*J. mar. biol. Ass. U.K.* (1957) 36, 663–693
Printed in Great Britain



# STUDIES IN THE GENUS *FUCUS* L.

## II. DISTRIBUTION AND ECOLOGY OF FORMS OF *FUCUS DISTICHUS* L. EMEND. POWELL IN BRITAIN AND IRELAND

By H. T. POWELL

The Marine Station, Millport

(With Plates I–IV and Text-figs. 1–5)

CONTENTS



## INTRODUCTION

In part I of this series (Powell, 1957) the species *Fucus distichus* L. was re-established and emended to include the following four subspecies: subsp. *distichus*, subsp. *anceps* (Harv. et Ward ex Carruthers) Powell, subsp. *edentatus* (De la Pyl.) Powell, and subsp. *evanescens* (C. Ag.) Powell. Of these subspecies, only *anceps*[1] and *edentatus* have been found in the British Isles. Their distribution and ecology in Britain and Ireland are now described.

[1] Throughout the text subspecific names have to be referred to constantly, and will be cited normally as a straight trinomial, e.g. *F(ucus) distichus anceps*. Forms and other lower categories are indicated in the usual way, e.g. *F. vesiculosus* f. *linearis*. Often, to avoid tedious repetition, it is adequate to refer simply to the final epithet, whether subspecies or form, e.g. *anceps*, or *linearis*, alone. Among names of other organisms there are some in which the genus here automatically indicates a single species (e.g. *Alaria esculenta*, *Chthamalus stellatus*), and the specific name can often be dropped.

It is probable that, until the present century, authentic specimens of any form of *Fucus distichus* L. emend. Powell were known in the British Isles only from Kilkee, Co. Clare, Ireland.[1] There, in 1863, W. H. Harvey and N. B. Ward found and described *F. anceps* (see Powell, 1957, for references). Many of the larger herbaria in Britain contain specimens of '*F. anceps*' from Kilkee, most of the specimens being distributed by E. M. Holmes (*Algae Britannicae Rariores Exsiccatae*, Fasc. X, No. 240). As the data on numerous herbarium specimens examined testify, several other collections were made at Kilkee later in the 19th century, the latest known date being September 1897 (collected by 'E. George').

The first authentic British record of *F. distichus edentatus* is that of Börgesen (1903) for the Shetland Islands (14–16 July 1902). He reported that 'well-developed, typical specimens, agreeing exactly with my Faeröese specimens referred to [*F. inflatus*] f. *edentata* (De la Pyl.) Rosenv., occurred abundantly near Lerwick'.

Batters (1902) and Newton (1931) both list *F. anceps* Harv. & Ward as a distinct species (with Kilkee as the only locality) and both mention, but with some doubt, a record by Traill (1885) of '*F. distichus*'.[2]

I first became interested in *F. distichus* during the summer of 1951 when with Dr J. R. Lewis (Leeds) I carried out an ecological survey of the north coast of Scotland. One of the most interesting findings of the survey was the discovery of *F. distichus anceps* along a limited and very exposed stretch of the north coast of Caithness. This remains the only record of any form of *F. distichus* for the mainland of Britain, and in a preliminary announcement of the find (Powell & Lewis, 1952) Börgesen's nomenclature was followed.

During succeeding years I have had opportunities of taking part in several phycological surveys of various parts of the coast of north and west Britain and Ireland, as follows: Fair Isle and part of the Mainland of Shetland in 1952, and parts of the west of Ireland in 1953, in each case with colleagues Dr E. M. Burrows (Liverpool), Dr E. Conway (Glasgow) and Dr S. M. Lodge (Liverpool); and the island of Lewis-Harris (Outer Hebrides) in 1954. These expeditions have yielded further information about the distribution

[1] All other early British records of fucoids that might possibly have referred to this species (e.g. the '*F. distichus*', '*F. inflatus*' and '*F. linearis*' of various authors) have been carefully considered, and almost certainly all refer to forms of either *F. ceranoides* L. or *F. vesiculosus* L. Thus '*F. distichus*' of Lightfoot (1777, p. 912) was probably a very narrow form of *F. ceranoides*; and '*F. inflatus*' Lightfoot (1777, p. 910) and '*F. linearis*' Hudson (1762, p. 467) were forms of *F. vesiculosus*.

[2] Traill (1885, p. 11) records '115. *Fucus distichus*. Cast ashore at Port-Seton (J. R. Henderson, 1882). Only one specimen found. Identified by E. M. Holmes.' I have made unsuccessful efforts to trace this specimen; it is *not* in Herb. Traill (University of Edinburgh), Herb. Holmes, Herb. Batters or General Algal Herb. (British Museum), or Herb. Kew. The specimen probably cannot be traced now and it would seem best to disregard this very doubtful record.


Text-fig. 1. Map to show localities (numbered 1–11) at which *Fucus distichus* has been found in Britain and Ireland. Subsp. *anceps* has been found at localities 1–9, and subsp. *edentatus* at localities 4, 10 and 11.

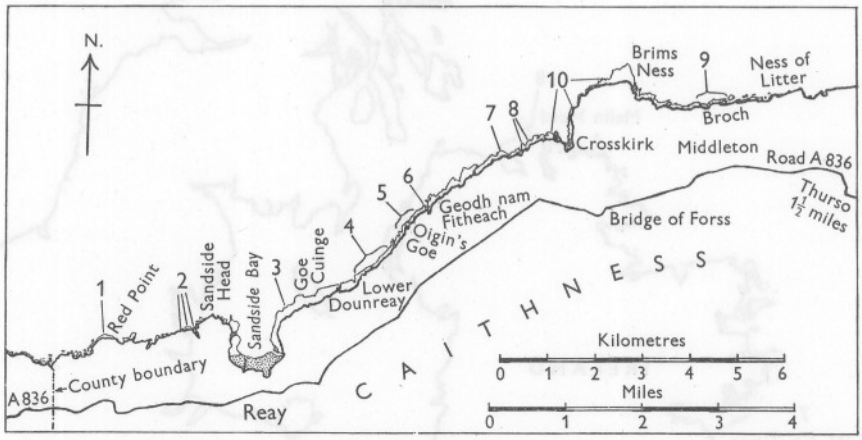
and ecology of forms of *F. distichus*; also, a number of additional valid British records have come to my notice from various sources and are discussed below.

## *FUCUS DISTICHUS* L. EMEND. POWELL, SUBSP. *ANCEPS* (HARV. ET WARD EX CARRUTHERS) POWELL (Pl. I)

### DISTRIBUTION

*Scotland* (see Text-figs. 1, 2)

CAITHNESS. Found, intermittently, only along a limited stretch (about 12 miles) of the north coast, from a point about 3 miles west of Holborn Head (near Thurso) westwards to near the county boundary with Sutherland (July–September 1951). It is possible that the range may extend slightly farther, both east and west, on reefs that are difficult to reach. The principal reefs on which *anceps* was found in the 1951 survey are shown in Text-fig. 2, sites 1–9; more recently (August 1954 and June 1956) Dr E. Conway (accompanied by my wife, Grace Powell, in 1956) has found the plant also at the three sites marked 10.




Text-fig. 2. Map of part of the north coast of Caithness. The principal sites at which subsp. *anceps* has been found are numbered 1–10 (see text).

ORKNEY ISLANDS. Recorded only from three sites, all on the west coast of the Mainland of Orkney. The plants from sites 1 and 2 (Text-fig. 1, locality 2), situated just south and just north of Bay of Skaill, were collected by James Sinclair (Orkney) in 1938 and 1939, respectively. I first heard of them through correspondence with Dr Søren Lund (Charlottenlund, Denmark), and later Mr Sinclair kindly allowed me to examine and identify his her-

barium specimens and to refer to his records here. Details are (1) Hole o'Rowe, Sandwick, Orkney (59° 3′ 4″ N., 3° 21′ 21″ W.), 16 October 1938, common in one spot on an exposed ledge of rock, material all sterile, sheet no. 445 in Herb. J. Sinclair; (2) exposed coast below Garson, Northdyke, Sandwick, Orkney (59° 3′ 40″ N., 3° 21′ W.), 7 May 1939, common on flat rocks, all five herbarium specimens fertile, sheet no. 511 in Herb. J. Sinclair.

For the third Orkney record I am indebted to Dr A. J. Southward (Plymouth), who in May 1953 found one small patch of *anceps* on an exposed reef near Brough Head, north-west Orkney Mainland (Text-fig. 1, locality 3; approximate position 59° 8′ 16″ N., 3° 19′ 39″ W.); the area occupied by the plant was several metres long by 0·5 m wide, on the upper shore among *Chthamalus stellatus* (Poli); material fertile.

FAIR ISLE. Found only at two sites in June–July 1952. At North Gavel, a very exposed site (59° 32′ 28″ N., 1° 35′ 49·5″ W.), *anceps* was fairly common on high-level ledges and rock steps (see Burrows, Conway, Lodge & Powell, 1954). At a second site, occasional scattered plants were found on extremely exposed reefs (59° 30′ 53″ N., 1° 39′ 7·5″ W.) immediately to the west of the South Lighthouse.

OUTER HEBRIDES. *Island of Lewis-Harris.* Cotton (1912, pp. 23–6), in relating the zonation of fucoids in parts of the west of Ireland to the rest of Britain,[1] and to other places in Europe, mentions (p. 23) 'An additional species, *F. inflatus*, was recorded by Börgesen for the Shetland Isles and Mr E. M. Holmes has lately received a specimen of this boreal species from Lewis, so possibly it is a regular constituent of the association in the north of Scotland.' The specimens from Lewis referred to by Cotton are now located in Herb. Kew, and detailed examination has proved that the plants are true *F. distichus* subsp. *anceps*. There are three specimens in Herb. Kew, on separate sheets, as follows: (*a*) a single narrow specimen, labelled '*Fucus inflatus* var. *distichus*, Butt of Lewis, N.B. Coll. W. J. Gibson. April 1909. Comm. E. M. Holmes.' Another label on the sheet indicates that the plant was actually named by F. Börgesen; and attached to the sheet is a letter from W. J. Gibson ('The Nicholson Institute, Stornoway') to E. M. Holmes dated 21 April 1909, stating that the material was collected 'last week' (i.e. about 14 April 1909). Specimen (*b*) is a duplicate of (*a*), labelled similarly, and mounted singly on a separate sheet. (*c*) On another sheet (beside three specimens of authentic '*Fucus anceps*, Kilkee') is mounted one plant labelled '*Fucus distichus*? Stornoway, N.B. Comm. E. M. H. May '09.' I am inclined to think that this is simply another duplicate Gibson specimen from 'Butt of Lewis' that Holmes sent on to someone else (or possibly to Kew) in May 1909; certainly it could not really have been collected in the sheltered environs of 'Stornoway'. All three specimens are fertile.

[1] Curiously, however, Cotton omits to mention in this general discussion Harvey's important record of '*F. anceps*' from Kilkee.

In July–August 1954 I was able to investigate the extreme northern tip of Lewis, but only the accessible parts of the shore north of a line running east to west from just south of Aird Dell on the west coast to just north of Port Skegirsta on the east coast. I found subsp. *anceps* only at two sites (close together; 58° 30′ 3″ N., 6° 13′ 19″ W.) on very exposed reefs, facing E.N.E., at the foot of the headland named Buaile na Faing, which is about 2 miles south-east of the Butt of Lewis. The littoral area of the actual headland and small islets comprising the true Butt of Lewis is precipitous and inaccessible without a rope or a boat and could not be investigated in 1954. Possibly the location 'Butt of Lewis' cited by W. J. Gibson is used in a broad sense, to include some few miles of the northern tip of Lewis.

*St Kilda.* Algae from the 1952 marine biological expedition to St Kilda (Gauld, Bagenal & Connell, 1953) were identified by me. *F. distichus* subsp. *anceps* (listed as *F. inflatus* f. *distichus*) was found in small quantity (a few plants) at one site only—at the top of the *Balanus balanoides* (L.) belt, on rather steeply sloping rocks at the head of Glen Bay, on the north side of Hirta (57° 49′ 16″ N., 8° 35′ 50″ W.). T. B. Bagenal (Millport) revisited the Glen Bay site on 14 July 1956 and again found *anceps*, in late fertile condition. He reports that the fucoid had greatly increased in amount since 1952, forming a belt up to 1 m wide at the head of the bay, and had spread (although not continuously) along about 100 m of shore altogether.

