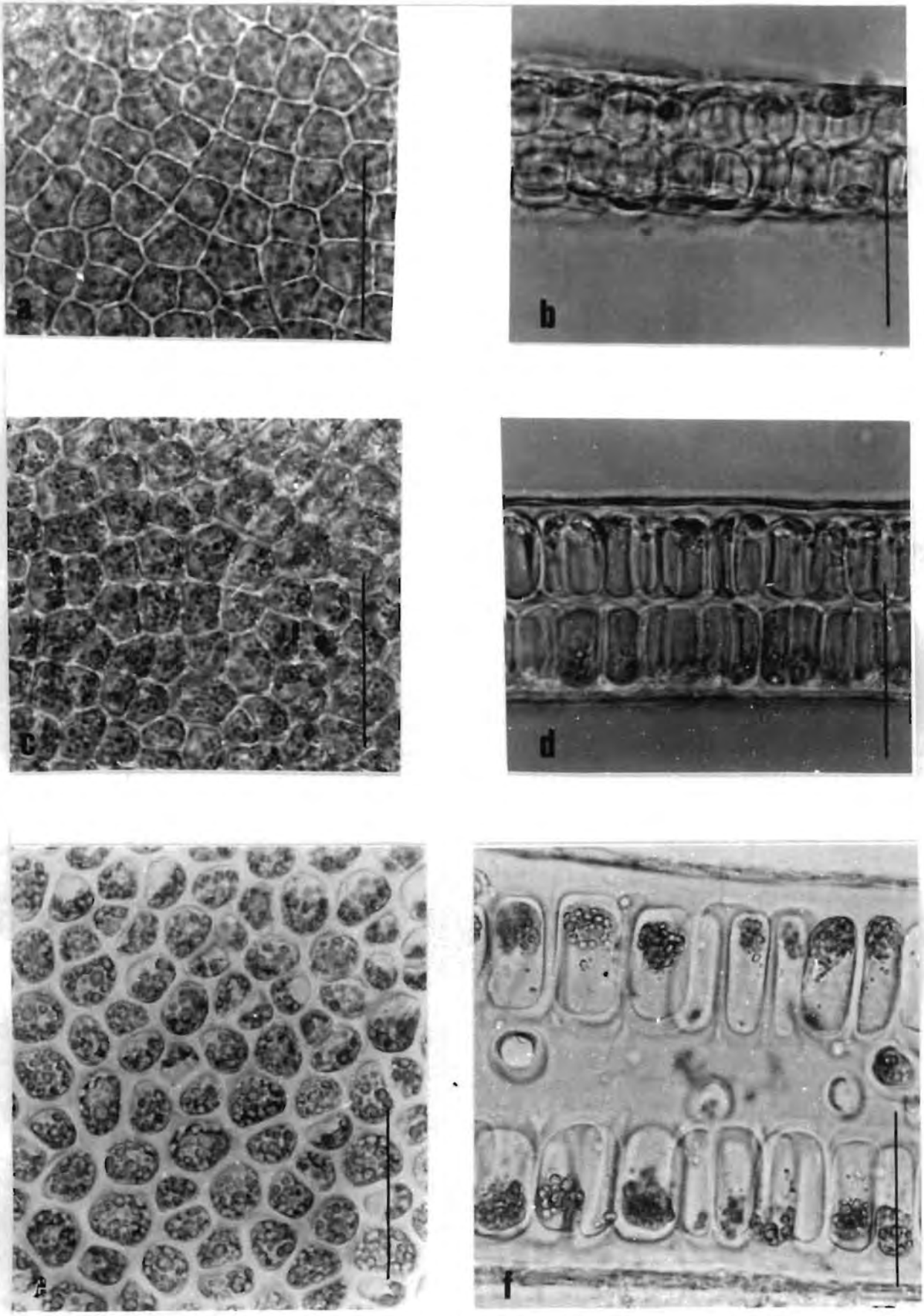


Plate 7. Ulva lactuca **a:** surface of apical thallus **b:** transverse section of apical thallus **c:** surface of mid thallus **d:** transverse section of mid thallus **e:** surface of basal thallus **f:** transverse section of basal thallus. (bar = 50 µm)

section are slightly rounded, quadrate to sub-quadrate with a L:B ratio of 1 - 1.2:1, 15-25 µm high, 12-22 µm wide (Plate 7b). Pyrenoids 1 to 2.

Mid thallus: 55-110 µm thick. Cells in surface view polygonal rounded to slightly angular, occasionally in short rows of two to four cells (Plate 7c). Cells in transverse section slightly rounded, quadrate to short rectangular with a L:B ratio of 1.5:1, cell height 18-22 µm, cell width 12-20 µm (Plate 7d). Usually one pyrenoid, rarely two or three.

Basal thallus: 70-120 µm thick. Cells in surface view polygonal, irregular (Plate 7e). Cells in transverse section rectangular with L:B ratio 2:1, 18-22 µm high, 11-22 µm wide (Plate 7f). Gametes and zoospores were seen to be released from separate plants but these were not placed in culture.

Ecology: U. lactuca has been recorded as a cosmopolitan species but its commonly reported occurrence has been questioned (Womersley, 1984). In the south western Cape this species has been recorded as commonly occuring by Pocock (1939) and Stephenson (1948). However, in this study this species was not commonly found in the south western Cape and only occurred in small discrete populations, usually in the mid to lower littoral zone.

The deeply lacinate palmate form as described by Bliding (1968) and as in the Type was not found. Intertidal specimens were found in the spring to early summer, but subtidal specimens were also found at Saldanha Bay in winter. Tanner (1979) did not find U. lactuca from Vancouver in the northeast Pacific although it was reported by Abbott & Hollenberg in California (1976). Phillips (1983) found U. lactuca to be an uncommon species in southern Australia. Krishnamurthy and Joshi (1969) found it to be a common species in India but seldom found the lanceolate form. Although most specimens were found on rocky substrates it was occasionaly found epiphytically and subtidally in loose sandy substrates, such as at Saldanha Bay. Although not common this species appears to occur along the entire south western Cape coastline.

Taxonomy: The identification of the Type specimen was only made by Papenfuss in 1960. However, the drawing and description by Kützing in his Abbildungen der Tange (1856) appear to have been made from the same Type as was found and illustrated by Papenfuss (1960). Early descriptions included many forms of U. lactuca (see Le Jolis, 1863; Agardh, 1883; De Toni, 1889; Hamel, 1931). These forms were designated as individual species by more modern taxonomists such as Bliding (1968) and Koeman (1985).

Distribution: Recorded worldwide, including the tropics, but many records are doubtful. In the south western Cape this species was found in Saldanha Bay and at Koppie Alleen. It is probably more widespread in this area.

Collection Sites in the south western Cape and Bolus Herbarium Number.

Saldanha Bay (54035,54034); Langebaan Lagoon (54039); Sea Point (54037); Kommetjie (54033); Clovelly (54036); Cape Hangklip (54038); Hermanus; Koppie Alleen 20°30' E 34°29'S.

ULVA RHACODES (Holmes)Papenfuss 1960. J.Linn.Soc p. 311

ENTEROMORPHA RHACODES Holmes 1894. Grevillea. 22:89-90.

(Plates 8 & 9)

Type: British Museum, Natural History, London!.

Type locality: Mouth of Kowie River, South Africa.

Description: Thalli of mature (reproductive) plants varying greatly in size. Epiphytic plants seldom > 10 cm in length and 1 cm in width. Larger plants found in drift, 10 - 20 cm in length and 10 - 15 cm in width. In small plants the thallus is macroscopically dentate, in larger plants dentation often becoming lappet-like. Pale yellowish green to grass green, the colour evenly distributed. Thallus thin and often ruffled with a very small holdfast usually without an obvious stipe.

Apical thallus: 40-60 µm wide. Cells in surface view closely packed, rounded, polygonal, some forming short rows of three cells. (Plate 9a). Cells in transverse section rounded short rectangular often almost spherical. L:B ratio

Plate 8. Ulva rhacodes collected at Scarborough.

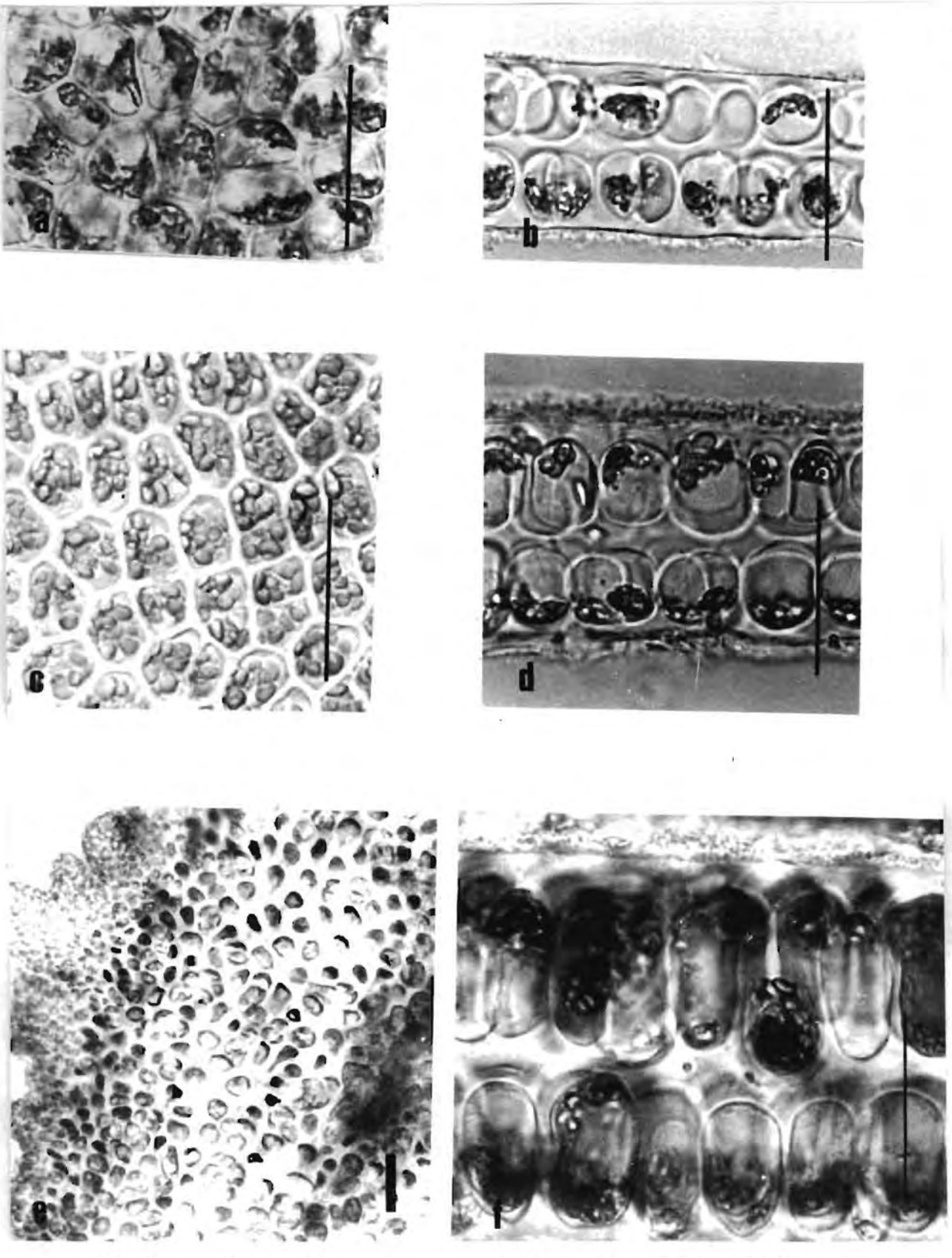


Plate 9. Ulva rhacodes **a:** surface of apical thallus **b:** transverse section of apical thallus **c:** surface of mid thallus **d:** transverse section of mid thallus **e:** surface of mid thallus showing smaller cells at toothed edge **f:** transverse section of basal thallus. (bar = 50 µm)

1.2:1. Cells 14-22 µm high, 10-22 µm wide (Plate 9b). Usually one, sometimes two pyrenoids.

Mid thallus: 50-65 µm thick. Cells in surface view polygonal, angular, closely packed, sometimes forming short rows of three to four cells decreasing in size from mid to edge of thallus rows (Plate 9 c,e). Cells in transverse section rounded, short rectangular. L:B ratio 1 - 1.5:1, 20-24 µm high, 12-24 µm wide (Plate 9d). Usually one pyrenoid.

Basal thallus: 65-110 µm thick, narrower at edge where cells are shorter. Cells in surface view rounded polygonal, decreasing in size from edge to mid thallus. Cells in transverse section rounded, short rectangular at the margins becoming more spherical in the central region. L:B ratio 1 - 1.5:1, 38-45 µm high, 18-20 µm wide. No "giant" cells observed as reported by v.d.Hoek and Donze (1968). Gametes and zoospores were seen to be released from separate plants and sporelings in culture showed the characteristic dentation within one month of growth.

Where sporelings from the Kowie estuary and Sea Point plants were grown through a range of temperatures, 4, 8, 12, 15, 19, 22, 26, 30°C, for 15 days with a L:D of 16:8, contrasting results were seen in the average growth rates. Sporelings from Sea Point failed to grow at either 4 or 30°C

whereas those from the Kowie survived for 10 days at 30°C and 15 days at 4°C. Greatest average growth rate was shown by the sporelings from Sea Point, in fact, the growth rate was nearly double that of the sporelings from the Kowie. This difference in growth rates of sporeling from plants in different areas would appear to indicate that there is genetic variation between populations of U. rhacodes on the South African coastline.

Ecology: This species was commonly found throughout the year in the south western Cape, from Table Bay to Hermanus. It is however apparently restricted to specific habitats and this could be the reason for its not being recorded here before this study. It does not occur in large, obvious populations, but in small aggregations, usually epiphytic (often on Cladophora spp.), in upper intertidal rockpools with constant water cover. Drift specimens were found and were always larger in size than attached specimens. A small number of specimens were found in sand inundated situations at Kalk Bay and Scarborough. The Type was collected in the lagoon-like mouth of the Kowie River where still water conditions prevail. Water temperatures in the Kowie estuary were found to vary on average 10°C daily in summer with a maximum water temperature of 24°C in summer and a low of 13°C in winter (Hill & Allanson, 1971). These temperature fluctuations are not generally found on the south western Cape coast except in upper intertidal

rockpools (Huggett & Griffiths,1986). Specimens from the Kowie River site were obtained during this study and these were notably larger than specimens collected in the south western Cape, often with lappet-like dentation and darker in colour. It is concluded that this species is restricted to areas of lesser wave stress, possibly due to its small holdfast, and that it is able to grow where water temperatures vary but do not drop below a critical level. Apart from southern Africa it has only been recorded from an estuary in Ria de Arosa on the north western coast of Spain (v.d.Hoek & Donze, 1968).