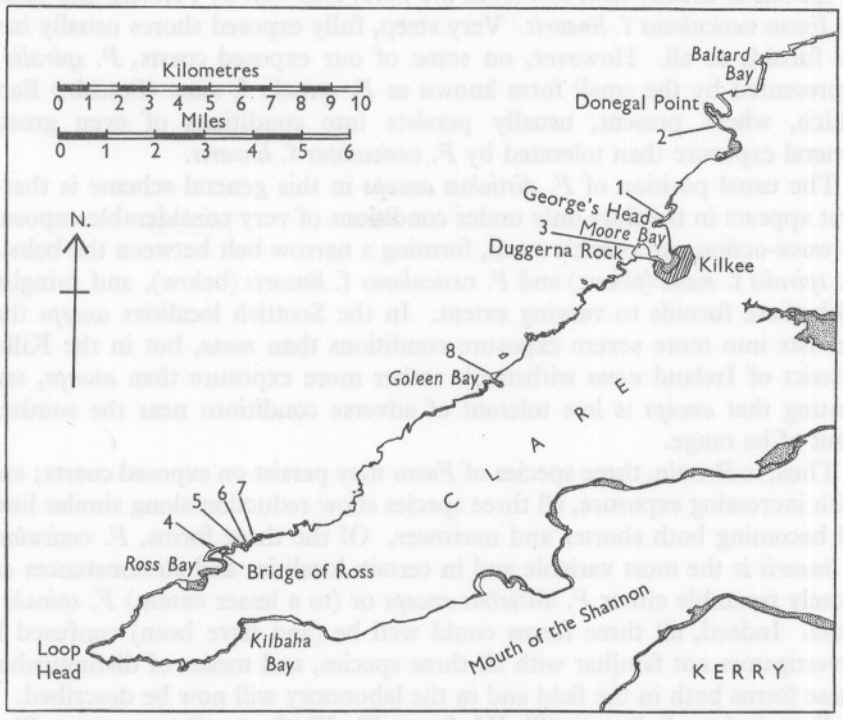
*Ireland* (see Text-figs. 1, 3)

KILKEE DISTRICT, Co. Clare. (Text-fig. 3.) In July 1953 *anceps* was found at the precise site (Duggerna Rock) at Kilkee where W. H. Harvey first recorded it 90 years before. During the 1953 survey the plant was found also on exposed rocks at several other localities in south-west Co. Clare, both north and south of Kilkee, between Donegal Point and Ross Bay, the exact sites being: (1) George's Head (north side, well inshore, on reefs facing N.N.W.); (2) Donegal Point (midway along south-west flank; the Point itself is a sheer 100 ft. cliff); (3) Duggerna Rock, Kilkee (and on two reefs immediately adjacent to and west of the Rock); (4)–(7) at four separate exposed sites, all within 1 mile of coast, just north of Ross Bay (i.e. from near Bridge of Ross, north-east for about a mile); (8) Goleen Bay (exposed reefs at northern entrance to Bay).

Also in 1953, J. R. Lewis surveyed other parts of the coast of Ireland and found *anceps* at two additional, isolated, exposed sites (Text-fig. 1, localities 8 and 9) as follows:

MALIN HEAD (the northernmost point of Co. Donegal), 4 July 1953, on reefs facing N.N.W. about 250 yards west of Malin Tower (55° 22′ 53″ N., 7° 22′ 56″ W.).

KERRY HEAD, Co. Kerry (52° 25′ 9″ N., 9° 56′ 44″ W.), 6 June 1953. This is the most southerly record of any form of *F. distichus* in Europe.




Text-fig. 3. Map of south-west part of Co. Clare. The sites at which subsp. *anceps* has been found are numbered 1–8 (see text).

## DISTINCTION FROM OTHER FUCOIDS

The distribution and ecology of *F. distichus anceps* is most conveniently considered in relation to the other fucoids found in Britain. On sheltered rocky shores, as is well known, the zonation of the littoral Fucaceae association follows a fairly standard pattern. The species occur in more or less well-defined belts in the following order from high-water level downwards: *Pelvetia canaliculata* (L.) Dec'ne et Thur., *Fucus spiralis* L., *Ascophyllum nodosum* (L.) Le Jol./*Fucus vesiculosus* L., *F. serratus* L. With increasing exposure to wave-action some of these dominants are replaced either by other algal species or by animals, but some persist usually in a modified and often reduced form. *Ascophyllum* is usually the first of the series to be eliminated by increasing exposure, followed by the normal bladdered form of *Fucus vesiculosus*, and then *F. serratus*; thus the fucoid zonation on fairly exposed and moderately steep shores is often as follows: *Pelvetia*, reduced plants of *Fucus spiralis*, *F. vesiculosus* f. *linearis* (Huds.) Powell (=f. *evesiculosus* auctt.). With further increase in exposure, or on steeper shores, the normal form of

*F. spiralis* is usually next lost from the flora, followed by *Pelvetia* and finally by *Fucus vesiculosus* f. *linearis*. Very steep, fully exposed shores usually have no fucoids at all. However, on some of our exposed coasts, *F. spiralis* is represented by the small form known as *F. spiralis* f. *nana* (Stackh.) Batt., which, where present, usually persists into conditions of even greater general exposure than tolerated by *F. vesiculosus* f. *linearis*.

The usual position of *F. distichus anceps* in this general scheme is that it first appears in the flora only under conditions of very considerable exposure to wave-action and oceanic swell, forming a narrow belt between the belts of *F. spiralis* f. *nana* (above) and *F. vesiculosus* f. *linearis* (below), and mingling with these fucoids to varying extent. In the Scottish localities *anceps* then persists into more severe exposure conditions than *nana*, but in the Kilkee district of Ireland *nana* withstands rather more exposure than *anceps*, suggesting that *anceps* is less tolerant of adverse conditions near the southern limit of its range.

Thus, in Britain, three species of *Fucus* may persist on exposed coasts; and, with increasing exposure, all three species show reduction along similar lines, all becoming both shorter and narrower. Of the three forms, *F. vesiculosus* f. *linearis* is the most variable and in certain localities and circumstances can closely resemble either *F. distichus anceps* or (to a lesser extent) *F. spiralis* f. *nana*. Indeed, all three forms could well be (and have been) confused by investigators not familiar with all three species, and means of distinguishing these forms both in the field and in the laboratory will now be described.

*F. vesiculosus* f. *linearis* (Pl. III, fig. 2, Pl. IV, fig. 1; Cotton, 1912, Pl. I; frontispiece, *Rev. Algologique*, T. 5, fasc. 3–4, 1931; Harvey, 1950, for photograph of plants on Lundy) is extremely variable in form and in conditions of considerable exposure may be reduced to rather erect stunted tufts only a few inches in length and with narrow fronds (but never so narrow as fronds of *anceps* growing at the same site). Fundamentally *linearis* is distinguished from *anceps* by the fact that it is unisexual and dioecious, while *anceps* is invariably hermaphrodite (it should be noted, however, that very old conceptacles of *anceps* may have released all antheridia and may then show a few remaining oogonia only). Also, the midrib in the younger branches of *linearis* is always very distinct and the lateral alae clearly differentiated (even in very narrow thalli), whereas in *anceps* the midrib and the lateral wings are not very sharply differentiated, the distal branches often being practically oval in section (see Plates I, III and IV). These two characters serve to distinguish the two forms in any circumstances and, in addition, *anceps* usually has a variable (small) number of small caecostomata (not present in either *linearis* or *nana*).

At certain exposed places in south-west England and Wales (e.g. the very exposed islands of Lundy and Skokholm) and in the west of Ireland, *linearis* may develop long, narrow, pointed receptacles, very reminiscent of *anceps* (see

Pl. IV, fig. 1). Gillham (1954, p. 217) records '*Fucus inflatus* L.? (*F. anceps* Harv. et Ward)' for Skokholm and Grassholm, but comments that 'it is possible that the plants are merely an extreme rough-water form of *F. vesiculosus*'. In view of the distribution of *anceps* outlined in the present paper, it is practically certain that the plants in question were merely small and narrow *F. vesiculosus* f. *linearis*;[1] Dr Gillham now agrees with this view.

*F. spiralis* f. *nana* (Pl. IV, fig. 2) varies in size from a few to *ca.* 10 cm in length and has narrow, strap-like thalli, either unbranched or with few dichotomies, and with very distinct midrib and lateral wings. The receptacles are usually small, terminal, globular, and have the sterile rim of tissue characteristic of this species; conceptacles hermaphrodite. The prominent midrib and the shape of receptacle readily distinguish this form from *anceps*; and the hermaphrodite conceptacles, and sterile rim to the receptacles, distinguish it from the most reduced forms of *linearis*.

It is usual for plants of *nana* to have all the apices fertile at the same time; this is a common feature also in *anceps*, and to a lesser extent in *linearis*, especially when the last two forms are growing under the most rigorous conditions that even they can tolerate. The development of this feature in the least favourable environmental circumstances is doubtless of value for the survival of the species.

## ECOLOGY AT PARTICULAR SITES

### *Scotland*

#### *Caithness*

The 1951 survey included an examination of many sites on the north, north-east and north-west coasts of Scotland (Sutherland and Caithness), but *F. distichus anceps* was found only on very exposed reefs at the sites indicated in Text-fig. 2. Geologically the reefs of the north coast of Caithness are formed of the remarkable Caithness Flagstones (a group of Middle Old Red Standstone), and form virtually unbroken and often very extensive sheets of rock, sloping either very gently or more or less steeply, sometimes from well above effective high-water level down into deep water. More usually, however, the reefs occur in a series one behind the other and more or less parallel with the coast-line, all dipping seawards and with the outermost being very much more exposed than the inner reefs which are comparatively sheltered.

Most of the reefs face north-west or north and, since they dip down directly into deep water and are not protected by offshore reefs or islands, are fully exposed both to oceanic swell and to all the wave-action produced by more local winds. Even during periods of local calm weather these reefs are constantly subject to oceanic swell which breaks as it travels inshore and on the gently inclined reefs sweeps upshore at great speed and may inundate all the lower half of the effective littoral zone even at low tide. As a result, there is a considerable increase in the effective height of the littoral zone, and the littoral plants and animals are able to occupy wider (vertical) zones without suffering undue desiccation. Also the communities of plants and animals present, in the upper littoral especially, are usually much more open than in sheltered localities. The

[1] This belief was strengthened when the author had an opportunity to examine some exposed parts of the shore of Skokholm during September 1956. *F. vesiculosus* f. *linearis* was common but no plants of *F. distichus anceps* were found.

general ecology of the dominant plants and animals found on these remarkable reefs has been described and illustrated by Lewis (1954).

In bays and other sheltered sites between the extensive Flagstone reefs, all the usual fucoids of sheltered British coasts were found. With increasing exposure, some of these were eliminated in the usual sequence and *F. vesiculosus* f. *linearis* became common in the upper part of the mid-littoral zone. On the upper shore, *Pelvetia canaliculata* and *Fucus spiralis* became represented by smaller plants, but *Pelvetia* was soon lost from the open reefs and *Fucus spiralis* persisted only as the small f. *nana*.

Moderately exposed (or very gently sloping) reefs characteristically showed the following zonation of dominant species from low-tide level upwards. *Sublittoral fringe*: dominated by *Alaria esculenta* (L.) Grev. *Mid-littoral zone*: first a broad belt of *Himanthalia elongata* (L.) S. F. Gray, merging upwards into a belt of *Rhodymenia palmata* (L.) Grev.; then a belt of *Gigartina stellata* (Stackh.) Batt./*Balanus balanoides*/*Mytilus edulis* L.; next a belt of *Fucus vesiculosus* f. *linearis*/*Balanus*/*Mytilus*, with the *Balanus* extending to a slightly higher level than the *Fucus*. *Supralittoral fringe*: dominated principally by a wide belt of *Porphyra umbilicalis* (L.) Kütz. (f. *umbilicalis*), with a weft of less conspicuous blue-green algae growing beneath the *Porphyra* plants and also extending to higher levels than *Porphyra*. Frequently patches of *Blidingia minima* (Näg.) Kylin occurred in the lower part of the *Porphyra* belt and extended into the upper part of the mid-littoral zone. Thus, *Fucus vesiculosus* f. *linearis* was often the only fucoid found on such a gently sloping reef.

On more exposed reefs (either those farther out or those with steeper slope) a belt of *F. spiralis* f. *nana* appeared in the lower half of the supralittoral *Porphyra* belt. (In some few instances it was possible to trace a full series of intermediate forms of *Fucus spiralis* from the typical form in shelter through to f. *nana* with more exposure, but more usually f. *nana* occurred as locally isolated populations on the more exposed reefs.) With still greater exposure (on the steeper reefs), *F. distichus anceps* appeared and formed a distinct belt, *ca.* 15–45 cm vertical range, at the level of the general upper limit of *Balanus balanoides*—i.e. between the belts of *Fucus spiralis* f. *nana* (above) and *F. vesiculosus* f. *linearis* (below) where these were also present. With still greater exposure, *F. vesiculosus* f. *linearis* and *F. spiralis* f. *nana* were in turn lost from the flora, leaving *F. distichus anceps* as the sole remaining fucoid on many of the steeper (most exposed) reefs. Still steeper reefs and vertical walls of rock had no fucoids at all; such sites were dominated principally by a high-level belt of *Porphyra*, mid-littoral *Balanus* and *Mytilus*, and *Alaria* on the lower shore.

On the more exposed reefs *Fucus distichus anceps* was often locally abundant (see Pl. I, fig. 1). The smallest plants were those growing at the most exposed sites; at rather less exposed sites the plants were larger and the largest of all were intermediate in size and habit between subsp. *anceps* and subsp. *edentatus* (see Pl. II, fig. 1). However, such large plants have been found at only a very few restricted sites where forms of *F. vesiculosus* and *F. spiralis* were less dominant than was usual with increasing shelter.

The uplifted, open communities of algae developed on the exposed reefs became confined to ever narrower and more exclusive belts on the more sheltered inshore reefs. It is possible that competition from forms of more successful fucoids (*F. spiralis* and *F. vesiculosus*) prevents the establishment (to any great extent) of intermediate forms of *F. distichus* on reefs with intermediate exposure conditions. Or, stated otherwise, *F. distichus anceps* is most abundant on the more exposed reefs probably because generally it is only on these reefs that a suitable 'ecological niche' is regularly available that it can successfully occupy; the equivalent (but narrower) zone on more sheltered reefs becomes increasingly occupied by forms of *F. spiralis* and *F. vesiculosus*.