Taxonomy: The Type specimen was collected by Dr.H. Becker in 1889. It was sent, with a number of other species to E.M. Holmes, an English amateur phycologist. Holmes considered it initially to be "an Ulva like U. fasciata" (letters from E.M.Holmes to Dr. Becker in UCT Manuscripts Dept.), but he described it formally as Enteromorpha rhacodes in 1894. In this formal description he also commented that it "bears a superficial resemblance to Letterstedtia insignis". His decision to place the species in the genus Enteromorpha rather than Ulva was probably based on the fact that he received the specimens long after preservation and mentions that they were very fragile (Holmes, 1894). It is interesting to note that J. Agardh, to whom Holmes sent a specimen of U. rhacodes, considered it to be in the genus Ulva, not Enteromorpha (letters of J.

Agardh in the British Museum). The Type specimen, which was examined in this study, is completely bleached with long lappet-like dentate extensions. It is likely that the distromatic thallus separated due to its condition. Papenfuss (1960) sectioned a specimen from Port Alfred, on the eastern Cape coast, and reassigned the species to the genus Ulva as he found the thallus to be distromatic.

Distribution: Blouberg to Cape Hangklip in the south western Cape, Kowie Lagoon and Port Alfred in the eastern Cape, and in Europe at Ria de Arosa on the north western coast of Spain. Possibly occurs in other similar sites on the African coast and in southern Europe on the Mediterranean coastline.

Collection Sites in the south western Cape and Bolus Herbarium Number where available.

Sea Point Nos.54080,54079,54078,54064,54075; Camps Bay Nos.54071,54066; Kommetjie No.54077; Olifantsbos Nos.54073,54072; Scarborough 18°20'E 33°12'S; Simonstown; Dalebrook Nos.54069,54069,54067,54065,54062; Pearly Beach; Hermanus No.2143.

ULVA RIGIDA C.Agardh 1822. Species Algarum p.410-411.

(Plates 10 - 12)

Thuret, 1854; Agardh, 1883; Setchell & Gardner, 1920b; Dangeard, 1958; Papenfuss, 1960; Bliding, 1968; Krishnamurthy & Joshi, 1969; Abbott & Hollenberg, 1976; Womersley, 1984; Koeman, 1985.

Lectotype: LD14294! Lund, Sweden

Lectotype Locality: Cadiz, Spain.

Synonyms: Phycoseris rigida Kützing, 1849.

Ulva lactuca var. rigida Le Jolis, 1864.

Ulva lactuca var. rigida Hamel, 1931.

Ulva laingii Chapman, 1956.

Ulva geminoidea var. dentata Chapman, 1956.

Description: This species shows a great variation in morphology, usually according to environmental conditions. Thallus may be short rosette-like, or elongate orbicular or lanceolate with a firm to rigid texture. Usually always with microscopically visible dentation, often only on the stipe and basal portions of the thallus. Occasionally some plants had no microscopic dentation whilst on

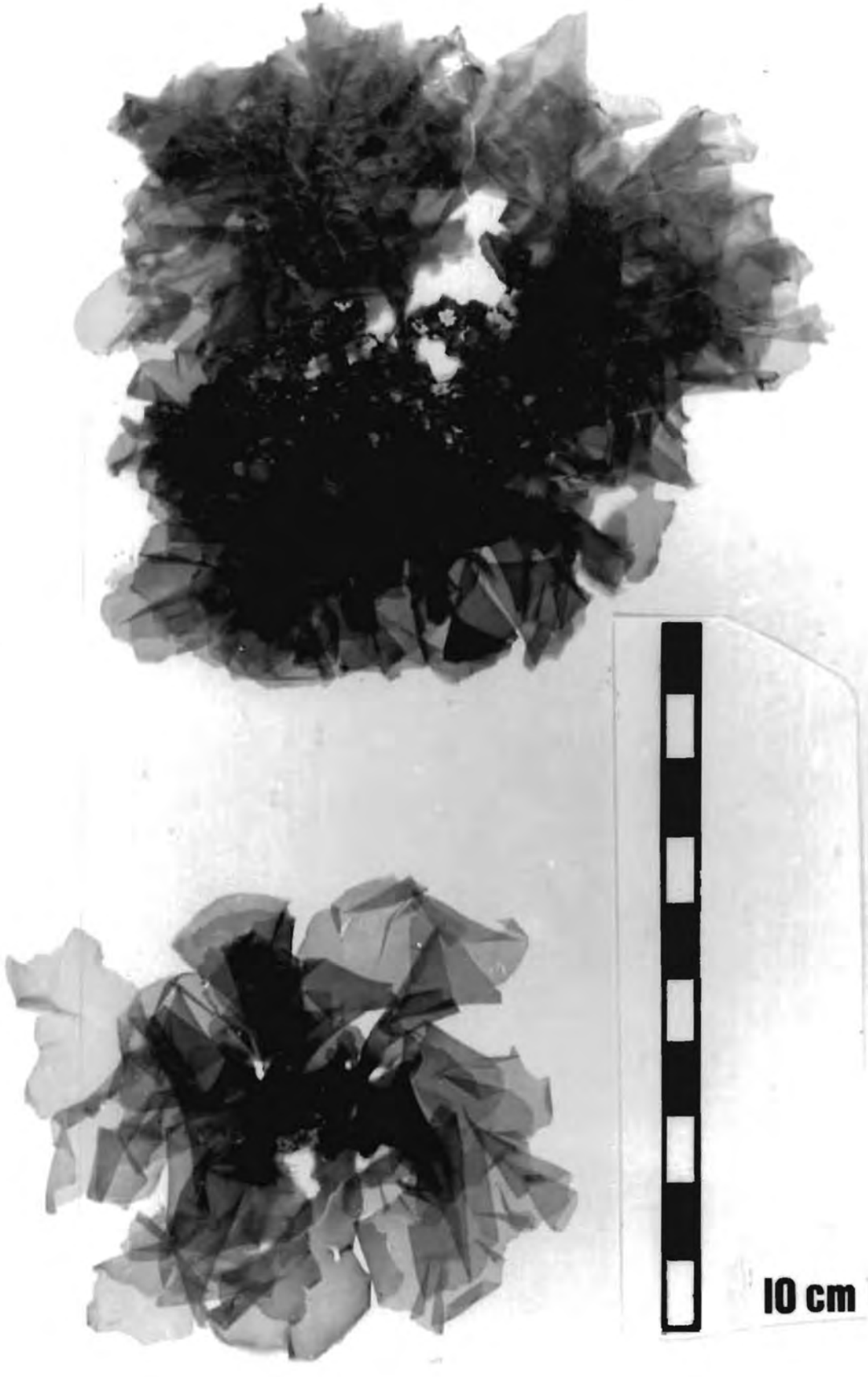


Plate 10. Ulva rigida collected at Dalebrook.

Plate 11. Ulva rigida collected at Rocklands in Table Bay.

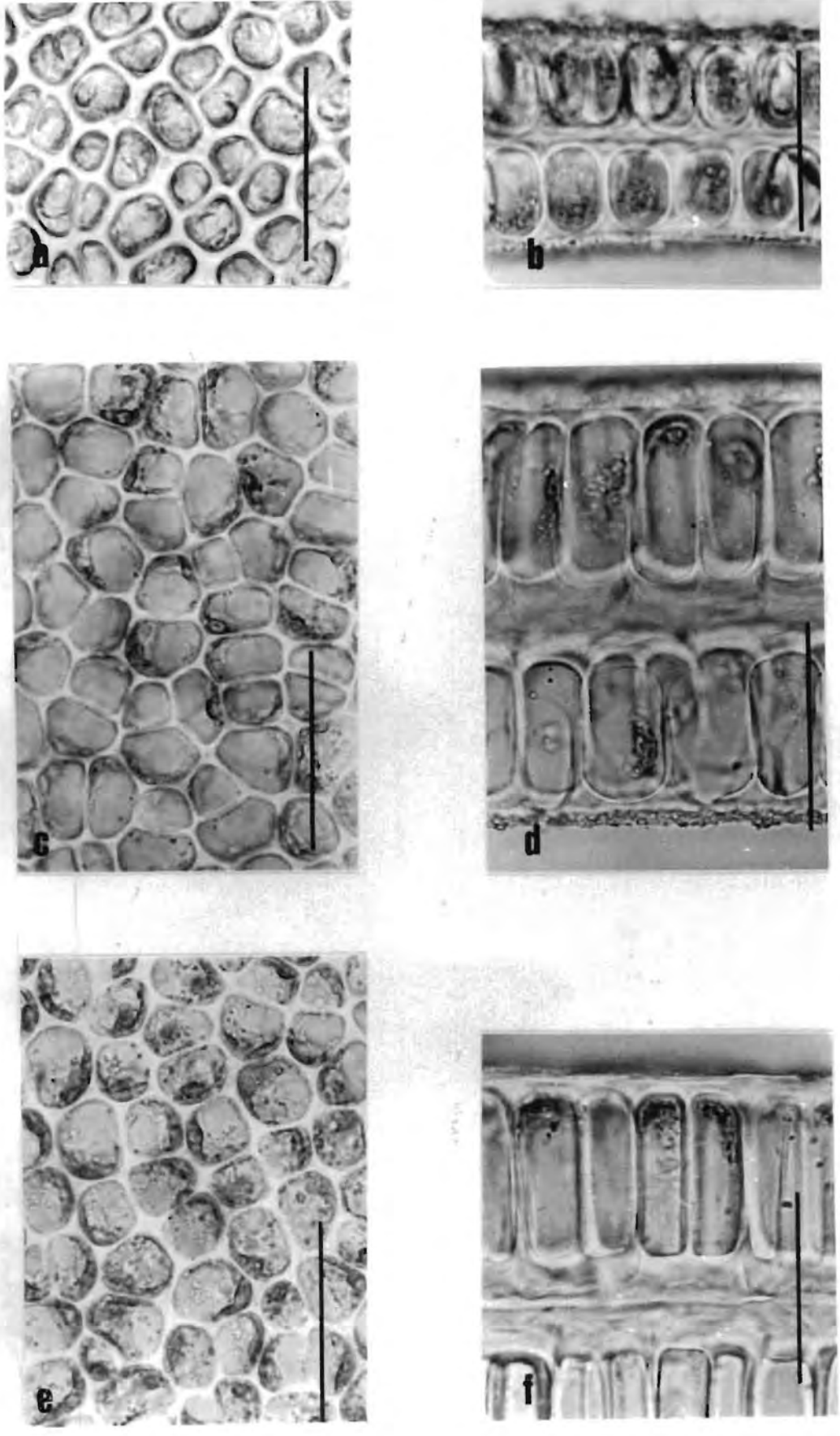


Plate 12. Ulva rigida **a:** surface of apical thallus **b:** transverse section of apical thallus **c:** surface of mid thallus **d:** transverse section of mid thallus **e:** surface of basal thallus **f:** transverse section of basal thallus. (bar = 50 µm)

others dentation was macroscopically visible. The thalli of larger plants were often found to have numerous perforations. Adult (reproductive) plants range in length from 2-30 cm. Width of rosette-like plants often greater than length and longer plants range from 2-15 cm in width. Holdfast usually well developed and a short, often curved, stipe present. Pale green to grass green, often darker in colour at the base, where marginal "wings" may be present in non-rosette type thalli.

Apical thallus: 50-95 µm thick. Cells in surface view polygonal, occasionally forming rows of three to five cells, but usually irregular (Plate 12a). Cells in transverse section well rounded, rectangular, L:B ratio 1.5-2:1, 24-30 µm high, 10-18 µm wide (Plate 12b). Pyrenoids 1 to 3.

Mid thallus: 70-110 µm thick. Cells in surface view polygonal, irregular, sometimes forming short rows (Plate 12c). Cells in transverse section rounded, rectangular, palisade-like, L:B ratio 2-2.5:1, 35-45 µm high, 15-20 µm wide (Plate 12d). Pyrenoids 1 to 2.

Basal thallus: 80-190 µm thick. Cells in surface view rounded polygonal (Plate 12e). Cells in transverse section, rounded, rectangular occasionally narrowing at the top, often shorter than in mid region (Plate 12f) with larger rhizoidal cells. Interstitial space wide sometimes

greater than single cell height. Biflagellate gametes and quadriflagellate zoospores were seen to be released from separate plants. Sporelings in culture were usually lanceolate, dark green in colour and without denticulation.

Ecology: This is one of the commonest Ulva species occuring throughout the year and at every site in the south western Cape. It is apparently physiologicaly and morphologicaly adaptable, enabling it to grow from the lower to upper intertidal regions, often forming dense populations. On flat wave exposed sites, especially where sandwash is prevalent e.g. Platboom, this species appears as a very short (2 cm), densely packed turf. Larger specimens were found where exposure was only for a brief period between tides. Smaller specimens were also found growing epiphytically on a range of other intertidal algae. At many lower intertidal sites this species often occurs with U. capensis. Its generally firm thallus and strong holdfast probably enable it to withstand the extremely strong wave action.

Taxonomy: Although this species is apparently cosmopolitan in occurrence it has been the source of some taxonomic controversy both in the past and in recent descriptions. Originally described by C.Agardh (1822) as occuring widely and "as far as the Cape of Good Hope" no original designated Type material has been located. J.Agardh described this

species as nearly always having crenate margins. It is uncertain as to who sent him these Cape of Good Hope specimens but he would possibly have seen Thunberg's Cape specimens, collected in Table Bay in 1773, in the Uppsala herbarium. Papenfuss (1960) examined specimens collected by Cabrera at Cadiz in Spain at the Agardh Herbarium and designated one, No. LD14294, as the Lectotype. Abbott & Hollenberg (1976) named the Type as coming from the Cape of Good Hope, possibly making this assumption from C.Agardh's original description (see Appendix II, page iii).