These general conclusions are based on an examination of many reefs. However, along the 12–15 miles of shoreline in question local variations from the zonation of Fucaceae outlined above were occasionally found. Sometimes these variations could be explained as the result of greater or less exposure very locally, caused by the particular configuration of the reef(s) in question (aspect, angle of slope, and relation to other nearby reefs)—e.g. the presence of a patch of *F. spiralis* f. *nana* above belts of *Pelvetia* and typical *Fucus spiralis* near the sheltered head of one of the inner reefs could be explained in terms of wave-action on the (more exposed) reef in front; waves and swell sweep up the outer reef and some splash dashes over and wets the small area of rock at a high level on the reef behind, just sufficiently for *F. spiralis* f. *nana* to develop there. Observations such as this serve to emphasize that, although *nana* and *anceps* were usually confined to the reefs most exposed to wave-action, these particular forms occur at a high level in a much extended littoral zone, and do not suffer most of the violence of swell and wave-action experienced by plants such as *Alaria* on the lower shore; on the other hand, the upper zones benefit from the almost constant spray of waves breaking lower down the shore.

On several very exposed reefs which otherwise lacked fucoids, patches of *anceps* were present only on the ends of the reefs most affected by spray from breaking waves; again it is probably the spray that is beneficial to this high-level form rather than any possible direct effect of wave-action.

Occasionally, both *linearis* and *nana* were absent from reefs where they were expected to occur. Possibly these reefs are stripped of such populations during exceptionally rough weather.

### *Fair Isle*

At the North Gavel site on Fair Isle (see Burrows *et al.*, 1954) the survey party made a fairly accurately levelled shore transect, to compare the vertical zonation of dominant algae with that developed at the sheltered North Haven not far away. The transects and vertical zonations are given in detail in Burrows *et al.* (1954), which also includes photographs (Pl. 15) of the upper and lower parts of the exposed North Gavel site. The belts of dominant algae present were very similar to those described above for Caithness, but the configuration of the shore was interestingly different. Thus the lower shore, covered with *Alaria esculenta*, consisted of a gently sloping platform, which below low-water level sloped very steeply into deep water; the whole of the *Alaria* platform was constantly washed by swell even on calm days. Above the wide belt of *Alaria* the shore consisted of a series of steep sloping walls and rather flat narrow ledges, backed finally by cliffs. On the line of the transect, the steep mid-littoral faces bore little else but scattered tufts of *Gigartina stellata*, but on less steep mid-littoral slopes nearby, *Balanus balanoides*, *Mytilus edulis* and *Patella aspera* Lamarck were common, together with *Rhodymenia palmata*, *Gigartina stellata*, *Acrosiphonia centralis* (Lyngb.) Kjellm., *Scytosiphon lomentaria* (Lyngb.) Endl., *Callithamnion arbuscula* (Dillw.) Lyngb. and *Ceramium acanthonotum* Carm. ex Harv.; the smaller of these mid-littoral algae were mostly attached to the animals (as often they were in Caithness). Higher still, *Fucus distichus anceps* formed a narrow belt (*ca.* 0·6 m in vertical extent) on rock steps, and among and above it *F. spiralis* f. *nana* was particularly well developed, dominating rock steps through a vertical range of about 1·5 m. A belt of mixed *Porphyra umbilicalis* and *Blidingia minima* extended upshore for 1·5–2·1 m (vertical) on rather steep rock faces above *Fucus spiralis* f. *nana*.

The range of spring tides quoted in *The Admiralty Tide Tables* (1956) for Fair Isle is 1·74 m, but the vertical height of rather steep shore occupied by algae at the exposed North Gavel site was up to 6·1 m (from low-water level to the top of the

*Blidingia minima* zone). As shown in Burrows *et al.* (1954), the top of the *Alaria* belt corresponded approximately to observed high-water of a neap tide on a calm day, but even on such a day swell broke continuously at this site, and at high-water repeatedly flooded a zone extending upwards for 1·2–1·5 m above the theoretical high-water level (up to the lowest *anceps* plants), and splash from these waves wetted plants growing up to 2·4–2·7 m above high-water level (including all of the *anceps* belt and most of the main *nana* belt). Throughout most of the year the amount of wave-action experienced at this site will be very much greater, and it may be supposed that the high-level belts of reduced fucoids are frequently within the zone flooded by breaking waves, but probably are not often subjected to the maximum violence of waves breaking directly on them. The survival of belts of algae at these very high levels depends upon their being frequently wetted by swell, waves and splash, or else moistened by mist or rain; and the North Gavel site (facing north-east) is also favoured by shade cast by the cliff behind. Some small plants of *nana* were found, in complete shade, in a small gulley as much as 7·5 m above the main *nana* belt on the open ledges below; a trickle of fresh water kept the plants in the shaded gulley moist.

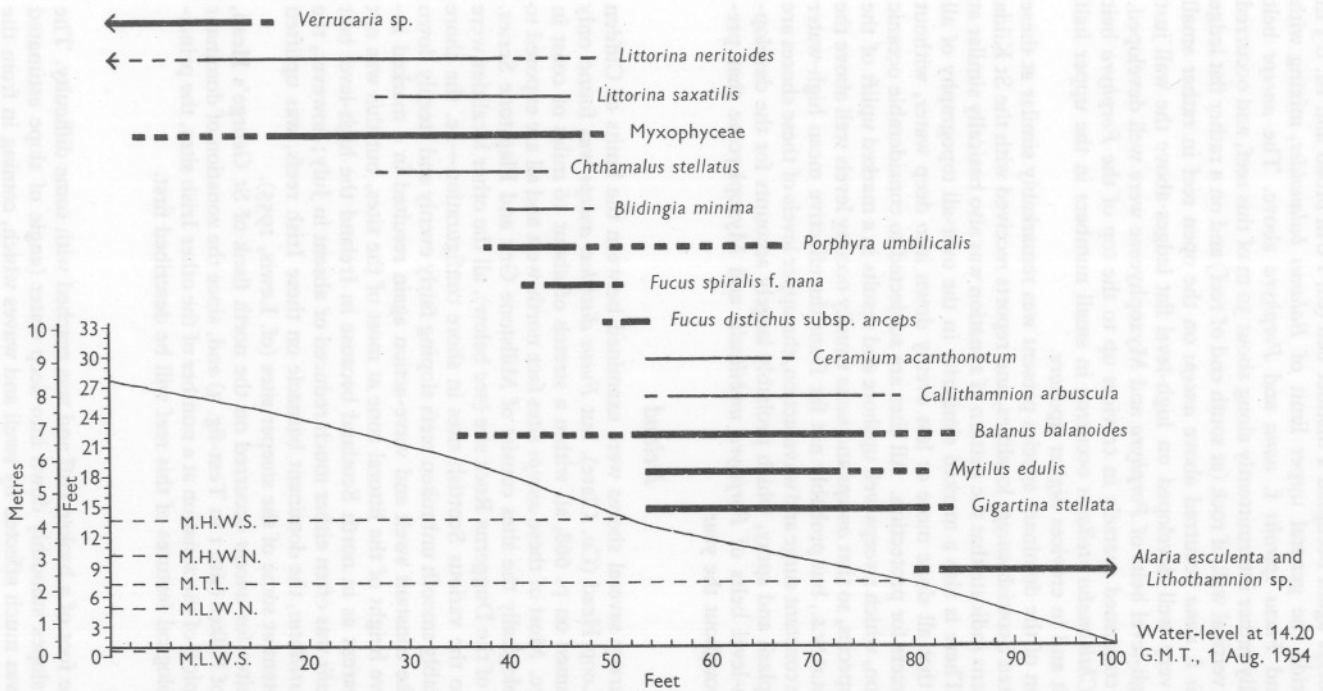
On the whole the plants of *anceps* were smaller than those found on the Caithness reefs and this is probably the result of more rigorous conditions at the North Gavel site, including relatively greater uplift of the whole belt as a result of the unusual (stepped) local rock configuration.

In a shallow high-level pool in the *anceps* belt at North Gavel, two plants of *Fucus distichus* were found which were distinctly narrower than the subsp. *anceps* of open rock and had much shorter receptacles; this narrow pool-plant was in fact intermediate in form between subsp. *anceps* and typical *F. distichus* (subsp. *distichus*) (see Powell, 1957).

At the second site on Fair Isle, a few patches only of *anceps* were found, on very exposed gently sloping reefs facing south-west. Neither *F. spiralis* f. *nana* nor *F. vesiculosus* f. *linearis* was found at or near this site and, as one moved toward more sheltered sites nearby, only one plant of *linearis* was observed. On broad flat reefs a short distance to the north, however, all the usual fucoids of shelter were found. *F. distichus anceps* seems to be only precariously established at this site, and was not found anywhere else on Fair Isle (much of the coast is precipitous and inaccessible); but, at Furse, some *F. spiralis* f. *nana* occurred on the upper shore and, passing into shelter nearby, a whole series of intermediate forms through to the typical form of *F. spiralis* was found.

### *Island of Lewis-Harris*

The site at which *anceps* was found on Lewis in 1954 is accessible from land only by climbing down a 20 m cliff with the aid of a rope. Both the cliff and the shore below are composed of Lewisian Gneiss. The configuration of the shore was very similar to parts of Caithness in that the whole of the littoral zone consisted of a single reef of rather gentle slope for the most part (average *ca.* 15°), with a remarkably smooth and unbroken surface, and dipping directly down into deep water. The whole formed a small natural amphitheatre, limited behind and at each end by steep cliffs. In spite of difficulties, a profile of the shore was made and the zonation of the dominant species measured (Text-fig. 4). The theoretical range of spring tides at this site is *ca.* 4 m, but the coast is very exposed and subject to heavy swell, even though it lies on the east side of the Butt of Lewis. However, it will be seen from Text-fig. 4 that the zones of algae were not uplifted to quite the same extent (in relation to theoretical mean tide levels) as they were at North Gavel, Fair Isle. Thus at the Lewis site the belt of *Alaria* was uplifted only to about theoretical M.T.L., compared with M.H.W.N. (theoretical level) at North Gavel.




Text-fig. 4. Transect at Buaile na Faing headland, Island of Lewis, 1 August 1954. The belts occupied by the dominant species are shown by thick continuous lines, while the zonation of some of the less common species is shown by thinner unbroken lines; in each case the broken lines indicate decreasing frequency of occurrence. The vertical heights of belts were measured from a datum corresponding to the observed level of the sea at 14.20 G.M.T. (approximate predicted time of low water at Stornoway); on the vertical scale, this datum has been made to correspond to the height for low water predicted for Stornoway that day (1·0 ft.). The mean tidal heights indicated against the vertical scale are those given in *The Admiralty Tide Tables* (1956) for Stornoway—a sheltered harbour some 25 miles south of the transect site.

*Fucus distichus anceps* again occupied a distinct belt (*ca.* 1·0 m broad and *ca.* 0·5 m vertical range) astride the general upper limit of *Balanus balanoides*, mixing with *Gigartina* below and *Fucus spiralis* f. *nana* and *Porphyra* above. The *anceps* belt extended horizontally rather intermittently along about 30 m of this reef, and occurred also on an adjacent vertical wall of rock (at south end of reef) and on a rather flat ledge above it. *F. spiralis* f. *nana* occurred above *anceps* on the open reef in rather small quantity, but was very well developed on high-level flat ledges above the wall just mentioned. The high-level belts of *Porphyra* and Myxophyceae were well developed. *Balanus balanoides* continued sparsely in crevices up to the top of the *Porphyra* belt and even higher. *Chthamalus stellatus* occurred in small numbers in the upper half of the *Porphyra* belt and in crevices higher upshore.

Thus the zonation of the dominant species present was remarkably similar at these three widely separated Scottish *anceps* localities, and reports received with the St Kilda and Orkney specimens indicate that the pattern of zonation was also basically similar at those *anceps* sites. There is also a marked similarity in the over-all topography of all the *anceps* reefs in that all slope more or less evenly down into deep water, without offshore islands or reefs for protection. All sites are subjected to considerable oceanic swell and wave-action, which sweeps well upshore and results in a marked uplift of the zones of dominant species, so that *anceps* and *nana* usually occupy levels well above the *theoretical* level of M.H.W.S., but probably not far from the effective mean high-water level. Because of the constant surge and wave-action, the upper levels of these shores are much affected by splash and spray, which probably largely accounts for the development of good high-level belts of *Porphyra umbilicalis* and Myxophyceae that presumably persist throughout the year.

## *Ireland*

During the 1953 survey several shores were examined between the limits of Clifden (Connemara) and Loop Head (Co. Clare), but *Fucus distichus anceps* was found only at the eight sites named on p. 668, all within a stretch of about 16 miles of coast in south-west Co. Clare. Most of these *anceps* sites face north-west and all are exposed to Atlantic swell. Geologically the sites consist of Millstone Grit and Flagstone Series. With the exception of the Duggerna Rock site (see below), all the other localities were essentially similar to the various Scottish sites in shore configuration—i.e. the shore consisted of remarkably smooth unbroken reefs sloping fairly evenly and steeply down into deep water. The constant swell and wave-action again resulted in a marked increase in the effective height of the littoral zone at most of the sites, but this was not so immediately apparent as in north Scotland because in Ireland the high-level belt of *Porphyra umbilicalis* was often either much reduced or absent in July; however, the belt of *Chthamalus stellatus*, the dominant barnacle on these Irish reefs, was uplifted to a considerable extent at some of the steeper sites (cf. Lewis, 1955).

One of the best sites for *anceps* occurred on the north flank of St George's Head, about 1 mile north of Kilkee (site 1 in Text-fig. 3) and, since the zonation of dominant species there was typical of the zonation at a number of the other Irish sites, the principal physical and ecological features of this reef will be described first.

### *St George's Head*

The site lies at the foot of a broken cliff and was reached with some difficulty. The reef faces N.N.W., slopes smoothly down into deep water (angle of slope estimated to be 10–15°), and was much affected by swell and waves which, coming in from the south-west, mostly ran along the reef as well as slightly up it; the greatest violence of

wave-action occurred at the western end of the reef and it was here that the uplift of zones was greatest. Farther inshore (in a north-east direction) the severity of wave-action was less and the reef also becomes less steep. At the most exposed (south-west) end of the reef the upper shore was dominated by *Chthamalus stellatus* and a quite well developed (for Ireland) high-level belt of *Porphyra umbilicalis*; an excellent belt of *Fucus spiralis* f. *nana* occurred in the lower part of the *Porphyra* belt. A few yards farther into 'shelter' a fine belt of *Fucus distichus anceps* came in, and mixed with *F. spiralis* f. *nana* above and *Gigartina stellata*/*Chthamalus*/*Mytilus edulis* below. *Ceramium acanthonotum* occurred on the higher *Mytilus*, and *Callithamnion arbuscula* on *Chthamalus* and rock slightly lower. The lower shore was dominated by *Alaria esculenta*, *Lithothamnion* sp. and frequent stunted *Corallina officinalis* L. Farther into shelter, *Fucus vesiculosus* f. *linearis* first appeared at about the upper limit of *Gigartina*, and gradually became dominant on the inner part of the reef where, as the whole littoral decreased in vertical extent, it soon entirely replaced *Fucus distichus anceps*—one of the best examples of this phenomenon seen anywhere. *Gigartina* also disappeared from the upper mid-littoral zone soon after the loss of *anceps*, as *linearis* came to dominate this level. Unfortunately, it was not possible to level accurately the zones of dominant species at this site, but uplift of the upper zones of algae was not nearly so marked as on some of the Caithness reefs, perhaps because of the oblique angle at which the prevailing swell hits the reef and runs along it rather than directly up it. The presence of a good high-level belt of *Porphyra* on the part of the reef most affected by spray from breaking waves was probably also a result of the relatively small amount of uplift of zones compared with some of the other Irish reefs described below; and, probably for the same reason, the *anceps* plants were rather larger than were found at some of the other Irish sites.

### *Donegal Point*

Most of the littoral zone of this headland is precipitous and inaccessible, and *anceps* was found only at one very restricted site about half-way along the south-west flank (site 2 in Text-fig. 3). The reef was rather steep (*ca.* 20°), fully exposed to violent swell, and dominated mainly by *Chthamalus* (with some few stunted algae) on the middle and upper shore, and by *Alaria* on the lower shore. Small and frequent plants of *Fucus spiralis* f. *nana* formed a fairly well-defined belt below a relatively narrow belt of *Porphyra*. The mid-littoral zone was dominated mainly by *Chthamalus* and *Mytilus*, but some few stunted, narrow plants of *Fucus vesiculosus* f. *linearis* were also present, and occasional tufts of *Gigartina* lower down. Several small patches of *Fucus distichus anceps* occurred, situated mostly between the very open 'belts' of *nana* and *linearis*; the individual plants of *anceps* were very small, mostly vegetative, and conspicuously yellow in colour. Farther along this difficult reef (north-west, towards the point) *linearis* and *anceps* were soon absent from the flora, but *nana* persisted on to steeper and even more wave-beaten reefs.

### *Duggerna Rock, Kilkee* (Text-fig. 3, site 3)

This type-locality for *anceps* is topographically one of the most anomalous, in the light of our recent knowledge of the distribution and ecology of this plant. The Duggerna Rock, situated at the southern entrance to Moore Bay, Kilkee, is a very extensive platform of intertidal rock, measuring approximately 550 m from east to west by about 500 m from north to south. Much of the inner part of this remarkable littoral plateau consists of relatively flat areas of broken rock (with deep pools, etc.) on which all of the fucoids of sheltered places occur, together with such species as

*Bifurcaria rotunda* (Huds.) Papenf. and *Himanthalia elongata* in deep, sheltered, mid-littoral pools. However, out towards the north-west extremity of the platform (about 320 m from the shore high-water line) the rocks become higher again over a quite small area and stick up as a small rock pinnacle which remains just above the surface at high tide, although waves usually wash over it. It was only on the steep seaward facing side of this 'offshore' elevation that *Fucus spiralis* f. *nana* and *F. distichus anceps* were found in typical narrow belts, although some few plants of *anceps* were found also on two narrow, exposed reefs immediately west of the elevation. Sometimes this particular offshore elevation is referred to as *the* Duggerna Rock and, judging by his description, this is undoubtedly the precise site at which W. H. Harvey first found *anceps* (see Carruthers, 1863; and Powell, 1957, for further references).

As already stated, however, the configuration of the shore at this site is somewhat different from that of most *anceps* sites in that, immediately to the west of the offshore elevation, lie two narrow reefs which slope gently *inshore*; these reefs are not very extensive and do not rise so high as the main offshore elevation so that they shelter from direct wave-crash only the lower parts of the Duggerna elevation. It was very interesting to find plants of *anceps* on the higher parts of both of these shallow inshore-facing reefs, in each case at a lower level than the *anceps* plants on Duggerna Rock itself.

Because of the unusual shore configuration, the zonation of dominants at this site was somewhat confused, but the salient features were as follows.

*The offshore elevation* (*Duggerna Rock*). The highest parts (flat) were covered with patches of *Chthamalus* and *Verrucaria* sp., and with frequent *Littorina saxatilis* (Olivi) and *L. neritoides* (Montagu). The western face of the elevation is steeply sloping or near vertical (for a vertical height of 2·7–3·1 m). The usual dominant species of such exposed Irish coasts occurred on this wall in a very open and mixed community, as follows: *Fucus spiralis* f. *nana* mostly in the uppermost 1·8 m (best developed on ledges) and *F. distichus anceps* in the lowermost 1·5 m, together with small plants of *F. vesiculosus* f. *linearis*, tufts of *Gigartina*, etc. The plants of *anceps* were rather small and had mostly ceased fruiting (17 July). Below the wall, on shallow ledges, *F. vesiculosus* f. *linearis* occurred in tufts, with barnacles, *Mytilus*, etc.

*The two inshore-facing reefs beyond.* The inner of the two reefs was about 18 m broad and, on the lower stretch of 12 m, was dominated principally by *Mytilus* and *Fucus vesiculosus* f. *linearis*, with frequent *Chthamalus*, *Gigartina*, etc., forming a dense closed community; on the higher part of the reef, however, about 6 m broad, these same species formed a much more open community (probably a direct result of severe wave-action) and here *Fucus distichus anceps* was found, either as isolated plants on small patches of otherwise bare rock, or else mixed with the other species in open communities.

The outer reef was about 30 m broad, and on the seaward side its uplifted western edge dipped quite steeply down into deep water; this western edge was dominated by *Alaria*. On the smooth inshore-facing surface of the reef the (lowermost) inner half was dominated by very crowded *Mytilus*, with scattered tufts of *Fucus vesiculosus* f. *linearis*, *Gigartina*, etc.; but throughout the higher half of the reef scattered plants of *Fucus distichus anceps* were again found, mixed with the above and other species of plants and animals in a rather open community.

Thus, on each of the two reefs, scattered plants of *anceps* occurred on the higher (least sheltered) parts only; it is of interest that the plants themselves were quite large (*ca.* 7–10 cm long) and that most were sterile, although some plants had precocious irregular areas of receptacular tissue some distance behind the apices; the deduced

age was 1 year—see p. 682). It is presumed that the relatively large size was a result of the plants growing at a relatively lower level on the shore than usual (less desiccation) and that they were able to do so because of the unusual configuration of the reefs at this otherwise very exposed site; however, since only very few fully fertile (2-year-old?) plants were found on the two outer reefs it may be assumed that conditions there are more hazardous (severe wave-action and intense competition from mid-littoral species) than subsp. *anceps* encounters at its more usual level.

It is of interest that on the outer reef one plant of *linearis* was found with several vegetative plants of *anceps* growing epiphytically on it; the two forms were readily distinguishable in the field by means of the midrib character (see p. 670). This is the only record of any form of *F. distichus* growing epiphytically on another large alga.

The remaining sites at which *anceps* was found in south-west Co. Clare are those numbered 4–8 in Text-fig. 3. Most of the intervening stretches of coast were either precipitous and inaccessible from land, or else were too sheltered for *anceps*.

### *Site* 4 (Text-fig. 3)

This is a broad reef, several 100 m long, on a very exposed coast just to the west of Bridge of Ross (a natural arch of rock); the reef again faces north-west so that oceanic swell approaching mainly from the south-west tends to run along as well as slightly up the reef. At the more sheltered north-east head of the reef, the belts of some of the dominant plants and animals were again obviously uplifted relative to theoretical tide-levels, but there was much evidence that the high-level belts of algae were very adversely affected (stunted and desiccated) by summer air temperatures.

The reef sloped very evenly, at an angle estimated to be *ca.* 10°. The lower shore was dominated by an uplifted belt (*ca.* 7·5 m broad) of sparse *Alaria*, merging upwards into a very open belt (*ca.* 3 m broad) of mixed *Gigartina*, *Mytilus*, *Corallina officinalis*, *Patella aspera*, *Nemalion elminthoides* (Vell.) Batt., *Callithamnion arbuscula*, *Polysiphonia macrocarpa* Harv., small *Scytosiphon lomentaria* and (unusually for an *anceps* site) frequent small plants of *Laurencia pinnatifida* (Huds.) Lamour., with *Chthamalus* largely confined to small pits and cracks in the otherwise very smooth surface of the rock. *Fucus distichus anceps* occurred in the zone next above (up to *ca.* 7·5 m wide), mixing with the above-named species and some few plants of *F. vesiculosus* f. *linearis* below, and with *F. spiralis* f. *nana* above; the maximum width of the *nana* belt was *ca.* 3·5 m. Both fucoid belts were very open. The plants of *anceps* appeared to comprise two distinct year-groups: (i) larger plants, mostly in the centre of the belt, which were in a late fruiting stage (2 years old?) and covered with brown epiphytes; (ii) younger vegetative plants (1 year old?) mainly above and below the belt of older plants, and with few or no epiphytes. The older plants particularly were very dried out on a warm day (18 July) and the epiphytes borne on the arched fronds had stuck to the rock in many instances. Above the two fucoid belts occurred a belt (*ca.* 7·5 m broad) of sparse and stunted *Porphyra* with *Chthamalus* (and some *Pygmaea pumila* (Huds.) Kuntze and *Blidingia minima*), while *Chthamalus* continued farther upshore for approximately 11 m, but strictly confined to crevices and altogether very inconspicuous. On the open rock in the upper part of the *Chthamalus* belt, patches of dried-out *Bangia fuscopurpurea* (Dillw.) Lyngb. and Myxophyceae indicated that earlier in the year algae had flourished at much higher levels on the open reef than they could in summer. *Littorina saxatilis* and *L. neritoides* continued in crevices very much higher upshore than *Chthamalus*. The theoretical range of spring tides in this area is about 4·3 m and from very approximate estimations it seems that most of the *anceps* belt probably occurred below the theoretical level of M.H.W.S. Unfortunately, *Balanus balanoides* was extremely scarce and no estimate could be made of its 'general upper

limit' to assist comparison of the levels occupied by *anceps* in Ireland and Scotland. However, there is little doubt that *anceps* generally occupies a somewhat lower zone (relative to both theoretical and effective mean high water levels) in south-west Co. Clare than it does in Scotland.

Toward the more exposed and wave-beaten south-west end of this same reef, the zones of dominant species were uplifted to a greater extent and first *anceps* and then *nana* were lost from the flora.

*Fucus distichus anceps* occurred also on the next reef immediately to the north.

### *Site* 5 (Text-fig. 3)

Here very good belts of *anceps* and *nana* were found on a rather steeper reef (estimated slope 15–20°), with the same associated dominant species above and below. At this site *anceps* again occurred in two distinct forms, apparent year-groups, the larger having mostly ceased fruiting and occurring mainly in the lower half of the *anceps* belt.

### *Site* 6 (east of site 5)

Here the littoral area is for the most part very steep (30–40°), but with flat ledges of rock at intervals; *anceps* was very well developed, especially on the ledges, and occurred in a zone at least 1·5 m in vertical extent (directly measurable at this site). Plants of the two apparent year-groups (see p. 682) were again present in about equal numbers, and at this site both young and old plants occurred throughout the 1·5 m range. In addition, many crowded groups of *anceps* sporelings occurred on *Chthamalus* and on rock in the *anceps* belt. This reef was examined during a heavy rain-storm, and it was noted that some *anceps* plants were growing in a depression completely submerged by a temporary strong stream of fresh water. Some specimens of *Balanus balanoides* were noted among the frequent *Chthamalus* in the *anceps* zone. It was again observed that *nana* persisted farther than *anceps* along the steeper and more wave-beaten part of this shore.