Kutzing (1849) placed this species in the genus Phycoseris and his drawing of the specimen on p.23 in his Phycoseris Generalis (1843) closely resembles the photograph of the Lectotype (Papenfuss, 1960). Areschoug (1851) considered U. rigida specimens from "the Cape" in Agardh's Herbarium to be U. capensis. He concluded that U. rigida Ag. "is a European species" (see Appendix II, page vi). Le Jolis (1863) considered rigida to be a form of U. lactuca. A Le Jolis specimen, labelled U. lactuca var rigida, collected at Cherbourg in 1873, which is in the Bolus Herbarium (No.28219) has very definite microscopic dentation on the margins and the cell shapes conform to those which are ascribed to U. rigida by Bliding (1968) and Koeman & v.d.Hoek (1980). Grunow (1867) examined Ulva specimens collected by Dr.Pappe in Table Bay. He maintained rigida as a separate species in the genus Phycoseris and states

that the basal cells are very different to those of U. capensis. J.Agardh (1883) maintained the position of rigida within the genus Ulva, but described this species as having many forms (see Appendix II). His drawings of U. rigida (Tab.IV.figs.119 - 122,1883) show the dentate (crenate) margins. De Toni (1889) maintained rigida as a form of U. lactuca. These early taxonomists found that U. rigida/U. lactuca var rigida was nearly always dentate and had a thallus thickness greater than that of U. lactuca.

Jaasund (1977) described U. rigida forma tropica, collected in Tanzania. He unfortunately failed to state the locality of the Holotype or where it was lodged but in this study I obtained two specimens, No. x63 and No.5-a, from the Gothenberg Herbarium which Jaasund had collected in Tanzania and annotated as U. rigida f. tropica. In his original description Jaasund (1977) stated that this form had smooth margins and in Jaasund (1976) the illustration of the basal cells shows them as being narrow elongate. On examination these specimens were all found to be microscopically dentate and only some of the cells in the base were narrow elongate. It was concluded therefore that these specimens did not conform to the description for U. rigida f. tropica as given by Jaasund and they should be annotated as U. rigida.

Chapman (1956) lists U. lactuca var. rigida (Ag.) Le Jol. as found in New Zealand, but does not mention dentation in the

species which was a feature mentioned by Le Jolis (1863). Chapman also described two new species, U. laingii and U. geminoidea var dentata from New Zealand. Their descriptions encompass the range of morphology of U. rigida found in this study and I consider them to be synonyms of U. rigida.

Bliding (1968) stated that U. rigida differed from other European species of Ulva in that it had dentate margins. Tanner (1979) found specimens of U. rigida in the north east Pacific to conform with the description given by Bliding. Koeman & v.d.Hoek (1980) stated that U. rigida may or may not be dentate, had distinct longitudinal ribs (a feature not mentioned by other taxonomists) and that the thallus in the basal region was thicker than other species examined in their study. Phillips (1983) considered that U. rigida sensu Bliding did "not agree with the type specimen of U. rigida C. Agardh" on the grounds that Bliding's (1968) description and drawing of the basal cells of U. rigida did not agree with those of Papenfuss's (1960) illustration of the cells from the Lectotype of U. rigida. It should be noted however that Papenfuss did not state that the cells illustrated were from the basal thallus. Papenfuss merely states that the drawing was made from a "section of the thallus". Phillips (1983) states that U. rigida in southern Australia "does not possess microscopic marginal teeth" which contradicts the original description by

C.Agardh (1822) and the description and illustration by J.Agardh (1883). Womersley (1984), who also examined species of Ulva in southern Australia, found that U. rigida usually had "microscopic spines on areas of intact margin". Phillips (1983) considered that U. rigida in southern Australia had palisade-like cells in the basal region (contrary to U. rigida of Bliding) which agreed with the description by J.Agardh (1883). This description (see Appendix II, page xiv) states that there is a wide range of forms and that the cells in the cells in the basal ("rigid part") region of the thallus may be "more or less quadrate or a little longer anticlinally than tangentially", "three times longer anticlinally than tangentially" or "attenuated towards the outside". In this study it was found the the shape of the basal cells was not constant for U. rigida and that the gross thallus morphology and appearance of the cells in transverse section of the apical, mid and basal regions must be assessed as a whole.

Distribution: Warm temperate to tropical seas. Namibia (Engledow pers. comm.), west coast of South Africa (R. Simons pers. comm.), eastern Cape (Seagrief, 1988), Natal (Levring, 1938) and the south western Cape from Paternoster to Cape Agulhas.

Collection Sites in the south western Cape and Bolus Herbarium Number where available.

Paternoster; Melbosstrand; Blouberg; Rocklands No.54087,54086; Sea Point; Oudekraal; Kommetjie No.54083; Platboom No.54090; Buffels Bay No.54091,54089; Dalebrook No.54088; Gansbaai No.54084; Koppie Alleen 20°30'E 34°29'S No.54081.

TAXONOMIC DISCUSSION OF *ULVA UNCIALIS*, *ENTEROMORPHA (ULVA) ATROVIRIDIS* AND *CHLOROPELTA CAESPITOSA*.

Ulva uncialis (Kützing) Montagne was originally acknowledged as a Suhr species by Kützing (1849), Areschoug (1851), Agardh (1883) and De Toni (1889). However, no record of Suhr's description can be found in his publications on Cape algae (1834, 1836, 1839, 1840, 1841). Authorship of this species is now attributed (Seagrief, 1984) to Kützing (1849) who described (p.475) and illustrated (plate 16) a specimen collected by Drege on the Kaffern Kuste (Transkei, Eastern Cape) as *Phycoseris uncialis*. Papenfuss designated this specimen, No.L910.187.352! in the Leiden Herbarium, as the Lectotype in 1955.

Kützing (1849) described the species as having a small thallus, irregularly lobed and with undulate margins. The name *uncialis* comes from the Latin "uncia", meaning the twelth part of a foot, and was probably first used by Drege, indicating that this is a small species reaching one inch in height.

The Lectotype, which was examined in this study, is a small (2.5 cm) specimen. The apical thallus is 35-40 µm thick in transverse section, with cells approximately 1.5 x higher than broad and with rounded corners. The basal thallus was approximately 100 µm thick with rectangular cells interspersed between rhizoidal cells whose basal extensions formed a thick mid interstitial layer. Unfortunately, due to the poor condition of the specimen it was not established whether there was any dentation. Areschoug (1851) considered U. uncialis to be a synonym of U. capensis ("a young form"). J.Agardh (1883) considered U. uncialis as a capensis form of U. rigida. In the Bolus Herbarium, a specimen labelled U. uncialis, which appears to have been sent by E.M.Holmes to J.Agardh is annotated in Agardh s hand "a juvenile form of U. rigida". De Toni (1889) lists U. uncialis in a group with U. capensis "species less well known or of uncertain affiliation".

Drege did list the collection of Ulva uncialis at Paardeneiland in Table Bay (Meyer, 1844). His collections were sold to many herbaria and Barton (1893) indicated that a Drege specimen of U. uncialis collected in Table Bay was in the British Museum. At the onset of this study it was considered possible that this species would be found in the south western Cape. Papenfuss (1940) states that "the plants distributed by Suhr are of

a species which is distinct from U. capensis". He unfortunately did not describe U. uncialis but did designate the Lectotype in 1955.

During this study no species of Ulva was found that had thalli which did not grow to a length greater than 3 cm and which had features making it distinct from other species. Some populations of U. rigida and U. rhacodes were only composed of small plants but this was due to environmental factors such as grazing, wave action etc. It would be expected that if, indeed, U. uncialis were a definitive species a distinct population of these plants would have been found as was the case with other species. According to the illustration made by Kützing (1849), sections made of the Lectotype and investigations made in this study it seems very likely that U. uncialis is a synonym of U. rigida.

Enteromorpha (Ulva) atroviridis (Levr.) Wynne comb.nov.

This species was originally described by Levring (1938) and the Type, from Port Nolloth, was seen in this study. It is readily discernable from Enteromorpha linza by its much darker colour and longer cell length in transverse section. Despite the fact that the cell layers are not joined in parts of the margin of the Type, Levring placed this species in the genus Ulva. Wynne

(1986) found this species in Swakopmund, Namibia, and reassigned it to the genus Enteromorpha because of the non-distromatic edges of part of the thallus and the hollow stipe.

This species was found at Langebaan, Sea Point and Kommetjie in the south western Cape. When the specimens were sectioned it was found that only parts of the upper margins of the thalli were not distromatic at the edges and that the stipe was only partially hollow in the very central region. Enteromorpha atroviridis and E. linza are different from other species of Enteromorpha in that they have unbranched thalli which are mainly distromatic. It is this feature which possibly prompted Kutzing to erect the genus Phycoseris where the stipe was hollow and the thallus was not entirely tubular but flattened and joined in parts. Silva (1952) was of the opinion that the differences between the two genera, Ulva and Enteromorpha, needed reassessment. Bliding (1968) and Womersley (1984) state that Ulva is entirely distromatic throughout, but Koeman and v.d.Hoek (1980) reported that Ulva curvata in the Netherlands had a hollow stipe. Bliding (1963), in his description of Enteromorpha, states that "the mature thallus is always hollow; either throughout cylindrical and tubulous or only in the stipe...but higher up flattened with the cavity sometimes divided into two".

Chloropelta caespitosa Tanner (1980) is a genus which has links with both *Enteromorpha* and *Ulva*. *C. caespitosa* was described by Tanner (1980) from a collection made in California. It was found during this study at Dalebrook near Kalk Bay on upper intertidal rocks and also at Cape Hangklip in upper intertidal rockpools (Joska & Bolton, 1992 - see Appendix I). In this genus the tubular germling, which is monostromatic, develops a distromatic thallus. Cells in the upper section of the tubular monostromatic plant start dividing parallel to the surface and the thallus thus becomes distromatic and commonly splits to form a flattened peltate blade. In both *Ulva* and *Enteromorpha* the initial monostromatic tubular germlings appear similar but whereas in *Ulva* a distromatic blade is formed from the collapsing and adherence of the monostromatic layers of the germling in *Chloropelta* the distromatic blade is formed from the cells of the monostromatic layer dividing in a plane parallel to the surface. In *Enteromorpha* the thallus remains monostromatic in its development and life history. Biflagellate gametes and quadriflagellate zoospores were released from separate plants while the plant was still hollow but distromatic, and germlings were also seen to develop from cells at the apex and at the base.

SUMMARY AND KEY TO THE SOUTH WESTERN CAPE SPECIES OF ULVA.

In this study, five species of Ulva were found to occur in the south western Cape, U. capensis, U. fasciata, U. lactuca, U. rhacodes and U. rigida. One species, U. rhacodes, had not been previously reported for this area and another, U. lactuca, was found to be rare despite its being commonly reported in past literature. It is likely that many specimens accredited to U. lactuca were, in fact, U. rigida. U. uncialis was considered not to be a valid species, and the assignment of U. atroviridis to Enteromorpha atroviridis (Wynne, 1986) is accepted.

This is a genus known for the "plastic" morphology of species. Although most recent taxonomic studies have given keys to the species (Tanner, 1979; Koeman & v.d.Hoek, 1980; Phillips,1983; Womersley,1984) a notable exception was Bliding (1968). Morphological criteria for these keys have not been the same, with emphasis being placed on thallus shape (Tanner, 1979; Womersley, 1984), thallus shape, chloroplast position and cells in the basal thallus (Phillips, 1983). Koeman & v.d.Hoek (1980) used a wide range of features, but used the number

of pyrenoids for initial distinction. With the benefit of the information from these modern studies it became evident that there was often variation within a species and also often similarity of features between species.

Thallus morphology showed greatest variation in U. rigida. Plants ranged from very short, turf-like populations with microscopic dentation to lanceolate forms with macroscopically visible dentation. This latter form of U. rigida appeared very similar to U. capensis in the field. Similarly, in the field, small plants of U. fasciata appeared the same as small plants of U. rigida. Dentation of the thallus which was always found to be macroscopic in U. capensis and U. rhacodes makes these species easily distinguished in the field. Where dentation was microscopic, as in U. rigida and U. fasciata, these species were often only distinguishable when sections were made and the thickened midrib cells of U. fasciata were seen. U. fasciata, although always having lanceolate thalli, showed variation in the amount of ruffling at the margins and at some sites a number of lanceolate thalli were formed above a short main thallus and these plants approached the form of some specimens of U. rigida. U. lactuca, which is not dentate, is very similar to some forms of U. rigida, where occasionally specimens had entire margins. It is only by sectioning

the thallus to measure thickness and comparing the apical cells that the difference may be seen.

Although colour variation was not objectively assessed it was noted that there is a general tendency towards specific colour in some species. It was also noted that U. rigida and U. fasciata commonly showed colour variation within the thallus. Short, turf-like forms of U. rigida were usually paler in the basal thallus and U. fasciata is always paler in the center, thicker, portions of the thallus.

South African specimens of both U. lactuca and U. rigida exhibited exactly the same basal anatomical features as found in European plants. Except for Enteromorpha atroviridis (formerly U. atroviridis), none of the species collected in the south western Cape had a basal central cavity. Very few specimens of any species examined in this study showed microscopic longitudinal ribs. "Wings" of small, non rhizoidal cells were found in a number of specimens in a variety of species but this was not found to be of such a consistent occurrence as to warrant its inclusion for species identification. Rhizoidal cells were commonly found to be larger than normal cells in all species. It was found in this study that the size of rhizoidal cells was generally variable

within and between species.

The length, breadth and shape of cells in transverse section was found to be the most consistent feature for species definition. However the cell shape and size in the apical, mid and basal sections of the thallus must all be considered. Surface view, showing arrangement and shape of cells in the thallus allowed some differentiation between species but was not absolute between U. rigida, U. fasciata and U. rhacodes. Form, size and arrangement of cells was found to be a limited guide to species when seen in surface view, but very important in transverse section of the apical, mid and basal thallus. Whilst the spindle-shaped cells of U. capensis and the spherical cells of U. rhacodes have a characteristic surface appearance the quadrate and rectangular cells of U. lactuca and U. rigida and U. fasciata, respectively, often appear the same in surface view. Also, U. capensis and U. rhacodes were sometimes found to have rectangular cells in the apical and mid thallus and thus the surface view appeared similar to that of the other three species. Transverse sections of the apical, mid and basal thallus which showed cell shape and size were found to be one of the most reliable comparative features for the species examined.

Although there was some similarity between species in

either the apical, mid or basal thallus, the cells of these regions showed definite trends within species. Additional features such as thallus morphology and ecological factors were taken into consideration.