### *Site* 7 (Text-fig. 3)

This site is extremely difficult of access, with a steep descent to a very exposed littoral zone. The reef is small in area, mostly steep in the lower littoral and affected by violent swell; however, the upper littoral area flattens out to a shallow slope and, at this level, on the more exposed part of the reef, good belts of *Fucus spiralis* f. *nana* and *Gigartina* (below) were developed. *Fucus distichus anceps* occurred below the *nana* only on a slightly more sheltered part of this restricted high-level platform; the plants were small and some were still in a late fertile stage.

### *Goleen Bay* (Text-fig. 3, site 8)

*F. distichus anceps* was found in quantity on the outer reefs of the rocky promontory at the northern entrance to the bay. The reefs at this site slope very steeply (20–30°) down into deep water, but they mostly face due north so that swell from the south-west again tends to run along them rather than directly upshore. The characteristic zonation of dominant species on the more exposed rock faces was as follows: *Chthamalus* on the upper shore; then *Chthamalus*/*Porphyra umbilicalis*; *Fucus spiralis* f. *nana*; *F. distichus anceps*; *Gigartina*, etc.; *Alaria*. The site was apparently too exposed for *Fucus vesiculosus* f. *linearis*. Again, *nana* was more tolerant than *anceps* of increasing exposure. The *anceps* formed an almost closed community and occurred in three

distinct colour shades: (i) light yellow—young, first-year vegetative plants; (ii) russet brown to orange—old plants, just ceasing to fruit; (iii) dark brown—old plants densely covered with epiphytic *Elachista fucicola* (Vell.) Aresch. and *Spongonema tomentosum* (Huds.) Kütz. Both young and old plants occurred throughout the *anceps* belt, and in general the plants of both age-groups were smaller towards the top of the belt. Epiphytes were most dense on the lowermost old plants. A large number of *anceps* sporelings were again observed, on *Chthamalus* and on rock, in the *anceps* belt.

The inner part of Goleen Bay is very sheltered and the shore consists of mixed boulders and reefs, covered with all the usual fucoids of sheltered Irish shores. Since *anceps* occurred in unusual abundance at the entrance to the narrow bay it was considered that, if sporelings of Irish *anceps* were able to develop into larger plants (approaching subsp. *edentatus* in form) under sheltered conditions, the inner part of Goleen Bay would be one of the most likely places to find such plants. No plants of *F. distichus* were found in the inner parts of the bay, however. Further, no intermediate forms between *anceps* and *edentatus* were found anywhere in Ireland.

At Baltard Bay (see Text-fig. 3) the shore configuration is very similar to some of the least steep Caithness reefs, and such reefs are extremely rare in the west of Ireland. The angle of slope was estimated as probably not more than 5° and the reef extends as an almost unbroken sheet of smooth Millstone Grit, from the base of low cliffs well above effective high-water level right down into deep water. The reef faces west and oceanic swell, running in along the southern flank of Baltard Bay, sweeps directly upshore. As in Caithness, these conditions result in a considerable uplift of the belts of dominant species, but the shallow reef is so extensive that the upper shore is not subjected to anything like the severity of swell and wave action experienced on the lower shore. Thus *F. vesiculosus* f. *linearis* was found to be well developed in the upper mid-littoral zone (mostly small, narrow plants), with *F. spiralis* f. *nana* frequent above it; subsp. *anceps*, however, was absent. The principal differences at this site, compared with sites of similar configuration in Caithness, were seen on the upper shore: *Chthamalus* was now the dominant barnacle and extended upshore (usually confined to cracks and hollows in the rock) for a considerable height above theoretical mean high-water level; and the high-level belts of *Porphyra* (above *nana*) and Myxophyceae were not nearly so well developed in summer (although *Porphyra umbilicalis* was abundant in the effective mid-littoral zone on such Irish shores).

## FRUITING RECORDS

Among the records and collections of subsp. *anceps* reported above, fertile plants have been found in all of the months from April to August. Only sterile plants were collected at Kilkee in 'September 1897' (by E. George); and J. Sinclair likewise found only sterile plants at Hole o'Rowe, Orkney, on 16 October 1938.

The only plants collected in the month of April (island of Lewis-Harris, *W. J. Gibson*, 1909—see p. 667) were fully mature, so it may be supposed that receptacles start to develop at least as early as January and probably a little earlier.[1] However, even though it is not known when fruiting starts, it is certain

[1] Börgesen (1902) reports that in the Faeröes fertile specimens of *Fucus distichus* were found from April to August; specimens gathered in October and November were sterile; in December a few specimens were found bearing young receptacles. However, Börgesen does not state which form of the species was examined in December.

that it largely ceases during August at all sites. There is a suggestion that the peak of fruiting is reached some few weeks earlier near the southern limits of distribution (the Kilkee district) than in the Scottish localities.

## POSSIBLE LONGEVITY

The observations on populations of *anceps* in south-west Co. Clare in July 1953 strongly suggest that there this plant has typically a 2- to 3-year life-span. Thus, at several sites, it was obvious that two distinct populations occurred intermixed: (i) relatively large, fully mature plants, frequently with all the apices fertile (or else with old receptacles dying back), and bearing many mature brown epiphytes (principally *Elachista fucicola* and *Spongonema tomentosum*); and (ii) shorter, vegetative plants, usually quite sterile, or else with only one or two (precocious) receptacles (often just part of a frond some way back from the apex), and with few or no epiphytes. Usually populations (i) and (ii) were quite intermixed, but occasionally, on reefs of even slope, belts of (ii)-type population occurred principally above and below a crowded main belt of (i)-type population. At several sites, crowded groups of really small sporelings were found in the *anceps* belt; length of sporelings (0·5–)4–10 (–13) mm, with one or two dichotomies and with prominent cryptostomata. It is thought that these small sporelings were probably not more than a few months old, population (ii) 1 year old, and population (i) 2 years old. After fruiting, the receptacles of the presumed 2-year-old plants die back and, since often no vegetative leaders are left to continue growth, it seems that the whole of such a plant usually dies back and is removed from the rock by wave-action during the third winter of its life. Indeed, vestiges of holdfast and stipe were seen at several sites in Ireland. However, some of the mature (i)-type Irish plants examined did show a few remaining vegetative leaders that could continue growth into a third year if the plants are able to survive the storms of a third winter; these leaders are usually lateral branches issuing from quite low down on the stipe.

At the Scottish sites, sterile (1-year-old) plants were again distinctive at all sites, but the fertile plants (probably at least 2 years old) commonly bore quite a number of vegetative leaders (again issuing mainly from the proximal rather than the distal parts of the plants) and it is probably more usual for plants to survive for at least 3 years, especially on many of the Caithness reefs where conditions are not quite so rigorous as at some of the other Scottish sites.

## DISCUSSION

*Fucus distichus* subsp. *anceps* thus shows a very discontinuous distribution in Britain and Ireland, being confined to some few isolated and usually very limited stretches of exposed coast in the north and west. The various centres of distribution are mostly geographically isolated from each other by con-

siderable distances, and locally the species is ecologically confined to very exposed reefs, that are often difficult of access.

At all the *anceps* sites described above, all or most of the littoral area of the shore slopes evenly and more or less steeply (5–40°) down into deep water, usually without any major offshore protection, and with the 5 and 10 fathom (9 and 18 m) isobaths usually close inshore. All of the sites are also subjected to constant and frequently violent oceanic swell, as well as severe wave-action, which sweep a long way up shores of this configuration and result in a marked upward extension of the littoral zone as a whole. The conditions of life for species growing in the upper littoral at such sites are obviously more rigorous than on more sheltered shores for, although frequently inundated during rough weather, and wetted by spray from breaking waves and swell even more often, there will be periods of relatively calm weather when the uplifted high-level species must suffer severe desiccation, especially in the warmer summer months, unless frequent rain or mist mitigates these conditions. In general, the desiccation will be a good deal more severe at the warmer southern (Irish) sites than at the cooler northern (Scottish) sites. Fucoids are only able to survive on such wave-beaten shores at the higher levels, where they develop into narrow dwarf forms such as *F. spiralis* f. *nana* and *F. distichus anceps*, and it is interesting that in Ireland the former with the more southerly over-all distribution tolerates rather more rigorous exposure conditions than the latter 'northern' species; whereas at the Scottish localities *anceps* persists farther into exposure than *nana*. It is very difficult to make comparisons of levels occupied by the same dominant species on shores such as these (with differing tidal ranges, aspect, angle of slope, etc.), but there were some indications that the two belts of high-level fucoids occur at relatively rather lower levels at some of the Irish sites than they do at the Scottish sites, and this could be a result of more severe desiccation at the Irish sites. Indeed, it seems that the eventual southern limit of *F. distichus anceps* is probably determined by increasingly severe desiccation at the high level occupied, retreat downshore being limited by the more severe wave-action and intense competition from other plant and animal species in the zone below.

This type of smooth shore configuration is very rare, and most of the exposed rocky shores of Britain and Ireland are very much more broken up. This usually means that much of the force of swell and wave-action is dissipated either on off-shore reefs or islands or, more often, in the lower littoral, with the result that the over-all height of the littoral zone is not raised to anything like the same extent; indeed, the upper shore is often comparatively sheltered from wave-action under these conditions, as is best indicated by the species that usually grow there (e.g. *Pelvetia canaliculata*). On such broken or flatter coasts, with intermediate exposure conditions prevailing at least in the mid- and upper littoral zones, *Fucus vesiculosus* f. *linearis* commonly

dominates the mid-littoral in Britain, with a zone of *F. spiralis* (or *F. spiralis* f. *nana*) above it.

Ecologically then *F. distichus anceps* appears to be confined to exposed sites (with extended littoral zone) largely as a result of competition from more successful forms of *F. vesiculosus* and *F. spiralis* on coasts of intermediate exposure; and intermediate forms of *F. distichus* (between subsp. *anceps* and subsp. *edentatus*) are largely absent from British coasts of intermediate exposure (except for a few instances in Caithness) probably for the same reason. It is very interesting that farther north, nearer to one of the centres of distribution of *F. distichus* (e.g. in the Faeröes, Iceland and northern Norway), intermediate forms of the species are commonly found on coasts of intermediate exposure and, although a form of *F. vesiculosus* without vesicles occurs commonly in these places, it is apparently restricted to more sheltered sites than in Britain (see Börgesen, 1902, p. 478; 1905, p. 720 *et seq.*).

Additional records of *F. distichus anceps* may be expected from certain restricted stretches of very exposed coast that have a similar configuration and ecology to that described above for the various sites known to date. However, in view of the over-all distribution, it is considered most unlikely that the form will be found anywhere else on the *mainland* of Britain other than on the north coast of Scotland. Additional records will probably come only from exposed coasts in the following areas: the Shetland and Orkney Islands, the Outer Hebrides (and possibly Tiree and Islay), and the north and west coasts (only) of Ireland. Even within these areas, however, the number of possible sites physically, and hence ecologically, suitable for *F. distichus anceps* are remarkably few as can be seen from large-scale maps and charts. Indeed, several of the Irish sites for *F. distichus anceps* were predicted from a study of fairly large-scale maps (1 in. to 1 mile, with contours, gives sufficient detail).

## *FUCUS DISTICHUS* L. EMEND. POWELL, SUBSP. *EDENTATUS* (DE LA PYL.) POWELL (Pl. II, fig. 2)

### DISTRIBUTION

In Britain, *F. distichus* subsp. *edentatus* has been found at the following three localities only: Lerwick and Scalloway, Shetland Islands, and North Haven, Fair Isle (Text-fig. 1).

In reporting the presence of the species at Lerwick in 1902, Börgesen (1903, p. 304) stated that 'it grew here at about low-water mark on the quay itself, as well as on stones opposite to it; but in spite of a very close search I did not succeed in finding it anywhere else, neither to the south-east of Lerwick, nor in the sound near Bressay, nor [at] Burra Voe, nor on Muckle Holm' (Yell Sound).

According to the printed label attached to specimens of *edentatus* distributed by E. M. Holmes as '*Fucus inflatus* Vahl' (*Alg. Brit. Rar. Exsicc.*,

Fasc. XII, No. 288), another collection of plants from Lerwick harbour was made in 'June 1908' by 'W. A. Russell'.

In June–July 1952, *edentatus* was found to be still abundant in the harbour at Lerwick and was found also at the following two new localities—in the shelter of the small harbour at Scalloway, a small fishing town not far from Lerwick, and in the sheltered North Haven on Fair Isle, which is the usual harbour for the island. The Fair Isle record represents a new southern limit for this form of the species on the British side of the North Sea and a preliminary notice of the record (under the name *F. inflatus* f. *edentatus*) was given in Burrows *et al.* (1954).