Although Koeman (1985) found that pyrenoid number was a reliable means of definition in species of Ulva in the Netherlands this was not found to be the case for species in the south western Cape. The number of pyrenoids often varied in different sections of the thallus of an individual species and a similar number of pyrenoids was found in different species. Chloroplast position was used by Phillips (1983, 1990) but not used by Womersley (1984) as a means of discriminating between species in southern Australia. In this study the chloroplast position in all species was too similar to use as a definitive feature. It was noted that the chloroplasts of the basal cells were very often "clotted" in appearance where the chloroplast had divided into many small granular bodies.

Method of reproduction for all species was the same with biflagellate and quadriflagellate zoids being formed in the margins of the apical thallus. As was reported by Tanner (1979) and Phillips (1983) the similarity in size of the biflagellate and quadriflagellate zoids between species did not allow for differentiation between

species. Biflagellate gametes in all species were seen to fuse or, occasionally, not fuse but develop into sporelings. There was also no notable difference in size between biflagellate gametes but quadriflagellate zoospores were always larger than the gametes. Zoospores ranged from 9 - 13 µm in length and 5 - 7 µm in width whilst gametes ranged from 7 - 10 µm in length and 3 - 5 µm in width.

It was noted in this study that if any section of the thallus, above the stipe, was removed/stressed and placed in culture medium the cells would often become sporogenous. Also, many specimens were found with small darkened areas in the base of the thallus, possibly an initial rhizoidal cell area. This ability of Ulva cells could possibly account for the "specialised regions" of reproductive cells or darkened areas that were found by Chapman (1952) and prompted his decision to erect a new genus, Gemina.

Sporelings were cultured in four species - U. capensis, U. fasciata, U. rhacodes and U. rigida. U. capensis and U. rhacodes had sporelings which were easily distinguishable with one month of growth. In both species dentation developed at an early stage, in U. capensis at the apex and on the entire margin in U. rhacodes. The sporelings of U. fasciata and U. rigida

were lanceolate and similar in shape, there was no dentation apparent after two months growth. In U. fasciata however, the sporelings remained very pale green in colour whilst U. rigida sporelings were a darker green.

It became apparent in this study that in the south western Cape ecological factors play an important role in the distribution of different species of Ulva. U. rigida with its range of morphology was cosmopolitan in its distribution on the rocky intertidal shore. U. capensis and U. fasciata occured only on the lower and subtidal regions of the shore. The latter species appears very locally restricted in its distribution however although the populations found remained constant. U. lactuca, rarely found, occured epilithically in mid intertidal exposed ares and unattached subtidally in sheltered areas. U. rhacodes was not known to occur in the south western Cape prior to this study. During the period of this study a specimen was also found in Swakopmund in Namibia (Pers.comm H.Engeldow) Usually always diminutive in size in the south western Cape, this species was probably overlooked because it occurs in the select habitat of upper intertidal rockpools, epiphytic on Cladophora sp. It is probable that the prevalent rough water conditions favour species with thicker thalli such as U. rigida and U. capensis. Thinner or

lanceolate thalli such as found in U. lactuca, U. fasciata and U. rhacodes preclude their common occurence except in select habitats.

Ulva is not an easy genus as has been commented on by Tanner (1979), Phillips (1983) and Koeman (1985). This can also be seen in the publications of older taxonomists (see Appendix II) where range of morphology and other limiting factors led to alternate "lumping" and "splitting" of species. What further complicates species definition is the lack of original Types. Only U. rhacodes has an known extant original Type. The Type for U. lactuca was "found" by Papenfuss (1960) and he too designated a Lectotype for U. capensis (Papenfuss,1940) and U. rigida (Papenfuss, 1960). U. fasciata also has no original Type, nor a designated Lectotype. This latter species was one of the first (1813) designated after U. lactuca and the contention of the status of U. nematoidea, U. costata, U. stenophylla, U.taeniata and U. dactylifera will probably remain as a result of this.

As a result of this study it is felt that U. capensis is not an endemic species, as was originally thought and probably occurs on other southern hemisphere coastlines where conditions are similar to those in the south western Cape Province. It is also possible that U. rhacodes may also have a wider distribution than was

originally thought. Considering that it was found in Spain (Hoek.v.d. & Donze, 1968) it is highly likely to occur in the Mediterranean as well. U. rigida, U. lactuca and U. fasciata, which were investigated in this study and by Tanner (1979) and Phillips (1983) remain species whose absolute definition is contentious.

KEY TO *ULVA* SPECIES IN THE SOUTH WESTERN CAPE.

---

1. Thallus multiple or occasionally single lanceolate with a paler thicker midrib. Margins moderately to markedly ruffled ... *U. fasciata*

   Thallus not multiple lanceolate and no paler midrib present. Margins not markedly ruffled. .... 2.

2. Thallus with macroscopically or microscopically dentate margins. ..... 3.

   Thallus without macroscopically or microscopically dentate margins. ..... 5.

3. Dentation macroscopic, often double. ..... 4.

   Dentation microscopic, often on basal margins only. ..... *U. rigida*

4. Cells in basal thallus distinctly elongate, spindle-shaped in transverse section. Thallus dark green, very firm to the feel. ..... *U. capensis*

   Cells in basal thallus rounded, often spherical, no higher than broad in transverse section. Thallus yellow green to grass green, even in colour, thin to the feel. ..... *U. rhacodes*

5. Thallus thin and soft, seldom thicker than 55 µm at the apical margin. Apical cells quadrate to subquadrate, barely rounded in transverse section. ..... *U. lactuca*

   Thallus not thin and soft, usually thicker than 55 µm at the apical margin. Apical cells rectangular, rounded, always longer than broad in transverse section. ..... *U. rigida*

ACKNOWLEDGEMENTS

I would like to thank Dr John Bolton for his patience, help and support enabling me to complete this study. Partial financial support was given by the FRD. I am indebted to Dr Herre Stegenga for the many taxonomic discussions and translations from French, Mr Richard Simons of the Seaweed Unit at the University of Cape Town for the translations of original descriptions in Latin, Mr Henry Botha and Mr Raymond Carelse of the Botany Department for technical help.

REFERENCES:

ABBOTT, I.A. & HOLLENBERG,G.J. 1976. Marine Algae of California. Stanford Univ. Press, Stanford. California. 827pp.

AGARDH, C.A. 1822. Species Algarum.1.Lund. 531pp.

AGARDH, J.G. 1883. Til Algernes Systematik.VI.Ulvaceae. Acta. Univ. Lund., 19(2).1-182 + plates.

ARASAKI, S. 1984. A new aspect of Ulva vegetation along the Japanese coast. Hydrobiologia, 116/117:229-232.

ARDRÉ, F. 1967. Une Ulve à thalle remarquable des cotes du Portugal. Rev. Algol. Nov. Ser. Tome VIII.Fasc.,4:292-296.

ARESCHOUG, J.E. 1851. Phyceae Capensis. Uppsala. pp 186.

ARESCHOUG, J.E. 1854. Phyceae novae et minus cognitae in maribus extraeuropaeis collectae. Act. Reg. Soc. Sci. Upsala, Series III, 1:329-372.

BARTON, E.S. 1893. A Provisional List of the Marine Algae of the Cape of Good Hope. J. Bot.,31:53-54.

BENNETT, B., GRIFFITHS, C.L. & PENRITH, M. 1983. The diets of littoral fish from the Cape Peninsula. S.Afr. J. Zoo. 18(4):343-352.

BLACKMAN, F.F. & TANSLEY, A.G. 1902. A revision of the classification of the green algae. New Phytol., 1:17-24, 133-144.

BLIDING, C. 1963. A Critical Survey of European taxa in Ulvales.1. Capsosiphon, Percursaria, Blidingia Enteromorpha. Op. Bot. Soc. Lund, 8:1-160.

BLIDING, C. 1968. A Critical Survey of European Taxa in Ulvales.II. Ulva, Ulvaria, Monostroma, Kornmannia. Bot. Notiser., 121:535-629.

BOLD, H.C.& WYNNE, M.J. 1985. Introduction to the Algae. 2nd.Ed. Prentice-Hall, New Jersey. 940pp.

BOLTON, J.J. 1986. Marine Phytogeography of the Benguela Upwelling Region on the West Coast of Southern Africa: A Temperature Dependent Approach. Bot. Mar. 29:251-256.

BOLTON, J.J. & ANDERSON, R.J. 1990. Correlation between Intertidal Seaweed Community Composition and Sea Water Temperature Patterns on a Geographical Scale. Bot. Mar. 33:447-457.

BOLTON, J.J. & STEGENGA, H. 1987. The marine algae of Hluleka (Transkei) and the warm temperate/subtropical transition on the east coast of southern Africa. Helgolander Meeresunters. 41:165-183.

BONNEAU, E.R. 1977. Polymorphic behaviour of Ulva lactuca (Chlorophyta) in axenic culture. 1.Occurrence of Enteromorpha-like plants in haploid clones. J. Phycol., 13:133-140.

BONNEAU, E.R. 1978. Asexual Reproductive Capabilites in Ulva lactuca L.(Chlorophyceae).Bot.mar.,21:117-121.

BORGESEN, F. 1914. The marine algae of the Danish West Indies. Part I. Chlorophyceae. Dansk. Bot. Arkiv. 1:1-158.

BORZI, A. 1895. Studi algologici Fasc.2, [i-viii], 121-378, pls. 10-31. Palermo.

BORY DE SAINT VINCENT, J.B. 1828. Cryptogamie. Voyage autour du Monde ... la corvette La Coquille. M.Duperrey,Paris.

BRITZ, S.J.& BRIGGS, W.R. 1976. Circadian Rhythms Chloroplast Orientation and Photosynthetic Capacity in Ulva. Plant Physiol., 58:22-27.

CHAMBERLAIN, Y.M. 1990. The genus Leptophytum (Rhodophyta, Corallinaceae) in the British Isles with descriptions of Leptophytum bornetii, L.elatum sp.nov. and L.laeve. Br. phycol. J. 25:179-199.

CHAPMAN, V.J. 1952. New entities in the Chlorophyceae of New Zealand. Trans. R. Soc. N.Z. 80:47-58.

CHAPMAN, V.J. 1956. The Marine Algae of New Zealand 1. Myxophyceae & Chlorophyceae. J. Linn. Soc., 55:331-501.

DANGEARD, P. 1951. Sur une espece d Ulva de nos cotes atlantiques (U.olivacea n.sp.). Botaniste, 35:27-34.

DANGEARD, P. 1958. Sur quelques especes d Ulva de la region de Dakar. Botaniste, 42:163-171.

DELF, E.M. 1921. Marine Algae of the Cape Peninsula. S.Afr. J. nat. Hist., 3(1):53-64.

DELF, E.M. & MICHELL, M.R. 1921. The Tyson Collection of Marine Algae. The Annals of the Bolus Herbarium, 111(2):89-121.

DELILE, A.R. 1813. Flore d'Egypte. Explication des Planches. In: France Description de l'égypte pendant l'Expedition de l'Armée Francaise. Histoire Naturelle, 2:145-320.

DE TONI, G.B. 1889. Sylloge Algarum. Vols.1 & 2. Padua. 1315pp.

FORTES, M.D. & LUNING, K. 1980. Growth rates of North Sea macroalgae in relation to temperature. irradiance and photoperiod. Helgolander Meeresunters. 34:15-29.

FØYN, B. 1934. Lebenszyklus, Cytologie und Sexualitat der Chlorophycee Ulva lactuca L. Protistenk. 83:154-177.

FØYN, B. 1955. Specific Differences between Northern & Southern European Populations of the Green Alga Ulva lactuca L. Pubbl. Staz. Zoo. Napoli., 27:261-270.

FØYN, B. 1960. Sex-linked Inheritance in Ulva. Biol. Bull., 118:407-411.

GAYRAL, P.& MAZANCOURT, J. 1959. Sur une espece nouvelle d'Ulva. Recoltee en estuarie au Maroc. Ulva dangeardii nov.sp. Botaniste, 42:131-141 + plates.

GERKING, S.D. 1984. Assimilation and Maintenance Ration of an Herbivorous Fish, Sarpa salpa, Feeding on a Green Alga. Trans. Am. Fish. Soc. 113:378-387.

GRIFFITHS, D.J. 1970. The Pyrenoid. Bot. Rev., 36:29.

GRIFFITHS, D.J. 1980. The pyrenoid and its role in algal metabolism. Sci. Prog., Oxf. 66:537-553.

GRUNOW, A. 1867. Reise Seine Majestat Fregatte Novara um die Erde. Botanische Theil.1 Band. Algen. Kaiserliche-koniglichen Hof und Staatsdrukerie, Vienna.

GUNN, M. & CODD, L.E. 1981. Botanical Exploration of Southern Africa. A.A. Balkema, Cape Town. 400 pp.

HAMEL, G. 1931. Chlorophycees des cotes francaises. Rev.algol., 5:1-54.

HILL, B.J.& ALLANSON, B.R. 1971. Temperature tolerance of the estuarine prawn Upogebia africana (Anomura, Crustacea). Mar. Biol., 11:337-343.

HINE, A.E. 1977. A Glossary of Phycological Terms for Students of Marine Macroalgae. St.Alden's in the Weeds, North Carolina. 90pp.

HOEK, C.van den 1964. Criteria and Procedures in present-day algal taxonomy.p.31-58.In: Algae and Man.(Ed: D.F.Jackson) Plenum Press,New York.

HOEK, C.v.d. & DONZE, M. 1968. A Contribution to the Knowledge of Ulva rhacodes (Chlorophyceae,Ulotrichales). Nova Hedwigia, 10(3/4):495-498 + plates 144-149.

HOEK, C.v.d., STAM, W.T. & OLSEN, J.L. 1988. The Emergence of a new chlorophytan system, and Dr.Kornmann's contribution thereto. Helgoländer Meeresunters, 42:339-383.

HOEKSMA, B.W. & HOEK, C.van den 1983. The Taxonomy of Ulva (Chlorophyceae) from the Coastal Region of Roscoff (Brittany, France). Bot. mar., 26:65-86.

HOLMES, E.M. 1894. A New Species of Enteromorpha. Grevillea 22:89-90.

HOWE, M.A. 1914. The Marine Algae of Peru. Mem. of the Torrey Bot. Club., 15:1-185.

HUGGETT, J. & GRIFFITHS, C.L. 1986. Some relationships between elevation, physico-chemical variables and biota of intertidal rock pools. Mar. Ecol. Prog. Ser. 29:189-197.

JAASUND, E. 1976. Intertidal Seaweeds in Tanzania.1st Ed. Univ. of Tromso, pp.160.

JAASUND, E. 1977. Marine Algae of Tanzania. V. Bot. mar., 20:333-338.

JOSKA, M.A.P. & BOLTON, J.J. 1992. Chloropelta caespitosa, a new record for southern Africa. S.A. J. Bot., 82:

KAPRAUN, D.F. 1970. Field and Cultural Studies of Ulva and Enteromorpha in the Vicinity of Port Arkansas, Texas. Contrb. Mar. Sci., 15:205-247.

KOEMAN, R.P.T. 1985. The taxonomy of Ulva Linnaeus and Enteromorpha Link,1820 (Chlorophyceae) in the Netherlands. Ph.D.Thesis. Rijks Univ.Groningen.201pp.

KOEMAN, R.P.T. & HOEK, C. van den 1981. The taxonomy of Ulva (Chlorophyceae) in the Netherlands. Br. Phycol. J., 16:9-53.

KORNMANN, P.& SAHLING, P.H. 1977. Meeresalgen von Helgoland. Wiss. Meeres-unters, 29:1-189.

KRISHNAMURTHY, V.& JOSHI, H.V. 1969. The species of Ulva from Indian waters. Bot. J. Linn. Soc., 62:123-130.

KUTZING, F.T. 1843. Phycologia generalis oder Anatomie, Physiologie und Systemkunde der Tange. Leipzig, Brockhaus.

KUTZING, F.T. 1849. Species Algarum. Brockhaus. Lipsiae 922pp.

KUTZING, F.T. 1856. Abbildungen der Tange. Tab. Phyc. VI. Band. Nordhausen. 95pp.

LAWSON, G.W.& JOHN, D.M. 1982. The Marine Algae and Coastal Environment of Tropical West Africa. 1st Ed. J.Cramer, Vaduz. 470pp.

LE JOLIS, A. 1863. Liste des algues marines de Cherbourg. Mem. Soc. Sci. Nat. Cherbourg, 10:1-168.

LEVRING, T. 1938. Verzeichnis einiger Chlorophycean und Phaeophycean von Sud Afrika. Lunds. Univ. Arsskr. N.F. Adv.2, 34(9):1-25.

LINK, H.F. 1820. Epistola...de algis aquatics in genera disponendis.p.1-8 In: Horae physicae berolinensis. C.G.D.Nees von Esenbeck.Bonn

LINNAEUS, C. 1753. Species plantarum...2. Stockholm.

LIPKIN, Y & SAFRIEL, U. 1972. Intertidal Zonation on Rocky Shores at Mikhmoret (Mediterranean, Israel) J. Ecol., 59:1-30.

MATHIESON, A.C., NORTON, T.A. & NEUSHUL, M. 1981. The Taxonomic Implications of Genetic and Environmentally Induced Variations in Seaweed Morphology. Bot. Rev., 47:313-347.

MATTOX, K.R. & STEWART, K.D. 1980. Comparative Cytology in the Taxonomy of the Ulvaceae and Certain other Green Algae. p.409-420. Proc.International Symposium on Taxonomy of Algae.1980 (Ed: T.V.Desibackery & Asst.Ed: V.N.Baja Rao).

MEYER, E. 1844. Zwei pflanzengeographische documente von J.F.Drege. Flora 1843 Band II, Leipzig. 52pp.

MIGITA, S. & FUJITA, Y. 1987. The life history of Ulva fasciata Delile (Chlorophyceae,Ulvales) in culture. Jap. J. Phycol., 35:226-230.

MSHIGENI, K.E. & KAJUMOLO, A.A. 1979. Effects of the environment on polymorphism in Ulva fasciata Delile (Chlorophyta,Ulvaceae). Bot. mar., 22:145-148.

MÜLLER, R.H.W. & ZAUNICK, R. 1960. Friedrich Traugott Kützing 1807 - 1893. Aufzeichnungen und Erinnerungen. J.A. Barth, Leipzig. pp.298.

PAPENFUSS, G.F. 1940. A revision of the South African marine algae in the herbarium Thunberg. Symb. bot. upsal., 4(3):1-18.

PAPENFUSS, G.F. 1960. On the genera of the Ulvales and the status of the order. J. Linn. Soc.(Bot.), 56:303-318.

PHILLIPS, J.A. 1983. Field, Anatomical and Cultural Studies of Southern Australian species of Ulva (Ulvaceae,Chlorophyta) Ph.D.Thesis. Monash Univ. 213 pp.

PHILLIPS, J.A. 1984. The Validity of Morphological and Anatomical Characters in Distinguishing Species of Ulva in Southern Australia. p.353-361 In: Systematics of the Green Algae. (Ed:D.E.G.Irvine & D.M. John) Academic Press, London.

PHILLIPS, J.A. 1988. Field, Anatomical and Developmental Studies on Southern Australian species of Ulva (Ulvaceae, Chlorophyta) Aust. Syst. Bot., 1:411-456.

PHILLIPS, J.A. 1990. Life history studies of Ulva rigida C.Ag. and Ulva stenophylla S. et G. in Southern Australia. Bot. mar., 33:79-84.

POCOCK, M.A. 1939. A Phenomenal Drift of Seaweed in False Bay. J. S.Afr. Bot., 7:75-79.

PROVASOLI, L. 1968. Media and prospects for cultivation of marine algae. p.47-44 In: Cultures and collections of algae. (Eds. A Watanabe and A Hattori). Tokyo: Japanese Society of Plant Physiology 1968.

REED, R.H.& RUSSELL, G. 1978. Salininity Fluctuations and their Influence on "Bottle Brush" Morphogenesis in Enteromorpha intestinalis (L) Link. Br. phycol. J., 13:149-153.

REED, R.H. & RUSSELL, G. 1979. Adaptation to Salinity Stress in Populations of Enteromorpha intestinalis (L) Link. Est. Coastal Mar. Sci., 8:251-258.

ROUND, F.E. 1984. Systematics of the Chlorophyta. p.1-27 In: Systematics of the Green Algae. (Ed:D.E.Irvine & D.M. John) Academic Press, London.

SEAGRIEF, S.C. 1984. A Catalogue of South African Green, Brown and Red Marine Algae. Memoirs of the Botanical Survey of South Africa. No.47. Botanical Research Institute Dept.of Agriculture, Pretoria. 72pp.

SEAGRIEF, S.C. 1988. Marine Algae. pp 35-72. In: A Field Guide to the Eastern Cape Coast (Eds. R.A. Lubke, F.W. Gess & M.N. Bruton) Wildlife Society of Southern Africa.

SETCHELL, W.A. & GARDNER, N.L. 1920a. Phycological Contributions.I. Univ. Calif. Publs. Bot., 7(9):279-324 + plates.

SETCHELL, W.A. & GARDNER, N.L. 1920b. Phycological Contributions.II. Chlorophyceae. Univ. Calif. Publs. Bot. 8(2):139-374.

SILVA, P.C. 1952. A Review of Nomenclatural Conservation in the Algae from the Point of View of the Type Method. Univ. Calif. Pub. Bot., 25(4):241-324.

STAEHELIN, L.A. 1988. Chloroplast Structure and Supremolecular Organization of Photosynthetic Membranes p.4-19 In: Encyclopedia of Plant Physiology Vol.19 (Eds: A.Pirson & M.H.Zimmerman) Springer-Verlag, Berlin.

STEFFENSEN, D.A. 1976. Morphological Variation of Ulva in the Avon-Heathcote Estuary, Christchurch. N.Z. J. Mar. Freshwat. Res., 10(2):329-341.

STEPHENSON, T.A. 1948. The Constitution of the Intetidal Fauna and Flora of South Africa.III. Ann. Natal Mus., 11(2):207-324.

SUBBARAMAIAH, K., KALE, S.R. & KRISHNAMURTHY, V. 1967. Gametes and Germlings of Ulva fasciata Delile. Current Science, 5: 128-129.

SUHR, J.N. VON. 1834. Ubersicht der Algen, welche von Hrn. Ecklon an der sudafrikanischen Kuste gefunden worden sind. Flora Jena 17:721-735,737-743.

SUHR, J.N. VON. 1836. Beitrage zur Algenkunde. 2. Flora Jena 19:337-350.

SUHR, J.N. VON. 1839. Beitrage zur Algenkunde. Flora Jena 22(5):65-75.

SUHR, J.N. VON. 1840. Beitrage zur Algenkunde.4-6. Flora Jena 23:257-265,273-282,289-298.

SUHR, J.N. VON. 1841. Beiträge zur Algenkunde. Verhandl. Kaiserl. Leopold.-Carol. Akad. d. Naturf. 18, suppl. 1:273-288.

TANNER, C. 1979. The Taxonomy & Morphological Variation of Distromatic Ulvaceous Algae (Chlorophyta) from the northeast Pacific.
Ph.D. Thesis.Univ.of British Columbia. 249 pp.

TANNER, C. 1980. Chloropelta gen.nov., an ulvaceous green Ulva with a different type of development. J. Phycol., 16:128-137.

TANNER, C. 1986. Investigations of the taxonomy and morphological variation of Ulva (Chlorophyta): Ulva californica Wille. Phycologia, 25(4): 510-520.

TAYLOR, W.R. 1937. Marine Algae of the Northeastern Coast of North America. Univ. of Michigan Press, Ann Arbor. 870pp.

THURET, G. 1854. Note sur la synonymie des Ulva lactuca et latissima L. suivie de quelques remarques sur la tribe des Ulvacees. Mem. Soc. Sci. Nat. Cherbourg., 2:17-32

WATSON, D.C. & NORTON, T.A. 1985. The Physical Characteristics of Seaweed Thalli as Deterrents to Littorine Grazers. Bot. mar., 28:383-397.

WOMERSLEY, H.B.S. 1984. The Marine Benthic Flora of Southern Australia. Part 1. Government Printer South Australia. 329 pp.

WYNNE, M.J. 1986. Report on a collection of benthic marine algae from the Namibian coast (south-western Africa). Nova Hedwiga, 43:311-355.

APPENDIX I Accepted for publication in S.A.J.Bot. Vol.58 1992

Chloropelta caespitosa Tanner 1980, an unusual Chlorophyte, newly reported for South Africa.

M.A.P. Joska & John J. Bolton

Department of Botany, University of Cape Town,
Rondebosch 7700.

Chloropelta caespitosa, was found at Dalebrook in False Bay and Cape Hangklip and represents the first record outside North America. This monospecific genus was first described by Tanner (1980) from California. This genus differs from other genera in the Ulvaceae in that young plants have an initial tubular monostromatic thallus which later becomes distromatic when cells divide in a plane parallel to the surface.

Chloropelta caespitosa was eers in Dalebrook in Valsbaai, en later by Cape Hangklip ontdek en dit verteenwordig die eerste waarneming buite Noord Amerika. Hierdie monospesifiese genus was eers beskryf van Kalifornië deur Tanner (1980). Hierdie genus verskil van ander genera in die Ulvaceae in dat jong plante 'n buisvormige monostromatiese tallus het wat later ontwikkel tot 'n distromatiese vorm wanneer die selle ewewydig aan die oppervlak deel.

Keywords: Chlorophyta, Chloropelta, South Africa.

In 1980, Tanner described a new genus and species of seaweed found in southern California. Because of its unusual developmental pattern he placed this species in the family Ulvaceae (Chlorophyta) in a new genus, Chloropelta. This genus has not, to our knowledge, been previously recorded outside North America.

The family Ulvaceae, sensu Bliding (1963; 1968) previously contained three genera, Ulva, Enteromorpha and Ulvaria. These three genera are characterised by the similar initial development of a uniseriate filament. Longitudinal cell division then takes place and eventually a hollow tubular thallus is formed, closed at both ends. In Ulva species the tube becomes flattened and cross sections of the thallus reveal a distromatic thallus. In Enteromorpha, the thallus remains hollow although species such as E. linza often have partially distromatic tissue (Kapraun, 1970). In Ulvaria species the monostromatic tube splits to form a monostromatic thallus. Tanner (1980) presents a more complete discussion.

In 1985, specimens which appeared similar to those described by Tanner (1980) were found in a green algal turf growing on small boulders in the upper intertidal zone at Dalebrook, in False Bay on the Cape Peninsula (34° 8'S, 18° 27'E) and have since been found at Cape Hangklip (34° 23'S, 18° 48'E). At both Dalebrook and Cape Hangklip, adult plants were found

with conical, peltate and flattened blades. Both sites experience extremely strong wave action. Plants and saccate germlings grew from a well developed rhizoidal system. Plants at Cape Hangklip were found growing epiphytically on Cladophora spp. in a midtidal rockpool.

Plants from Dalebrook were placed, individually, in 200 ml crystallizing dishes containing Provasoli ES medium (Provasoli, 1968) at 15° C and 30 - 40 µmol $m^{-2}.s^{-1}$, and sectioned during various stages of development.