## ECOLOGY

### *Lerwick, Shetland*

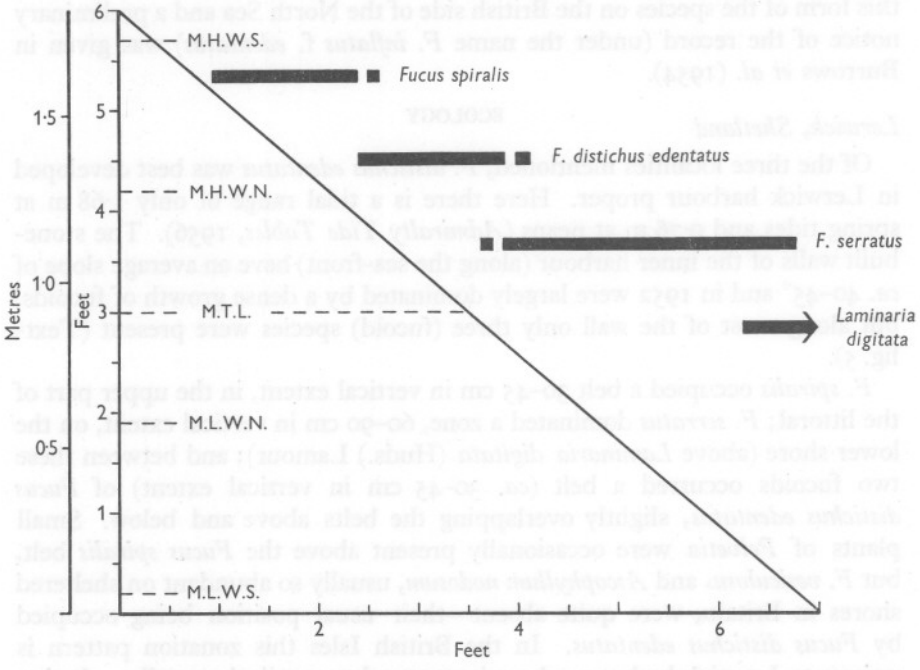
Of the three localities mentioned, *F. distichus edentatus* was best developed in Lerwick harbour proper. Here there is a tidal range of only 1·68 m at spring tides and 0·76 m at neaps (*Admiralty Tide Tables*, 1956). The stone-built walls of the inner harbour (along the sea-front) have an average slope of *ca.* 40–45° and in 1952 were largely dominated by a dense growth of fucoids, but along most of the wall only three (fucoid) species were present (Text-fig. 5).

*F. spiralis* occupied a belt 30–45 cm in vertical extent, in the upper part of the littoral; *F. serratus* dominated a zone, 60–90 cm in vertical extent, on the lower shore (above *Laminaria digitata* (Huds.) Lamour); and between these two fucoids occurred a belt (*ca.* 30–45 cm in vertical extent) of *Fucus distichus edentatus*, slightly overlapping the belts above and below. Small plants of *Pelvetia* were occasionally present above the *Fucus spiralis* belt, but *F. vesiculosus* and *Ascophyllum nodosum*, usually so abundant on sheltered shores in Britain, were quite absent—their usual position being occupied by *Fucus distichus edentatus*. In the British Isles this zonation pattern is unique to Lerwick harbour, where it occurred on vertical as well as sloping walls. Tracing the fucoids south-eastwards beyond the built-up walls of the harbour proper, it was found first that, on a more open (but still comparatively sheltered) and gently sloping shore (of natural reefs, boulders and sand), near Queen's Hotel (Leag beach), *edentatus* occurred down to lower levels and the individual plants were then larger; again *F. spiralis* occurred on the upper shore and *F. serratus* (here with very deeply incised serrations) on the lower shore, and no other fucoids were present. Continuing south-eastwards along the shore, however, *F. vesiculosus* quite soon appeared in the mid-littoral zone and, as it increased in amount, so the *F. distichus edentatus* decreased until, within a few hundred metres of Lerwick harbour, it disappeared from the flora. (*Pelvetia* appeared just before *Fucus vesiculosus*, and some plants of *Ascophyllum* were found with the first *Fucus vesiculosus*).

On the Leag shore especially, plants of *edentatus* frequently had irregular inflations in the distal parts of the fronds, and sometimes grew in shallow

pools. *F. serratus* also frequently had inflated apices at this site (observed on a rather warm day).

These observations at Lerwick could suggest that *F. distichus edentatus* may compete with *F. vesiculosus* and *Ascophyllum* for the available space in parts of the *outer* harbour area, but on the *inner* harbour wall the complete replacement of the other two species by *edentatus* is altogether unusual, and




Text-fig. 5. Diagram to show zonation of the dominant algae on the wall of the inner harbour at Lerwick, June 1952, and the approximate relation of the algal belts to the mean tidal levels there (mean levels derived from *The Admiralty Tide Tables*).

is almost certainly not entirely (and perhaps not at all) the result of competition. There is very considerable pollution in Lerwick harbour caused particularly by effluent pouring directly into the harbour from the fish factories that line the quays, and it would seem that *edentatus* is more tolerant of this pollution than is either *Fucus vesiculosus* or *Ascophyllum*. It is interesting that Lund (1949*a*, *b*) also has noted that *Fucus distichus edentatus* in Copenhagen harbour shows greater tolerance of polluted water than does *F. vesiculosus* or *F. serratus*; the individual plants of *edentatus* were also smaller at such polluted localities (Copenhagen) than at less polluted places nearby.

*Scalloway, Shetland*

During a brief visit to Scalloway on 3 July 1952, patches of rather small plants of *edentatus* were found in the sheltered harbour. The plants occurred on a gently sloping shore composed of boulders, shingle and sand, at the western head of the bay between the two piers. The tidal range is small (only 1·13 m at springs), and it is probable that these waters were again somewhat polluted. The fucoids present in open communities on this rather unstable shore were: *F. spiralis* forming a belt on the upper shore; small amounts of both *F. distichus edentatus* and *F. vesiculosus* intermixed in the middle part of the littoral; and plentiful *F. serratus* on the lower shore. The small plants of *edentatus* had almost ceased fruiting, and many plants had irregular inflations. It was most unusual (for Britain) to find that nearly all of the plants of *F. serratus* had inflated apices.

*North Haven, Fair Isle*

In the sheltered North Haven on Fair Isle (a small and predominantly sandy bay), *edentatus* was again not very abundant compared with Lerwick, although it was found on rocks or boulders at both the east and west sides of the bay, on the boat-slip at the centre of the bay and on the stone landing jetty in the south-east corner of the bay. The tidal range is 1·74 m at springs, and the Haven is not polluted. On the west side of the Haven the rock face above the sandy beach is very steep or vertical; here *F. spiralis* occurred in the uppermost 30–45 cm of the *Balanus balanoides* belt, and occasional plants of *Fucus distichus edentatus* were found below the *F. spiralis* belt and farther down to about M.T.L.; the lower plants of *edentatus* were larger than those growing higher up; no other fucoids occurred on this steep face, the lower levels being occupied by *Gigartina stellata*, *Acrosiphonia centralis* and *Enteromorpha* spp.

The boat-slip in the centre of the bay is made of concrete and iron and runs down the sandy beach into deep water. The cement was well covered with *Balanus balanoides*; *Pelvetia* and *Ascophyllum* were absent; on the inshore end of the sides of the slip occurred a belt of *Fucus spiralis* (30–45 cm vertical extent) and below this a belt of *edentatus* (30–38 cm vertical); farther out on the slip and at a lower level, *edentatus* occurred mixed with *F. vesiculosus* and occasional *F. serratus*, with an undergrowth of *Gigartina*, *Lomentaria articulata* (Huds.) Lyngb., etc.

In the south-east corner of the bay the nearly vertical sides of the stone-built landing jetty showed the following zonation of fucoids: a narrow belt of *Fucus spiralis* above, then a belt of *F. vesiculosus* but with a small amount of intermixed *Ascophyllum*, and finally some plants of *Fucus distichus edentatus* on the lower part of the wall.

On the shore nearby (just a few metres to the west of the jetty) the zonation

of the dominant algae was worked out in detail and is recorded in Burrows *et al.* (1954, see especially Figs. 4, 5). The shore here sloped very gently; the upper part consisted of a broken rocky reef and the lower part of rounded boulders and rock outcrops embedded in sand. *F. spiralis* formed a good belt (38–45 cm vertical extent) on the reef; *F. vesiculosus* and some *Ascophyllum* dominated the mid-littoral rock and boulders (0·9–1·2 m vertical extent), with associated *Gigartina*, *Cladophora rupestris* (L.) Kütz, *Enteromorpha* spp., *Acrosiphonia centralis*, etc.; while *Fucus distichus edentatus* (large plants) occurred only on boulders on the lower shore, together with *F. vesiculosus* and some *F. serratus*.

Just beyond the jetty, the eastern shore of the Haven (rock reefs and boulders) is very broken, and here only one small group of plants of *edentatus* was present, on the lower shore.

Thus *edentatus* appeared to be fairly well-established in the North Haven: in the most sheltered corner (near the landing jetty) frequent *F. vesiculosus* and some *Ascophyllum* dominated a zone below *Fucus spiralis*, and *edentatus* was confined to more open communities on boulders embedded in sand on the lower shore; but, at the rather more exposed (also steep) sites in the bay, *edentatus* appeared to be more successful than *F. vesiculosus* in colonizing the zone immediately below *F. spiralis*.

## FRUITING RECORDS

The plants collected at Lerwick by F. Börgesen in 1902,[1] and by W. A. Russell in June 1908, were both fertile; otherwise records are limited to the 1952 observations when, during the period 24 June–3 July, fully fertile plants were noted at Lerwick, Scalloway and North Haven; at Scalloway, however, most of the receptacles were old and the fruiting period appeared to be nearing an end.

## DISCUSSION

These three records of *F. distichus edentatus* represent the southern limit of this form of the species on the British side of the North Sea; the southern limit on the eastern shores of the North Sea is in Copenhagen harbour (Lund, 1949*a*,*b*). In the Faeröe Islands (about 250 miles to the north-west) and in Norway (a similar distance to the east) the plant is plentiful, and it has very probably been introduced accidentally to the three Shetland harbours by the fishing vessels which ply between them, and the Faeröes, and Norway.

There are several ways in which this could happen: pieces of (fertile) *edentatus* could be scraped from a jetty wall by the hull of a fishing vessel (perhaps itself roughened with attached barnacles) and be carried about to some other

[1] In his paper Börgesen (1903, p. 300) states that he visited Lerwick 14–16 July [1902]; a fully mature specimen of subsp. *edentatus* in Herb. Kew, however, is labelled by Börgesen 'Lerwick, 16. 6. 1902'.

harbour where the pieces could readily be scraped off against another quay. The chances of subsequent establishment would be increased by the fact that the species is hermaphrodite. Alternatively, as Hylmö (1933) suggests (with reference to the recent spread of the plant on the west coast of Sweden), it could be taken onto fishing vessels, growing on the shells of *Mytilus edulis* (used for bait), and later be jettisoned with the empty shells perhaps in another harbour. Introduction by fishing vessels seems a more likely possibility than introduction by floating plants, although the terminal parts of fertile plants (with swollen receptacles, and often with irregular inflations in the thallus) probably could float and be carried for considerable distances by surface currents.

It is fairly safe to assume that *Fucus distichus edentatus* has been present in Lerwick harbour for the past 55 years at least. However, we cannot judge from Börgesen's limited observations whether or not the species has increased in quantity in this time; he may not have seen those parts of the inner harbour wall where the species now forms a definite belt between *F. spiralis* and *F. serratus*.

The size and vigour of the British specimens indicate that such physical conditions of the environment as sea and air temperatures do not directly determine the present southern limits of *edentatus*. Perhaps rather the limits to further spread (very locally) are imposed principally by increasingly severe competition from species that are more successful locally. If this is a correct interpretation of the observations, it would be an excellent illustration of Gause's (1934) contention that two species with similar ecology cannot live together in the same place. On a broader scale in northern Britain, the further spread of *edentatus* southwards (to other sheltered sites, where for one reason or another conditions are not favourable for *F. vesiculosus*) is doubtless limited to a large extent by sea-barriers.

If *edentatus* were to spread further in Britain, and if fishing boats are indeed the principal means of dispersion, it might be supposed that the plant would appear next in harbours (especially those that are more or less polluted) in the south of Shetland, in the Orkney Islands (e.g. Kirkwall and Stromness), or even in harbours in north-east Scotland such as at Thurso and Wick. I have looked for the species but not found it in the following likely places. (1) Grutness Voe (south end of Shetland Mainland), 1952. (2) Kirkwall harbour (Orkney), 1952, a brief examination of the vertical harbour wall showed very few fucoids present at all, and much oily pollution. (3) Stromness harbour (Orkney), 1952; a rather more careful search here showed, very interestingly, that *F. vesiculosus* and *Ascophyllum* were absent from the harbour area; on parts of the harbour wall (tidal range 3·08 m at springs) a wide belt of *Fucus spiralis* above merged into a wide belt of *F. serratus* below, but very often there was a 'gap' between the two belts occupied in part by *Balanus balanoides* but quite devoid of fucoids. Stromness harbour appeared to be polluted, and

is a likely place for *Fucus distichus edentatus* to become established if ever it were introduced, there being a suitable vacant 'ecological niche'. (4) The harbour at Scrabster (near Thurso), 1951.

There is no evidence to suggest that *edentatus* is actively extending its range southwards in Britain at the present time.

## TAXONOMIC CONSIDERATIONS

The distribution and ecology of forms of *F. distichus* in Britain and Ireland, described above, is a good illustration of the fact that, towards the southern limits of distribution, the species is represented by populations of only one or two of the best adapted forms, confined to restricted habitats and often geographically isolated. It may well be that such ecological restriction and geographical isolation (particularly of subsp. *anceps* in Ireland) could result in the gradual evolution of genetically distinct ecotypes or even species.