The tubular germlings collected from Dalebrook developed a characteristic "baseball bat" shape when 3mm to 5mm in length (Fig.1.) Transverse sections of these germlings revealed a hollow monostromatic tube. Larger plants at a later stage of development were more bulbous at the upper half of the thallus. Transverse sections made of these thalli showed that cells just above the rhizoidal region were dividing parallel to the surface and thus a distromatic thallus was being formed (Fig.2). Biflagellate zoids were released singly through papillae on some cells at the apex. The sporangia contained only 6 - 8 zoids. It was also noted that some germlings developed directly from cells at the apex. With disintegration of the apex a "raft" of germlings was released. Quadriflagellate zoospores were not seen to be released although Tanner (1980) found these in field specimens in California. Once zoids had been released the rounded top section of the tubular thallus

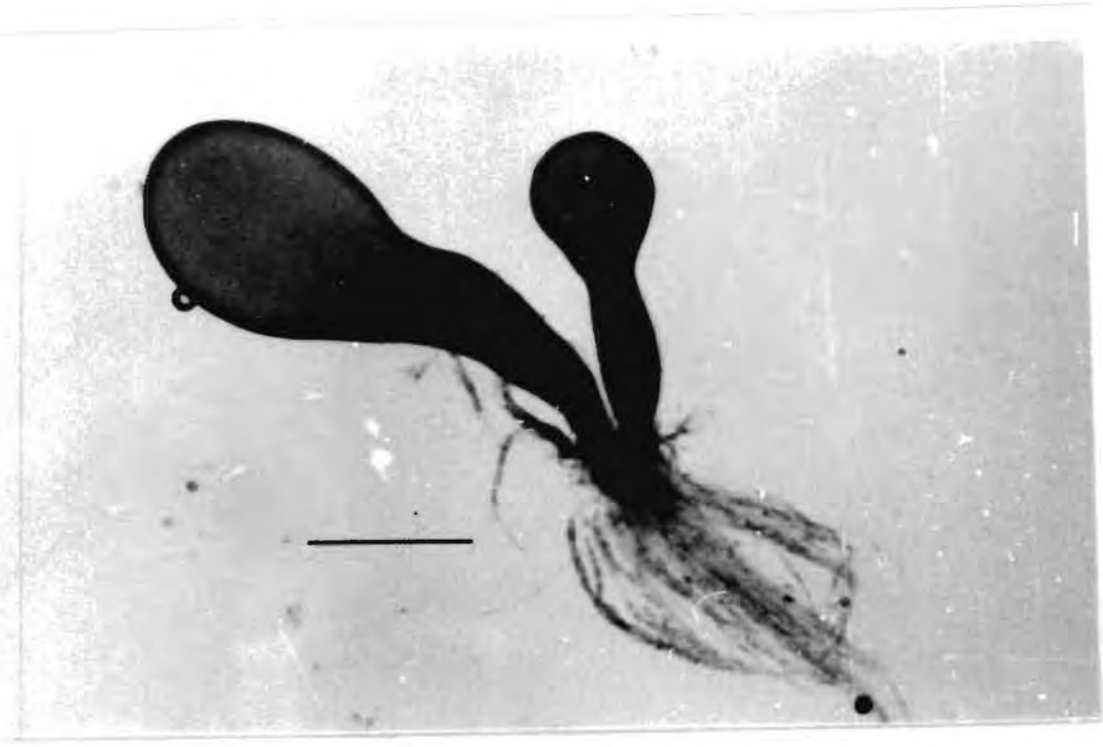


Figure 1: Young, tubular Chloropelta caespitosa plant from Dalebrook with characteristic "baseball bat" shape (bar = 1 mm).

Figure 2: Transverse section of adult thallus from Dalebrook plant showing both monostromatic and distromatic cell layers (bar = 10 µm).

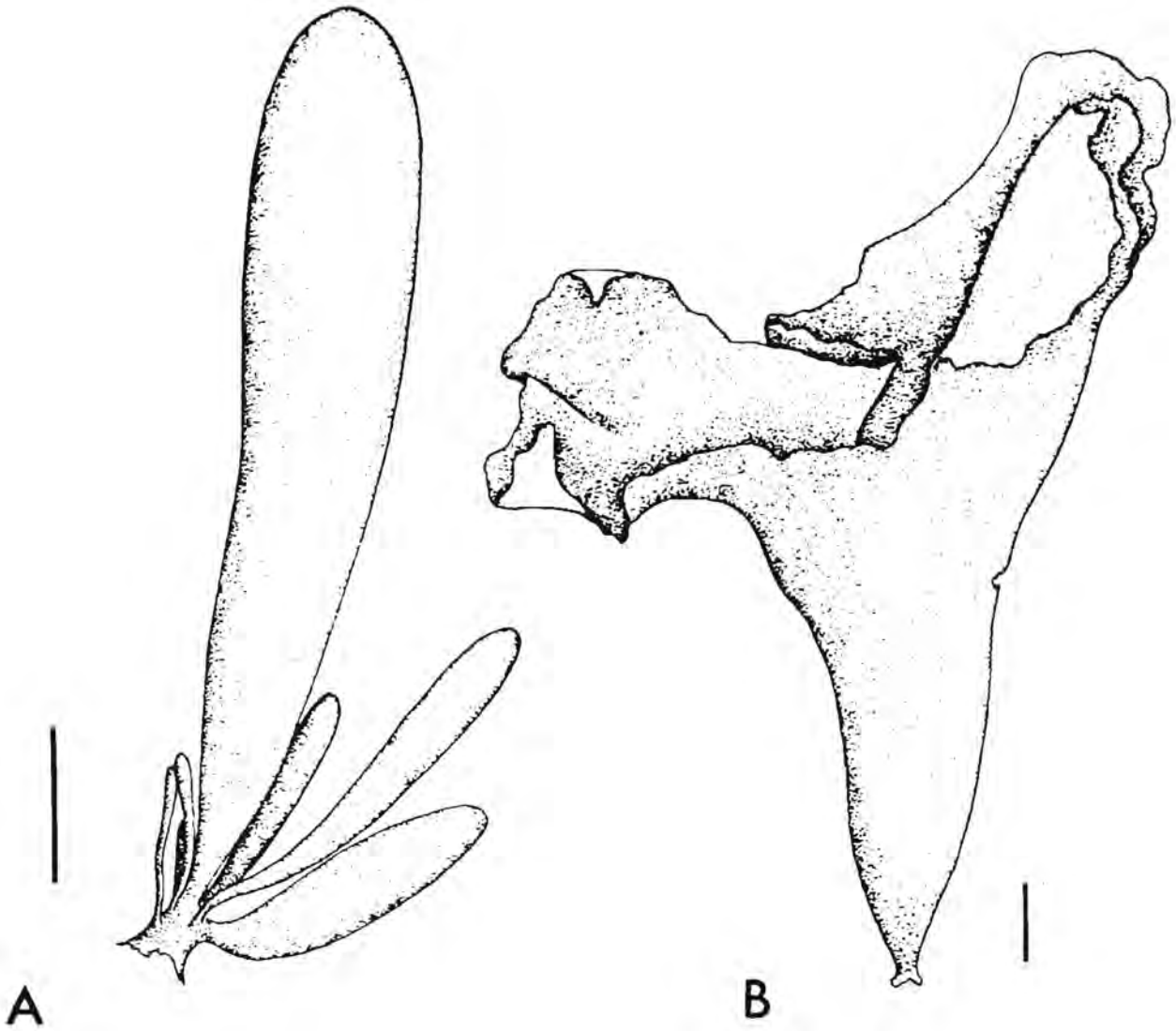


Figure 3: Habitat drawing showing, A. young tubular plant (bar = 0.5 mm) B. adult conical plant (bar = 1 mm). (Drawing by H. Stegenga)

degenerated and the opened tube became conical (Fig.3), or in some cases a flattened, distromatic thallus. Zoids released from reproductive cells were not seen to fuse in specimens from the field and in the one generation cultured. Adult specimens found at the original sites in Dalebrook and Cape Hangklip were seldom greater than 12 mm in length. A very well developed rhizoidal system with septa often produced sporelings.

Except for the fact that the specimens collected at Dalebrook released only biflagellate zoids rather than biflagellate and quadriflagellate zoids, it was concluded that they otherwise conform to the developmental and morphological pattern as described for C. caespitosa by Tanner (1980). Preserved specimens have been placed in the marine algal collection at the Bolus Herbarium (BOL) in the Botany Department of the University of Cape Town (Dalebrook: Bol.No.54111, Cape Hangklip: Bol.No.52655).

References:

BLIDING, C. 1963. A critical survey of European taxa in Ulvales, Part I. Capsosiphon, Percursaria, Blidingia, Enteromorpha. Op. bot. soc. bot. Lund. 8: 1-160.

BLIDING, C. 1968. A critical survey of European taxa in Ulvales, Part II. Ulva, Ulvaria, Monostroma, Kornmannia. Bot. Not. 121: 535-629.

KAPRAUN, D.F. 1970. Field and cultural studies of Ulva and Entermorpha in the vicinity of Port Aransas, Texas. Contrib. Mar. Sci. 15: 205-295.

PROVASOLI, L. 1968. Media and prospects for the cultivation of marine algae. In: Cultures and collection of algae. Proceedings of the U.S.-Japan conference, Hakone. Sept. 1966. eds. Watanabe, A. & Hattori, A. Jap. Soc. Plant Physiol. 1968: 63-75.

TANNER, C.E. 1980. Chloropelta gen. nov., an ulvaceous green alga with a different type of development. J. Phycol. 16: 128-137.

APPENDIX II

Translations from the original Latin were made by Mr Richard Simons and from the original French and German by Dr Herre Stegenga of some descriptions of Ulva species applicable to this study. They have been included as an appendix in that they were of value and have been referred to in the main text.

Author	Ulva (Phycoseris)	Page
Delile, M. (1813)	fasciata.	ii
Agardh, C. (1822)	rigida.	iii
Bory de St. V., J.B.. (1828)	nematoidea.	iv
Kützing, F.T. (1849)	rigida, lobata β	v
	africana, fasciata,	
	linza.	v
Areschoug, J.E. (1851)	capensis, uncialis.	vi
Le Jolis, A. (1863)	lactuca α rigida,	
	lactuca τ lactuca.	viii
Grunow, A. (1867)	capensis, nematoidea.	xii
Agardh, J.G. (1883)	rigida, capensis, linza,	
	fasciata,uncialis.	xiv
De Toni, J.B. (1889)	capensis, fasciata, linza,	
	lactuca. uncialis.	xxv
Hamel, G. (1931)	fasciata, lactuca.	xxx

Delile, M. 1813 Flore D'Egypte

Explication des Planches

Pages 153 and 154.

ULVA FASCIATA

This plant is membranous, not very tough (coriaceous) having nevertheless more consistence than Ulva lactuca. Its stems are three to ten decimetres long (1 to 3 feet), digitated into long strips which are curly (curled) on the edges, sinuous and briefly toothed (i.e. with small "teeth"), 3 to eight centimeters wide (one to three inches), narrowing insensibly towards the tip, terminating in sharp thin strips. The branches or long narrow strips of this plant are of a slightly darker and less transparent green on the edges than in the middle (of the blades).

Ulva fasciata carpets the bottom of the new port of Alexandria, from the town pier (Quoy) to the mooring ground of the boats/vessels near the lighthouse. Several persons, while swimming, have torn from the bottom of the clear and limpid water, this plant of a very beautiful green like that of ivy.

Agardh, C. 1822 Species Algarum

Vol. 11

Page 410

Ulva rigida, frond split into lobes towards the base, the lobes curved-curled and rigid.

U. plicata Roth Cat. 1.p.208 & fl. Germ. p.539

U. lactuca Engl.Bot.t. 1551? - Dec.Syn. p.3

In the Atlantic Ocean as far as Cape of Good Hope. - In the Mediterranean and Black Seas. Desfontaines and Cabrera donated the specimens.

This species is immediately distinguishable by its rigidity, thickness and dark colour; much smaller than Ulva latissima. The frond torn into lobes almost to the shield-shaped attachment, the lobes of various lengths, 4-7 inches, and gradually dilating from a narrowed base, curled or curly, often crenate, if not indeed ciliate along the margins. Points or seeds of the frond larger than those of U. latissima and U. lactuca, thickly scattered. The substance is thicker than that of the last two species, though the frond is evidently composed of two layers easily separating. Gaudichaud collected a specimen of a similar Ulva at the Sandwich Islands. Also this umbilicate species is often encountered with lobes expanded into circular discs. Though the figure from Engl.Bot (not seen) is cited, it may better apply to U. plicata fl. Dan.

Bory de Saint Vincent, J.B. 1828. Cryptogamie.
Voyage autour du
Monde la corvette La Coquille.
Page 190.

75. Ulve nematoide, Ulva (Nematoidea).

It is from Conception, on the coast of Chile that M.d'Urville has brought back this elegant species. We have learnt, from another voyager (sailor), who found it at the Bay de los Chorillos, that the inhabitants of the Peruvian coast call it Cucha-luio - which they pronounce Chutcha-louio. The second word signifies, in the language of the country: grass or weed: .....Ulva nematoidea derives this name from the form of its divisions, which resemble pretty green ribbons curled at the edges. These divisions are about two feet long and one inch wide; they originate from the margins of the frond (thallus) in a confused manner - however apparently in pairs; the frond (thallus) is fixed laterally and its form could be said to be palmate if the divisions were not so irregular as they issued from it. Sometimes these straps (divisions) are enlarged (wider) and forked at their extremities, which are normally obtuse and very rounded too. The colour is of a beautiful bright grass-green, uniform throughout; it is this (the colour) which principally distinguishes it from the following.

13. Phycoseris rigida Kg. Phyc. gener. p. 298. - P. tissue tough and cartilaginous, deeply lobed, lobes curved, undulate; stipe flat, thickish; cells rounded-cuboid. - Ulva rigida Ag. - in the mediterranean (v.s.)

19. Ph. lobata Kg. - P. tissue shortly stipitate, soon very broadly expanded, divided many times, segments broad, lobed, and sinuous, rounded obtusely at the apex, contracted at the base. Chile (v.s.)

β africana; tissue rigid, dilated, irregularly ovate or elliptic, lobed or variously split. (Blade often perforated so as to look rather like a sieve, now and then irregularly dentate or ciliate at the margins.). Pappe collected it in Table Bay, Pappe No. 87 (v.s.)

20. Ph. fasciata Mont.Fl. d'Alger. p.151. - P. tissue stipitate, shortly cuneate at the base, elongate, linear. attenuated, acute. -
Ulva fasciata Delile Egypt p.153. - Ulva divisa Suhr - Ulva nematoidea Bory. - segments dilated, short, curly-undulate. - In the Mediterranean, Adriatic and tropical Atlantic on the shores of both Europe and Africa; in the Pacific in Chile. (v.s.)

Areschoug, J.E. 1851 Phyceae Capensis
Uppsala.
Pages 15 & 16.

1. ULVA CAPENSIS Aresch.

Thallus intensely green, formed of two layers of cells 0,05 mm to 0,10 mm thick, affixed by a navel-like pad from which it expands into variously torn lobes, finally elongate with linear stipes elliptical entire or lobed undulate, at the margin lacerate. At the base attenuated into a linear stipe, cells vertically linear and very dense.

Synonyms include: Ulva lactuca sensu Thunberg for the Cape
U. rigida Ag. ref to the Cape.
U. uncialis Suhr.
etc.

From Table Bay, where it is very common, along all shores in the south as far as Algoa Bay and perhaps further. If the synonym of Krauss truly belongs to this taxon then the distribution extends into Natal. Younger thalli are about one inch high, attached to the rocks by a navel-like pad from which it expands in every direction, lobed and variously torn; this form includes, at least in part, Ulva uncialis Suhr, that contains young forms of many different species, distinguished by size rather than by other characters. Fully developed, truly this thallus is a foot or even up to 2 feet high and 6-8 inches wide, oblong elliptic, simple or lobed and the undulate margin of the

same entire or shredded, intensely green, more or less attenuated at the base into a linear flat stipe, thicker below than above, rigid and firm, constructed of two cell layers, and hence corresponds to Phycoseris of Kützing. The synonymy suggested here is not advanced with any great certainty. I am convinced, though, that among the many collections available to us from the Cape that none is either Ulva latissima or U. sordida (cfr. Enum. Phyc. Scand.) - U. rigida Ag. is a European species and according to specimens that J. Agardh has given us entirely different from our Cape species.