It is probably safe to assume that *anceps* has been present in Ireland since 1863 at least, and it is highly possible that it may even be a survivor there from a time when the seas around Britain were much colder, but able to exist now only under the extraordinarily narrow range of habitat conditions described in the present paper. It is a well-known phenomenon that species or subspecies that are represented by a single ecotype confined to a limited area frequently exhibit exceptionally small 'ecological amplitude' (i.e. the range of habitat variation that a plant can tolerate; see Daubenmire, 1947) compared with others which, by means of genetic diversification, are represented in a variety of habitats. The apparent genetic impoverishment of these entities may arise by either of two courses of events: (i) catastrophes destroy most of the population and the remnants are *depleted species* or *relicts*, with only limited genetical possibilities for morphological variation; or (ii) an ecotype of small ecological amplitude may result from a very limited crossing of an effective geographical barrier. The population descending from such a single introduction can have no greater genetic heterogeneity than that possessed by the individuals that immigrated (subsequent mutations excluded). Certainly *anceps* shows very limited ecological amplitude in Ireland, but rather more in Caithness. Wherever it occurs in Britain and Ireland, however, *anceps* seems more likely to be a relict form, rather than an introduction of recent centuries. That it may be actively extending its range southwards at the present time is considered very unlikely.

The *edentatus* in Shetland and Fair Isle harbours, on the other hand, has more probably been introduced to those places in comparatively recent times, but certainly before 1902 in Lerwick harbour.

## ACKNOWLEDGEMENTS

This paper brings together information from many sources, including field observations made during several surveys of parts of the coasts of north Scotland and west Ireland, and I wish to record my thanks to all the colleagues who participated in the various expeditions—Dr E. M. Burrows, Dr E. Conway, Dr J. R. Lewis, Dr S. M. Lodge, Dr M. de Valéra (Galway), and my wife, Grace Powell—for help of various kinds and for permission to include here some of the observations made on the surveys; these colleagues, however, are not responsible for the views here expressed.

I wish to thank also: Dr Burrows and Dr Lewis for the photographs shown as Pl. II, fig. 2, and Pl. I, fig. 1, respectively; Dr Mary Parke (Plymouth) and Dr A. P. Orr (Millport) for helpful criticism of the typescript; Dr Burrows and Prof. L. A. Harvey (Exeter) for material of *F. vesiculosus* f. *linearis* from Lundy; and Miss C. I. Dickinson (Kew) for help in tracing herbarium specimens.

Finally the author gratefully acknowledges grants received from the Browne Fund of the Royal Society toward expenses incurred in the surveys of the north coast of Scotland and parts of the west coast of Ireland.

## SUMMARY

The distribution and ecology of subspp. *anceps* and *edentatus* of *F. distichus* L. emend. Powell (1957) in Britain and Ireland is described in detail, based on recent ecological surveys and critical examination of all past records.

*F. distichus anceps* is a small form confined to certain very exposed coasts in the north and west of Scotland and Ireland, where it reaches the southern limit of its geographical range. This plant may be a relict form in Britain, existing now only under an extraordinarily narrow range of rigorous habitat conditions; it is not thought to be actively extending its range southwards at the present time. The ecology of subsp. *anceps* is considered principally in relation to that of other reduced fucoids found on exposed British shores, viz. *F. spiralis* f. *nana* and *F. vesiculosus* f. *linearis*; all three forms are illustrated by photographs and means of distinguishing them are described. The life-span of subsp. *anceps* is thought to be 2 to 3 years at some Irish sites, but may be longer at some of the Scottish sites.

*F. distichus edentatus* is a large, sheltered-water form, and has been found only in the harbours of Lerwick and Scalloway (Shetland Islands) and North Haven (Fair Isle), which mark the southern limits of this subspecies on the British side of the North Sea. It is best developed in Lerwick harbour where it forms a belt between *F. spiralis* and *F. serratus* and appears to be very tolerant of water polluted by effluent from fish factories. *F. distichus edentatus* has possibly been introduced to these three harbours within recent centuries,

perhaps by fishing vessels; it is not thought to be actively extending its range southwards in Britain.

The facts presented show that, at the southern limits of its distribution in Britain, *F. distichus* is represented by populations of only one or two of the best adapted forms, confined to restricted habitats and often geographically isolated. It may be that such restriction and isolation (particularly of subsp. *anceps* in Ireland) could result in the gradual evolution of genetically distinct ecotypes or even species.

## REFERENCES


ADMIRALTY, HYDROGRAPHIC DEPARTMENT, 1956. *The Admiralty Tide Tables, Vol. I, European Waters, 1957*, London.

BATTERS, E. A. L., 1902. A catalogue of the British marine algae. *J. Bot., Lond.*, Vol. 40, Supplement, 107 pp.

BÖRGESEN, F., 1902. Marine algae. *Botany of the Faeröes*, Part II, pp. 339–532, pls. XIII–XXIV. Copenhagen (1903). (Issued separately.)

—— 1903. The marine algae of the Shetlands. *J. Bot., Lond.*, Vol. 41, pp. 300–6.

—— 1905. The algae-vegetation of the Faeröese coasts, with remarks on the phytogeography. *Botany of the Faeröes*, Part III, pp. 683–834. Copenhagen (1908). (Issued separately.)

BURROWS, E. M., CONWAY, E., LODGE, S. M. & POWELL, H. T., 1954. The raising of intertidal algal zones on Fair Isle. *J. Ecol.*, Vol. 42, pp. 283–8.

CARRUTHERS, W., 1863. *Fucus distichus* Linn. as an Irish plant. *J. Bot., Lond.*, Vol. 1, pp. 353–5, pl. 12.

COTTON, A. D., 1912. Clare Island Survey: Marine Algae. *Proc. R. Irish Acad.*, Vol. 31, Part 15, 178 pp., 11 pls.

DAUBENMIRE, R. F., 1947. *Plants and Environment. A Textbook of Plant Autecology*. xiii, 424 pp. New York and London.

GAULD, D. T., BAGENAL, T. B. & CONNELL, J. H., 1953. The marine fauna and flora of St Kilda, 1952. *Scot. Nat.*, Vol. 65, pp. 29–49.

GAUSE, G. F., 1934. *The Struggle for Existence*. Baltimore.

GILLHAM, M. E., 1954. The marine algae of Skokholm and Grassholm Islands, Pembrokeshire. *Northw. Nat.*, Vol. 25, pp. 204–25, pls. 3–5.

HARVEY, L. A., 1950. The granite shores of Lundy. *Ann. Rep. Lundy Field Soc.*, Year 4 (1950), pp. 34–44, 1 pl.

HUDSON, W., 1762. *Flora Anglica*. xv, 506 pp. London.

HYLMÖ, D. E., 1933. Algenimmigration nach der schwedischen Westküste. *Bot. Notiser*, 1933, pp. 377–90.

LEWIS, J. R., 1954. The ecology of exposed rocky shores of Caithness. *Trans. roy. Soc. Edinb.*, Vol. 62, pp. 695–723, 4 pls.

—— 1955. The mode of occurrence of the universal intertidal zones in Great Britain. *J. Ecol.*, Vol. 43, pp. 270–90.

LIGHTFOOT, J., 1777. *Flora Scotica*. 2 Vols. London.

LUND, S., 1949*a*. Nye Alger for de danske Farvande. (With summary in English.) *Bot. Tidsskr.*, Bd. 48, Hft. 3, pp. 231–53.

—— 1949*b*. Immigration of algae into Danish waters. *Nature, Lond.*, Vol. 164, p. 616.

NEWTON, L., 1931. *A Handbook of the British Seaweeds*. xiii, 478 pp. London.

POWELL, H. T., 1957. Studies in the genus *Fucus* L. I. *Fucus distichus* L. emend. Powell. *J. mar. biol. Ass. U.K.*, Vol. 36, pp. 407–32.

POWELL, H. T. & LEWIS, J. R., 1952. Occurrence of *Fucus inflatus* L. forma *distichus* (L.) Börgesen on the north coast of Scotland. *Nature, Lond.*, Vol. 169, p. 508.

TRAILL, G. W., 1885. *A Monograph of the Algae of the Firth of Forth.* 17 pp. and 4 pp. of mounted algae. Edinburgh.

## EXPLANATION OF PLATES

### PLATE I

*Fucus distichus* L. emend. Powell, subsp. *anceps* (Harv. et Ward ex Carruthers) Powell

Fig. 1. Photograph of part of a belt of plants growing on an exposed reef near Lower Dounreay, Caithness, Scotland (site 4 in Text-fig. 2), July 1951, showing characteristic arching of the fronds. (Photograph J. R. Lewis.)

Fig. 2. Photograph of a typical mature Caithness plant (preserved in formalin/seawater, but not pressed), collected just west of Sandside Head, Caithness (site 2 in Text-fig. 2), July 1951, *H. T. Powell* (MILL). Greatest length of plant 17·4 cm; most of the apices are fertile; plant probably *ca.* 2 years old. The scale is 15 cm long.

### PLATE II

Fig. 1. *Fucus distichus* L. emend. Powell, subsp. *anceps*. Photograph of a living mature plant from a reef just east of Brims Ness, Caithness (site 9 in Text-fig. 2), June 1956, *Mrs Grace Powell* (MILL). Greatest length of plant 23·7 cm; receptacles up to 5·7 cm long and up to 6 mm broad; some of the branches have been cut off. This is the longest plant of subsp. *anceps* found so far in Britain and it was growing on a reef slightly sheltered from direct wave-crash; all of the apices were fertile. In certain respects the plant is intermediate in form between subsp. *anceps* and subsp. *edentatus* (see p. 672).

Fig. 2. *F. distichus* L. emend. Powell, subsp. *edentatus* (De la Pyl.) Powell. Photograph of a mature plant growing on a fairly sheltered shore at Leag, just to the south of Lerwick harbour, Shetland Islands, 3 July 1952. Some plants of *F. spiralis* are present in top right background; the barnacles are *Balanus balanoides*. (Photograph E. M. Burrows.)

### PLATE III

Fig. 1. *Fucus distichus* subsp. *anceps*. Same plant as in Pl. I, fig. 2, with some of the branches cut off, spread out and photographed under conditions similar to those for the lower illustration. Note that in the distal branches the midribs are scarcely distinct from the alae.

Fig. 2. *F. vesiculosus* L., f. *linearis* (Huds.) Powell. Photograph of a very reduced plant (preserved in formalin/seawater, but not pressed), from very exposed coast at Jenny's Cove, Lundy, Bristol Channel, *L. A. Harvey* (MILL). April 1949, with young receptacles. Greatest length of plant 14·4 cm. Some of the branches have been cut off. Note the very distinct midribs in the distal branches, and the absence of vesicles (see p. 670).

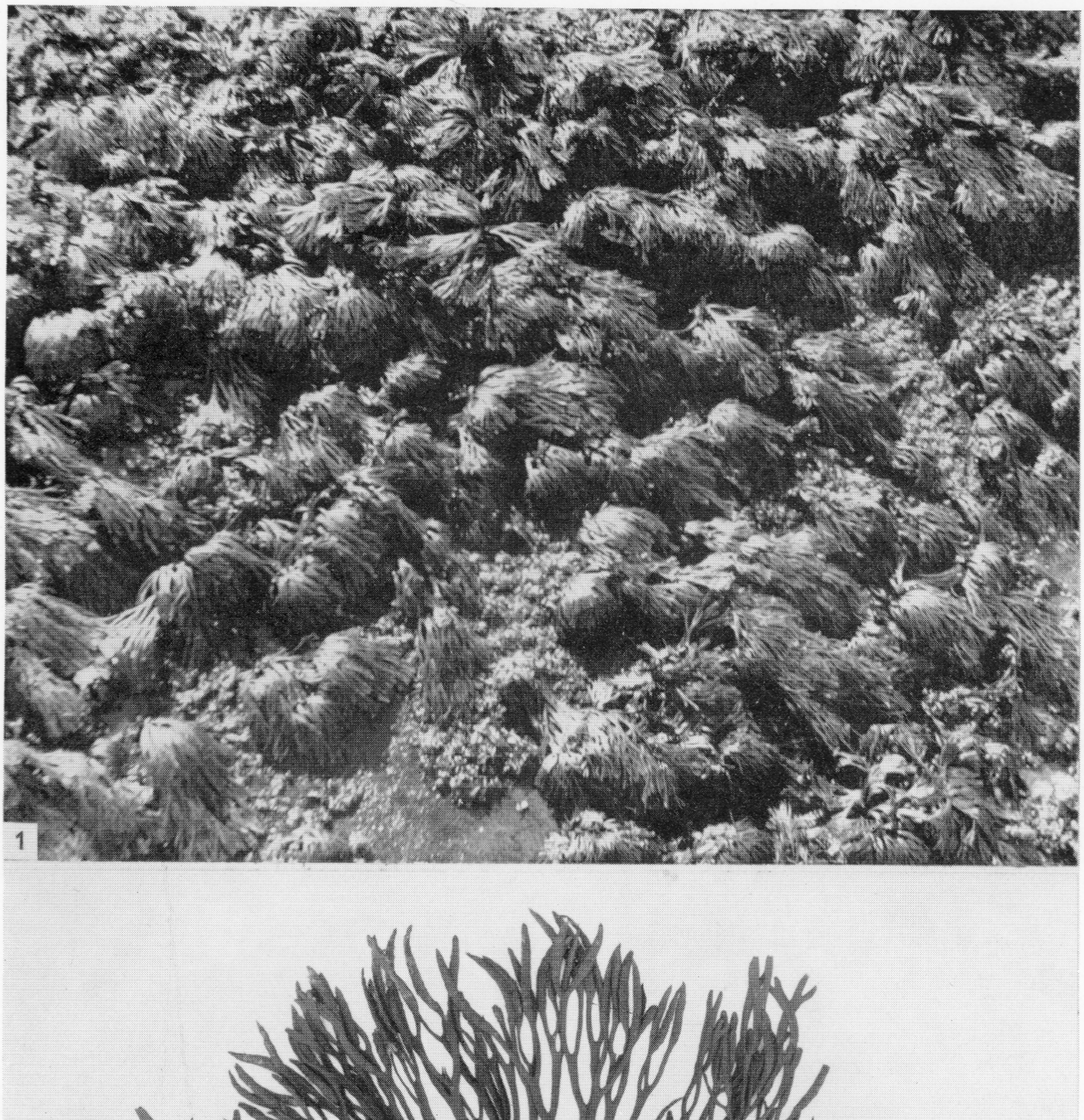
The scales show cm and mm.