Forma ß africana of U. lobata Kütz. spec. l.c. is certainly synonymous, but the primary (and perhaps only) form of U. lobata collected on Chilean shores, can scarcely be the same if one takes into account the description, for which reason we are necessarily erecting a new name. In the name U. uncialis Suhr, we are being badly deceived because it represents the juvenile forms of many species. I hope specimens of U. uncialis sent to us by the author are of our species U. capensis.

Obs.: U. latissima Thunberg Fl. Cap. ed. Schultes p.741 is, according to the description, our U. capensis, though it is stored in Thunberg's herbarium as Iridaea orbitosa Suhr. His herbarium is not always useful to gain an understanding of species described in Flora Capensis.

Le Jolis, A. 1863 Liste des algues marines de Cherbourg. Page 38.

U. lactuca - α rigida (Ag.) - U. Lactuca Linn. Spec.plant.II, p.1163; Light. Flocs II, p.970; DC.Fl.fr.I, p.9 (pro parte). - U. plicata Roth Catal.bot.I, p.208. - U. rigida Ag. Spec.alg.I, p.410; J.Ag. Alg.mar.med. p.17; Le Jol. Alg.mar.Cherb. No.239. - U. latissima Grev. Alg.brit. p.171; De Not. Alg.mar.ligust. p.26; Harv. Phyc.brit. pl.171 (pro parte); Chauv. Alg.Normand. No.39; Lloyd Alg.de l'Ouest, No.24. - Phycoseris australis Ktz. Spec.alg. p.477 (non Ulva australis Aresch. Phyc.nov. p.44).

Thallus thick and rigid, for the most part with many deep splits, irregularly lacinate and eroded at the margins or may be entire, intensely darker in colour at the base.

On rocks and stones; at low tide level. All the year through. - C

I have understood here Ulva rigida in the sense of the modern authors, since the phrase of C.Agardh "Ulva Lactuca multo minor" is not at all in agreement with this plant, or rather, undoubtedly concerned some form of small size. I have not been able to see differences between the plant of the Ocean and that of the Mediterranean; and the same herbarium specimens of our coast, labeled Ulva rigida by Mr J. Agardh, have been named Phycoseris australis by Mr

Kützing. Ulva rigida was certainly included in Ulva lactuca palmata prolifera of Linnaeus and of (the) old authors, and even these days the English algologists confuse it (or: mix it up) with the two following varieties under the general name of U. latissima. Although there exist no clear cut characters between those three plants that allow to separate them specifically, yet Ulva rigida shows a denser tissue, a more rigid and coriaceous consistency especially near the base; most often it forms tufts proliferating in all directions, (consisting of) fronds that are irregularly incised and eroded along the edges; but those margins are flat or little folded, and not regularly undulate as in the 3e variety. The colour of U. rigida is of an intense green and blueish near the base when it grows at very low tide level.

p. 40

- γ Lactuca (Linn.). - Ulva Lactuca Linn. Spec.plant.ii, p.1163(partim); Esper Ic.fuc. p.3, t.3; Smith. Engl.Bot. T.1551; Thur. in Mem.soc.sc.nat.Cherb.II, p23. - U. latissima σ palmata Ag. Spec.alg.I. p.409 (pro parte excl. syn. plurim.). - U. latissima Grev. l.c.; Harv. l.c. (partim). - U. lactuca marina a Nacc. Algol.adriat. p. 49. - Phycoseris gigantea Ktz. Spec.alg. p.476 (partim). - Ulva Linza Auct.veter. (forma peculiaris).

on stones and algae, at high tide level and low tide level. All year through. - CC. - Form c on Napoleon beach; forms d and f in sandy places; form e almost always parasitic (translator:probably means epiphytic).

The various forms of the 3° group (Lactuca) are in general distinguished by a softer consistency, a less dense tissue, a less intense green colour, approaching yellowish, and especially by their fronds with entire and undulate margins (;) (fronds) having a very outspoken tendency to lengthen into ribbons twisted along their (length) axis (Translator: sentence structure changed!). Sometimes the marginal folds largely project from the holdfast of the thallus and it (the thallus) looks umbilicate; sometimes, on the other hand, it (the thallus) is narrowing towards the base into a sort of stipe. Forma multifida is often flat on the margins and thus approaches Ulva rigida; but its consistency is soft and its ribbons retain a clear tendency to twist; it sometimes resembles certain herbarium specimens from the Mediterranean, which have been assigned to Ulva fasciata. Forma amplissima, distinguishable from U. latissima only in its youth, at that time presents a nearly round thallus with entire margins and large radiating folds. Forma simplex, often of umbilicate appearance, is more or less folded on the margins which are entire and continuous (;) it (f. simplex) merges into forma contorta when lengthening. The latter presents during all stages of its development long fluted and spirally twisted ribbons; in

herbaria one finds it often enough under the name Ulva linza, just like, for that matter, the other ribbon-shaped forms of U. lactuca. As for forma Dillenii, in my opinion it is certainly the plant illustrated by Dillen under the name Tremella marina fasciata, on which Linne has established his Ulva linza; it represents the transition of the distromatic Ulvas in which the two cell layers are joined in all parts of the thallus, to the Ulvas that are tubular at least at the base, and which for that reason are included in the next species.

Grunow, A. 1867 Reise Seine Majestat
Fregatte um die Erde.
I Band. Algen. 42-43.

2. Ph. capensis (Areschoug). - Ulva capensis Aresch.
Phyc. novae et min. cogn. - Areschoug.
Phyc. extraeurop. exsic. No. 59.
Cape of Good Hope.

Large form with long lanceolate fronds (lobes). A similar species from Table Bay, Cape was given to the Novara-Expedition by Dr. Pappe as Ulva rigida Ag. to which this specimen possibly belongs as a variety. But I find that a cross section of the lower parts in Kützing's drawings of Ph. rigida as well as the one that J.Agardh named as a specimen of this species in Hohenacker's Meeresalgen No. 207, different. In Ph. rigida the cells are here (in the lower parts) rounded, but Ph. capensis, in contrast, are elongated - rather like Kützing has shown in Ph. planifolia and Ph. Ligula in his Tab. phyc. VI. t.18,f. l.c. and f.2.

3. Ph. nematoida (Bory) Mont.
Var. latior: laciniis brevioribus. -
Phycoseris lobata Kg. Tab. phyc. VI.t 27. Madeira.
Forma brevior: tenuius membranacea.Madeira.

These specimens agree extremely well with a similar soft (pliant) form which Gaudichaud had collected at Rio de Janeiro (Herb. Berol.)

Var. augustior: laciniis longioribus. Gibraltar, New Zealand and Chile.

The specimens from Chile are similar to the previous variety. These from Gibraltar and New Zealand have narrowed, up to 7 inches long, stongly undulated, fronds — and so are much more similar to specimens which Gaudichaud collected in Peru and have more than 1 foot long fronds. According to Montagne Ph. nematoidea (Bory) is not identical with U. fasciata Delile (in Hohenacker's Meeresalgen No.261 as Ulva nematoidea Bory as attested by J.Agardh). As far as I can see, the latter (Ulva fasciata) is somewhat more rigid, less wavy and distinctly toothed, however, in some forms it is very difficult to separate them.

Agardh, J.G. 1883 Till Algernes Systematik. Volume VI: 168 - 174.

** Cells gradually elongating in an anticlinal direction until they are about or somewhat more than double their tangential dimension; at the surface they appear round-angled.

6. ULVA RIGIDA (C. Ag. Sp. p. 410) somewhat erect, stipulate, stipes at length obvious, when young, fronds are pale green slender and membranous, with ageing (and chiefly in the lower parts) darkening, firm and finally indeed almost cartilaginous, broadly expanded and lobed, wider lobes rounded, or if narrower then elongated, the thallus more often more or less perforated with rounded holes, cells anticlinally elongated, up to 3 times longer than the diameter, the interstitial space in the lower parts densely crammed with rhizoids (Tab. IV. Fig. 119-122).Forms of this differ to quite a degree:

a. Firmer substance, somewhat rigid when dried

α Rigida frond more firmly membranous, obovate-dilated, lobed and either folded or curly at the margins.

U. lactuca Wulf. Crypt. aquat. p.3. Thuret Etud. Phyc p.5. Tab II. & III. (with a wondrous lustre! excl. synon.)

U. lactuca α rigida Le Jolis Alg. Mar. de Cherb. p. 38 (excl.syn.)Phycoseris rigida Keutz. Tab. Phyc. Vol. VI. tab. 23. II

ß Cribosa frond more firmly membranous obovate-dilated, broadly lobed, sieve-like, holes numerous, round but often crenulate-margined. Ulva. reticulata Salzm. et. auct. Phycos reticulata Kuetz. Sp.? (as concerns only the Mediterranean forms.).

Ulv. rigida var. Welw. Phyc. lusit. n:o 179.

τ Fimbriata substance more firmly membranous, deeply lacinate, lacinae sublinear, perforate and frilled by marginal lacerations.

Ulv. fimbriata Welw. Phyc.lusit. n:o 217 and 282.

b. More delicate, membranous when dried.

σ Myriotrema frond somewhat rigid below and blackish green, above more delicately membranous, broadly expanded, lobed and undulate at the margins, sieve-like with numerous flattish-margined holes.

Ulv. myriotrema Crouan mscr. and Florul.Finist. p.131 Zanard. Icon. adriat. tab. XI!

Phycoseris myriotrema Kuetz. tab.phycol.Vol. V1. tab 23. 1.

Ulv. latissima var. umbilicalis Ag. Sp. p.408

Ulv. latissima (of most authors) Harv. Phyc. Brit. tab. 171? (as far as specimens labelled thus by most authors but scarcely applying to this illustration). Crouan Florul. Finist. Pl.10 fig.71!

Ulv. lactuca β latissima Le Jolis Alg.Mar.de Cherb. p.39 (excl. syn.). Exsicc. (herbarium specimens): Crouan Alg. Mar. Finist. n:o 389 and 390.

∈ Laciniata frond somewhat rigid below, blackish green, above, more delicately membranous broadly expanded, deeply lobed, lobes lacinate and with undulate margins.

U. laciniata Wulf. Crypt. Aquat. n:o 5 page 3. U. latissima var. palmata Ag. Sp. p.409 (in part and excl.syn.). U. australis Kuetz. Tab.phyc. Vol.V1. tab.24.II

The following also occur:

a. Capensis

U. capensis Aresch. Phyc. Cap. p.15 ;Phyc. nov. p. 43

U. uncialis Suhr Kuetz. l.c. tab. 16

b. Australis

U. australis Aresch. Phyc.nov. p.44?

U. latissima var. Harv.Alg. austr. exs. n:o 601.D

Phycoseris Ulva Sond. Alg. Preiss. p.6?

c. Pacifica

U. latissima Rupr. Alg. Ochot. p. 203

U. latissima var. Harv. Fr. Isl. n:o 122

U. reticulum Tiles. mscr. (from Japan)

U. fenestrata Post. and Rupr.

Phycoseris lobata Keutz. Tab.Phyc. Vol.VI tab.27.

As I understand Ulva rigida, it is the most common of all species, occuring as it does in all warm seas around the globe. I have attempted to show the full range of forms, those from Europe, the Cape, the South, the Pacific; those with few and those with many perforations; those delicate and those more tough. Of course if one were to judge from a sight of only the extremes one would conclude that they are entirely different taxa, but confronted with the full range one is impressed by the continuity that it shows and to conclude that they fall within the ambit of a single species. My observations on site, unless I am misled, convinces me that their texture is simply an expression of the conditions in which they grew: if in calm or deep water, then delicate; if in exposed places then robust and more or less contracted or even (as in the case of U. uncialis Suhr) bunching together so as to succeed in the harsher conditions. According to his field notes, Welwitsch

collected cartilaginous rigid forms in Winter in the month of November; I myself at Marseilles, in the month of May, collected a form remarkable for the delicateness of its upper frond. Thus it may be believed that age and situation can influence or induce a habit. (Crouan in Florul.Finist. said as much in regard to U. rigida and U. myriotrema.)

Further, it must be admitted that even in more delicate plants, the lower parts often differ remarkably from the upper; not only because it is darker green while the upper is pale, but also because it is obviously firmer and curled, as much in fact, as that of a tougher form, growing in more exposed conditions. The greater age of this lower portion (in the case of a plant with a more delicate uper portion) is confirmed by both the structure itself and the appearance of the cells. Indeed in the upper portion of the more delicate plant, I have seen a distromatic membrane consisting of cells almost twice as long tangentially as anticlinally, and, in addition, with thinner cuticle and interstitial layer in that place; in the more rigid part of the same specimens I have seen in transverse section, cells that are more or less quadrate or a little longer anticlinally than tangentially and, where the hyaline cuticle and interstitial layer are very conspicuous and sometimes even very thick; at the surface, all cells are equally round-angled. The upper parts and edges of the entire plant become fertile when mature and, the spores

having been shed, they appear as a decolorised band up to one-half inch wide. In time, this process is repeated centripetally until at length the entire upper portion of the plant has been evacuated; with that I suspect the dead tissue is sloughed off leaving a persisting basal portion that regenerates a fresh upper blade. The same observations have been made on the more rigid forms but in this case the cells are differently shaped being up to 3 times longer anticlinally than tangentially and the cuticle is better developed. The young plant is entirely and more intensely greenish and by no means somewhat golden green, though with aging it becomes somewhat yellow. The endochrome of dried plants appear not at all rarely to be attenuated towards the outside (centrifugally) (subconical); this so far as I have been able to make out is the result of a contraction of the cuticular layer caused by drying. Foramina almost always, though not indeed in young or slightly dilated forms, present and have been held by some (very many) to indicate a separate species. These perforations cannot be interpreted as the effects of grazing by animals as was done by Greville for U. reticulata but perhaps the explanation lies in differential development by which some situations in the frond are favoured while others are not and as a consequence in the latter places cells become moribund and eventually disintergrate thus forming the holes. Certainly I have seen on a frond distinguished by more numerous foramina, scattered cells obviously

deprived of their green endochrome, that I could easily accept as the forerunners of foramina. I have seen foramina, in more slender fronds, that are surrounded by a hyaline margin..... ; in a somewhat rigid plant I have observed cells of a similar kind produced along a margin, sometimes indeed deflected upwards and downwards and sufficiently numerous as to make prominent minutely crenulated margins on each surface. Chiefly in a thicker plant that I think was more exposed to violent wave action, not only has perforations in the disc but also becomes variously frilled at the margins. By building up a wealth of cells in these places margins are strengthened; a necessity, I should think, if fronds are not to be entirely destroyed through severe battering. As concerns the Australian form that doubtfully belongs to U. rigida, Areshoug (Phyc. nov. p.44) declared that it is always parasitic on the stems of Caulinia, whereas U. capensis (U. rigida) truly is a rock dweller, and a frond initially umbilicate, finally splits into several parts. U. rigida is almost always primarily attached to rock though I have also seen it on other algae. Young plantlets so attached and no more than one-half an inch high have a lanceolate-oblong frond lightly lacerated at the margin and already perforated by one or more holes, contracted into a wedge-like stipe. In plantlets of two or three inches the stipes are more conspicuous and the frond broader and almost kidney-shaped, more deeply torn and with lots of

perforations. In sections cut about half an inch above the holdfast I have seen two cell-layers in which the cells have a subquadrate outline and homogenous rounded endochrome. Rock-attached plants frequently have fronds crispately lobed right at the base with less conspicuous stipes; some lobes of this frond become very large, while others remain small until such time as they, too, enlarge in no particular sequence (unless I am mistaken). As the plant ages so much the more does the basal area expand in thickness by the development gradually of ever more numerous interior filaments in the central part of the blade; by this means the cuneate stipe becomes gradually ever more conspicuous with definite internal structure, which is why old fronds appear very evidently (obviously) stipitate above the holdfast itself. - In the Australasian species, that I have considered to be assignable to genus Letterstedtia, fronds at first look very much like those of U. rigida, but as they develop they gradually change in the lower parts to compounded, almost linear, stems, structurally very much like the stipes of U. rigida; whether or not the Areschoug species recalled above may be referred to this species, I have not dared to say.

One may understand from what has been said above that authors diverge very greatly as to the limits of the species. Because most have attempted to qualify their identifications by superficial characteristics, they have had difficulties in understanding the true identities of the

various species. I might have thought that most contemporary algologists would have understood our species (singular) as Ulva lactuca and U. latissima. Among U. latissima (the one I describe above) and more slender forms of U. rigida very few authors make a distinction. I suspect that ours was described as U. plicata by Roth. What the identity of Phycoseris gigantea Kütz. Tab Phyc. tab 22, is I cannot say for certain; I consider that its habit and habitat (North Sea) make it likely that it is probably a form of U. latissima; yet a specimen from the Arctic (Greenland) that is in my possession and that is more likely U. crassa Kjellm. is so like the Kuetzing illustration that I am in doubt. I am equally puzzled by Harvey's U. latissima in Phyc. Brit. I suspect, too, that Crouan, in Florul. Finist., included in U. latissima both our U. latissima and the more slender membranous forms of U. rigida. The specimen distributed as no 387 in Alg. Marin. Finist. is, I believe, U. latissima. Which plant, however, drawn by the same (authors?) and provided with an evident stipe and vertically elongated cells, for me belong to forms of U. rigida. The same report a form described and distributed in Alg. Marin. Finist. sub. n:o 387, as doubtfully of U. lanceolata Linn. and consider identical with Ph.(ycoseris) Smargadina Kuetz. Tab. Phyc. Vol. VI. tab. 19, but I think is a juvenile of U. rigida. It may happen that his form occurs in certain places, as they state in Florula Finist.; structural characteristics and formation

of a stipe, however, convince me that it is U. rigida. Transverse sections of the stipe can be plain and stuffed with a conspicuous layer of intercellular material that contains numerous rhizoids. As far as the identity of Phy. smaragdina, given me by Kützing,is concerned, I find it fits Ent.(enteromorpha) linza in all respects. As to the Ulva lanceolata of Linnaeus, very shortly diagnosed in the XIIth. edition of the Natural System, most algologists appear to have dismissed it; most consider it to be a form of Ent. linza. Areschoug's Ulva stipitata (Phyc. Scand. p. 185) was later considered by its author to be a juvenile form of Ulva latissima. If I were to indicate a certain difference among forms derived from different oceans and often under various names in collections, then I should say that those from the Pacific tend to be olive while those from Australasia appear palely bluish-grey.

7. ULVA FASCIATA Delile Egypt. tab. 58. fig. 5.

Occurrence:

Mediterranean ...

Ulva fasciata Del. l.c. Mont. Fl. Alger. p.151.tab.14.fig.1.2.

Phycoseris fasciata Kütz. Tab. phyc. Vol. VI. tab.28

Ulva latissima var. palmata Ag. Sp. (partim).

Atlantic .....

Ulva divisa Suhr in Bot. Zeit. 1831 n:o 39.

Pacific .....

Ulva nematoidea Bory Voy. Coqu. n:o 75.

Phycoseris lobata Kütz.Sp. & Tab.phycol.Vol.VI tab.27?

Indian .....

Ulva fasciata Harv. Alg. Ceyl. n:o 100

In its whole structure U. fasciata approaches Ulv. rigida; it differs from other Ulvas in its unusual habit. Truly the lacinae are much better defined than those of other species of Ulva; also, there is at the margins a minute canal around which the cells form a semicircle; in this latter respect it seems to be transitional with Ulv. (=Enteromorpha) linza; but among these marginal cells the outermost two or three are displaced so as to form almost a double row by alternating with those in the semicircle. Such a disposition is not visible in Ent. linza where anaogous cells make or describe a perfect semicircle. The marginal filaments of Ulva rigida have a disposition of cells similar to that of U. fasciata thus showing an affinity, not apparent in U. (=Enteromorpha) linza. I am not yet aware of the occurrence of U. fasciata on the shores of Britain nor on the upper shores of France, which leads me to believe it is characteristic of warmer seas. I find no differences between forms recovered from the different oceans.

De-Toni, J.B. 1889 Sylloge Algarum

Volume 1. pages 110-112

ULVA L. (1737) Gen. p.236 em. J.Ag. (1883) Till Algernes Systematik VI. p. 160. (Etym. Latin Ulva - a bog plant - and is like Celtic Ul. meaning water), Ardiss. Phyc. Medt.II. page 190, excl. p. Hauck Meeresalgen p.435, De-Toni from Levi Fl. Alg. Ven. III, page 184, excl. p. , Borzi Studi algol. I, page 1. -

Thallus greening, expanding into a membrane sessile or shortly stalked above a holdfast, sometimes broadly expanded and lobed here and there, at other times more definitely lacinate and subpalmate, the membrane either continuous or perforate, germlings (uniserate) threads that soon become multicellular by repeated division of the segments, distromatic by coalition of the two monostromatic membranes; cells of the basal region produce inwardly and then downwardly projected rhizoids filling the interstices. Reproduction by bicilliate zoospores that conjugate to make quadricilliate zygotes; zoospores in any but the basal cells of the tissue, escape in a swarm through a pore near the middle of the outside wall; the mother cells persist causing the flesh in the area to be flaccid and whitish.

Section I. Cells rounded and almost cuboid, anticlinally scarcely longer than the tangential.

1. Ulva lactuca L. Sp. II, page 1163 ex parte, Le Jolis List Alg. Cherb. p. 38, Thur. et Born. Et phyc. page 5, t. 2 and 3, Hauck Meeresalgen p.435, Ardiss. Phyc. Medit. II, page 193. -

Thallus 1-6 diameters long or more, variable in outline, sometimes rounded, ovate, oblong, kidney-shaped or lanceolate, simple or irregularly lacinate, immediately perforate, more or less undulately folded, more often twisted, shortly stiped at a more often than not firmer base that is heart- or wedge-shaped, otherwise subsessile, smooth edged and rarely crenate or irregularly dentate. -

forma genuina Hauck Meeresalgen p. 435, f. 194, Ulva lactuca ß latissima Ardiss. Phyc. Medit. II, p. 194. Ulva latissima L. Fl. Suec.Ed. II, p.431 ex parte, nec Grev. (fide Le Jol.), J. Ag. Till Algernes Systematik VI, p. 168. t.4, f. 119-122, Ulva Lactuca var. rigida Ardiss. Phyc. Medit. I. p.123, De-Toni e Levi Fl. Alg. Ven III, p. 186.

Erect, stipitate, stipe eventually very obvious, juvenile frond delicately membranous, paler, when older more darkly green especially in the lower portions, stiffish, finally indeed almost cartilaginous, broadly expanded and lobed, lobes broad and rounded or narrower and elongated, thallus more often more or less perforated; cells anticlinally elongated, at length 2-3 times longer than diameter, interstitial space of a piece that eventually becomes

crammed with rhizoids. These forms seem very different in aspect: a. firmer substance, somewhat rigid when dried. - Forma rigida: Ulva Lactuca Wulf. Crypt. aquat. p.3, Thur. et Born. tud. phyc. p.5,t. II and III excl.synon!, Ulva Lactuca α rigida Le Jolis Alg. Mar. Cherb. p.38 excl. synon., Phycoseris rigida Kütz. Tab. Phyc. VI, t. 23, f. 2: frond more firmly membranous, obovate-dilated, lobed and either folded or curled at the margin. In Atlantic and Mediterranean; at 'P.Arenas' in the Magellan Straits (Piccone), on the shores of Brazil (Martens), Mocamedes, Angola (Henriques).

Section 2. Cells anticlinally and gradually elongating until finally about or even more than double the tangential dimension; in surface view appearing round-angled (cf. Ulva Lactuca var. in Section 1.).

7. Ulva fasciata Delile Egypt. page 153, t.58, f.5, J.Ag. Till Algernes Systematik VI, p. 173, Mont. Fl. d'Algeria p.151, t.14, f.1-2, Phycoseris fasciata Kütz. Tab. Phyc. VI, t.28 (mediterranea), Ulva latissima var. palmata Ag. Sp. p. 409 pro parte, Ulva divisa Suhr in Botanishe Zeitung 1831, n. 39 (atlantica), Ulva nematoidea Bory Voyage de le Coquille n.75 (pacifica), Phycoseris lobata Kütz. Sp. et Tab. Phyc. VI, t. 27? (pacifica), Ulva fasciata Harv. Alg.Ceyl. N. 100 (indica). -

Frond stipitate, at the base shortly cuneate, divided into opposite, simple or dichotomous, elongate, linear, attenuated, acute segments.

Hab: In the Mediterranean, Adriatic, Atlantic European and African coasts, in the Pacific on the shores of Chile, on the Island of Taprobanem (Ceylon)(Piccone);.....on Barbados in the Antilles (Dickie), on the island of St. Vincent (Caribbean)(Piccone), at Algarve, Portugal (De-Toni, Moller), on the coast of California (Dickie) and at Paita on the Island of St. Laurence (Peru)(Marcacci sec. Piccone) and Rio de Janeiro at Mache, Brazil (S. Hilaire sec. Martens, Piccone). -

According to J. Agardh (l.c.): this plant has so far (1889), not been discovered in Britain or on the northern French shores. To quote further from J. Agardh (l.c.):nothing really distinguishes this species from Ulva Lactuca var. rigida, though the lacinae are better defined and at their margins the two membranes separate to form a more or less cylindrical space, thus forging a link with Enteromorpha Linza; but among the radiating cells around the marginal lacuna, 2-3 (cells), at most, seem to project beyond the arch in such a way as almost to suggest a distromatic membrane instead of the single-layered membrane that characterises E. Linza.

Species less well known or of uncertain affiliation

.....

8. Ulva uncialis Suhr in Kütz. Species p. 475.

Phycoseris uncialis (Suhr) Kuetz., l.c.

Ulva capensis Aresch. Phyc. Capensis p. 15, Phyc. extraeurop. p.43, -

Frond 2,5 cm. or a little longer, broadish, irregularly split and lacerated, segments (lobes) undulating.

Hab: on the Cape shores of South Africa (Drege) - intensely green, formed of two layers of cells. 0,5 to 0,10 mm. thick, the expanded and variously lobed blade attached by a navel-like holdfast. The lobes finally linear-stipitate, elliptic, entire or again lobed, undulate and lacerate at the margins, attenuated at the base to form linear stipes, containing densely packed cells that are linear in the anticlinal direction.

HAMEL, G. 1931 Chlorophycees des cotes francaises.
p. 43.

2. - Ulva fasciata Delile.

Fronds 20-40 cm long and more either composed of a single thallus or strap, long and narrow, or if a number of thalli held by a common disc. The base region shows over a number of centimetres descending rhizoids. The thalli are yellow-green but the margins are usually darker green and, in addition often have spiny projections. In thin section, the cells are very elongated and the frond is thick, 135 um in the middle; on the margins it is only 95 um. At this position the two layers come apart easily which is often evident by a marginal and longitudinal swelling. By this characteristic, Ulva fasciata resembles E. linza but does not have, which the latter has, a tubular base.

3. Ulva Lactuca

Highly polymorphic fronds, more or less widely spread out, dark green or yellowish, made up of two adhering layers of cells held by a disc that consolidates the rhizoids; does not have a margin with darker colour as in U. fasciata, nor a differentiation into axis or stem and leaves as in U. Schousboei.

Le Jolis distinguishes in U. Lactuca a number of varieties:

Var.rigida (Ag.) Le Jol. - Tissue more tough, more rigid and coriaceous specially at the base; fronds forming

tufts proliferating in all directions, irregularly lacinate and eroded on the edges which are smooth or lightly folded. Intense green and bluish colour at the base, when it grows at very low tide region.

Var. latissima (L.) DC.Fl.fr.I, p.9 - when young, has a single thallus, complete, smooth on the edges, often narrower at the base to form a cuniform stipe; thick and rigid consistency, close to var. rigida. Later it spreads in all directions and ends up having enormous sizes; it is then highly creased, papery, fragile and breaks easily. Often it shows regular perforations, which is the f. myriotrema.

Var. Lactuca (Linn.) Le Jolis. - fronds softer consistency, less intense green tending to yellow, and mainly complete and undulous margins of the thalli, having a marked tendency to elongate itself in ribbons, twisted on the axis.

Two forms are noticable: f. amplissima with big suborbicular frond with large radiating folds; f. contorta with spiral linear thallus.

Ulva Lactuca is one of the most common of our algae; found from Dunkerque to Hendaye and in the Mediterranean, on all the French and African coasts. It grows at mid tide, at low tide and can be found in dredgings.