### PLATE IV

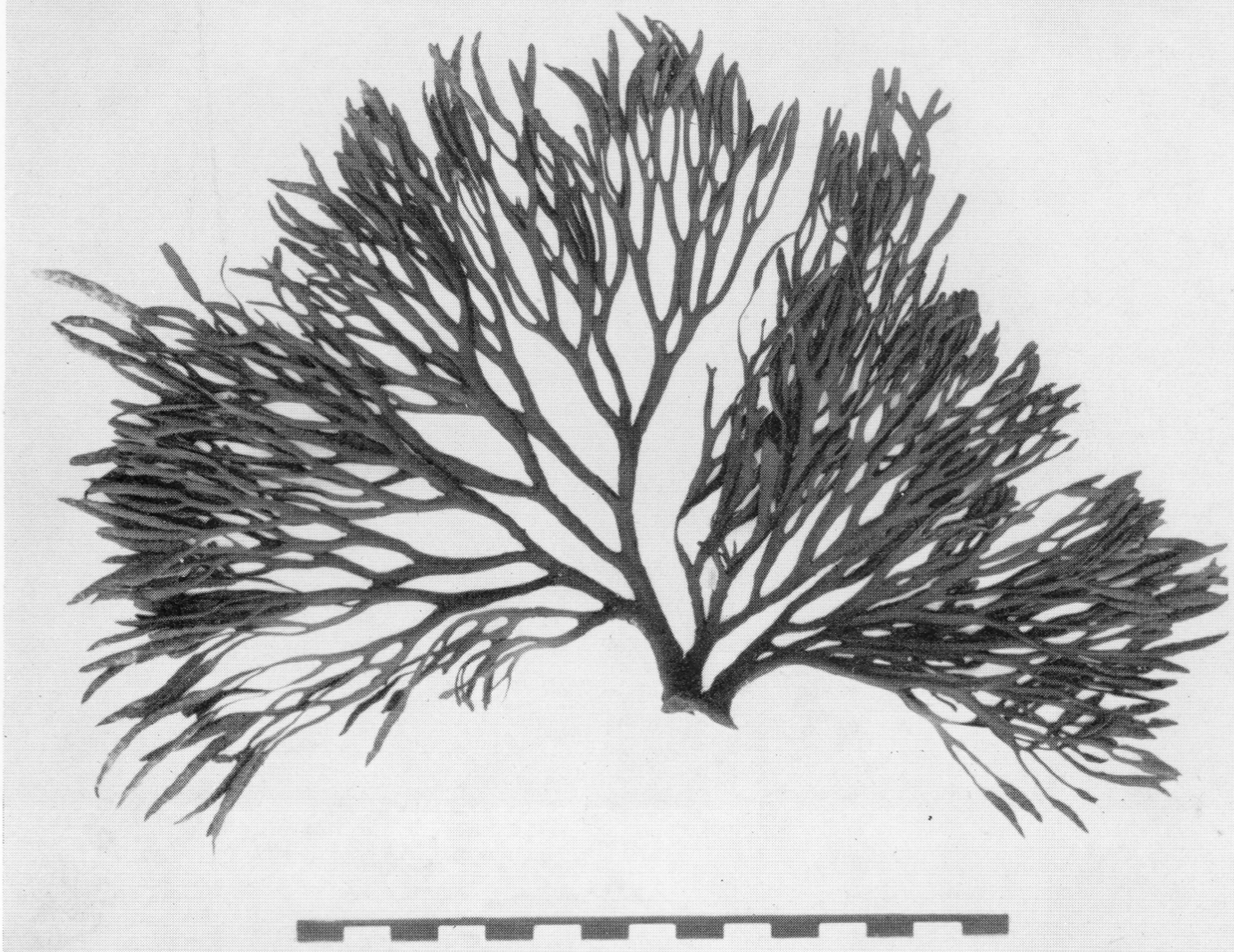
Fig. 1. *Fucus vesiculosus* f. *linearis*. Photograph of a very reduced plant (preserved in formalin/seawater, but not pressed) from exposed coast at Jenny's Cove, Lundy, Bristol Channel, August 1950, *L. A. Harvey* (MILL). Greatest length of plant 15·0 cm. Note the long, narrow receptacles, most of which are mature, the prominent midribs and the absence of vesicles (see p. 670). Some of the branches have been cut off.

Fig. 2. *F. spiralis* L., f. *nana* (Stackh.) Batt. Photograph of several plants (preserved but not pressed) from exposed reefs near Lower Dounreay, Caithness (site 4 in Text-fig. 2), July 1951, *H. T. Powell* (MILL) (see p. 671). Greatest length of right-hand plant 12·9 cm.; most of its apices are fertile.

The scales show cm and mm.

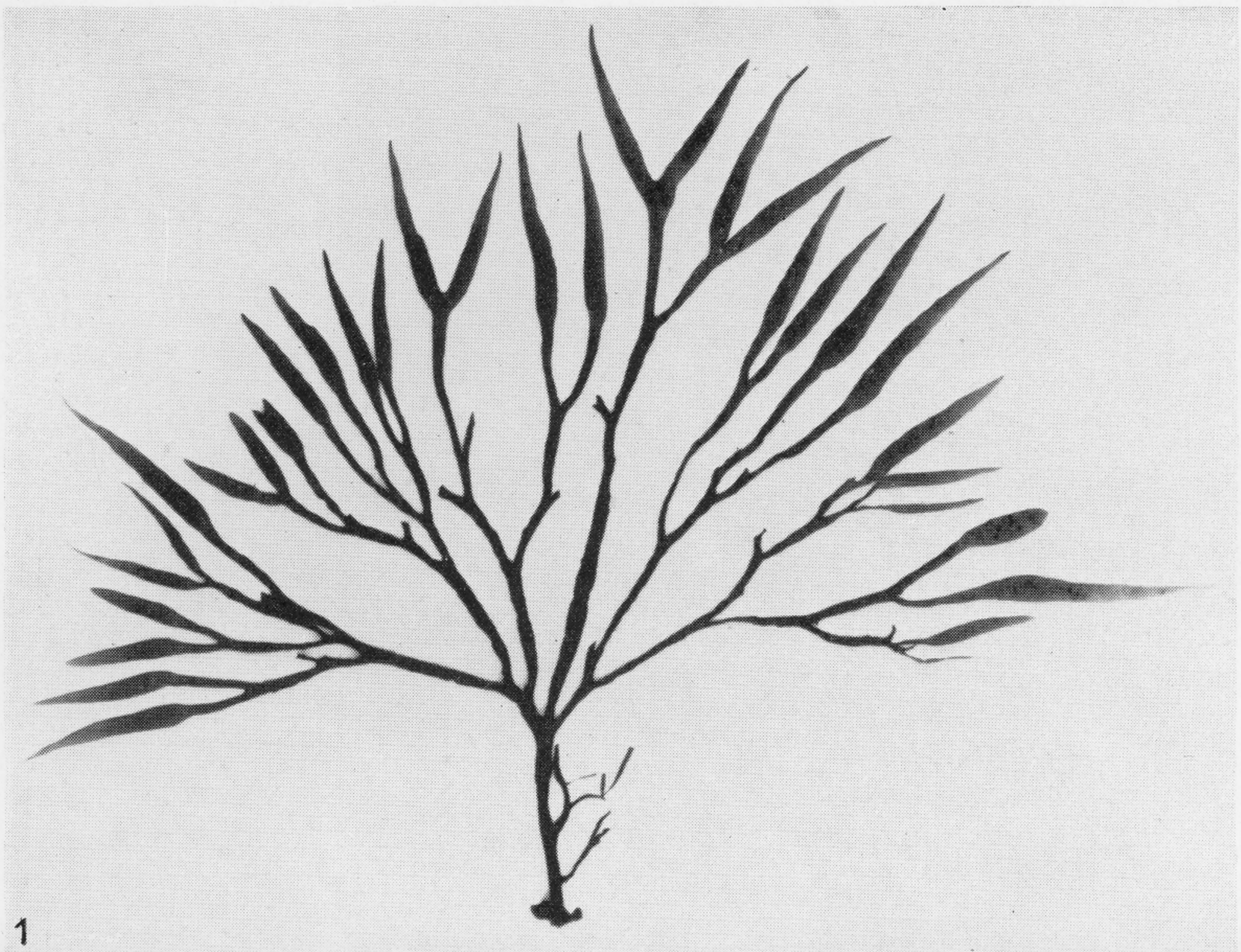


1



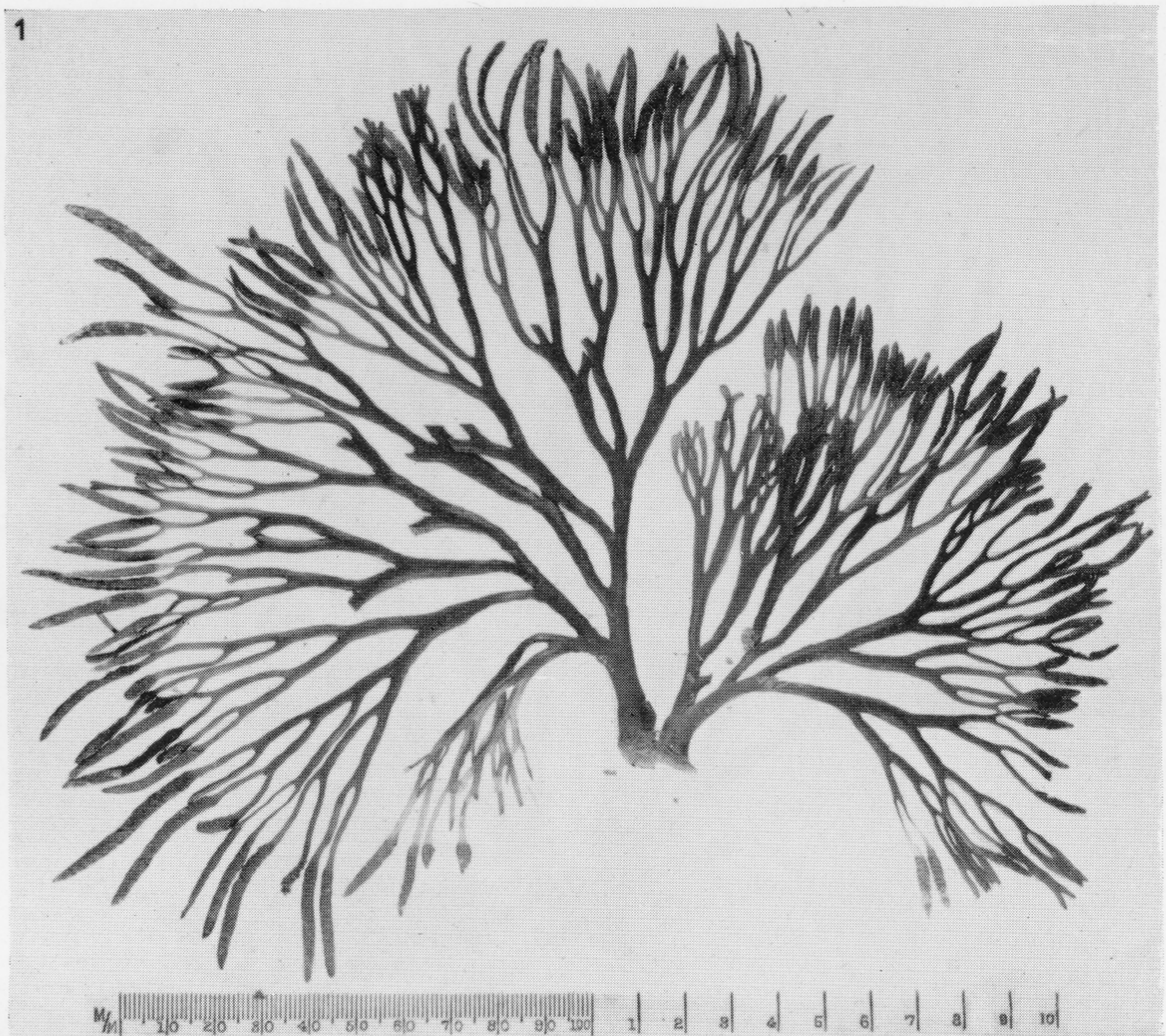
2

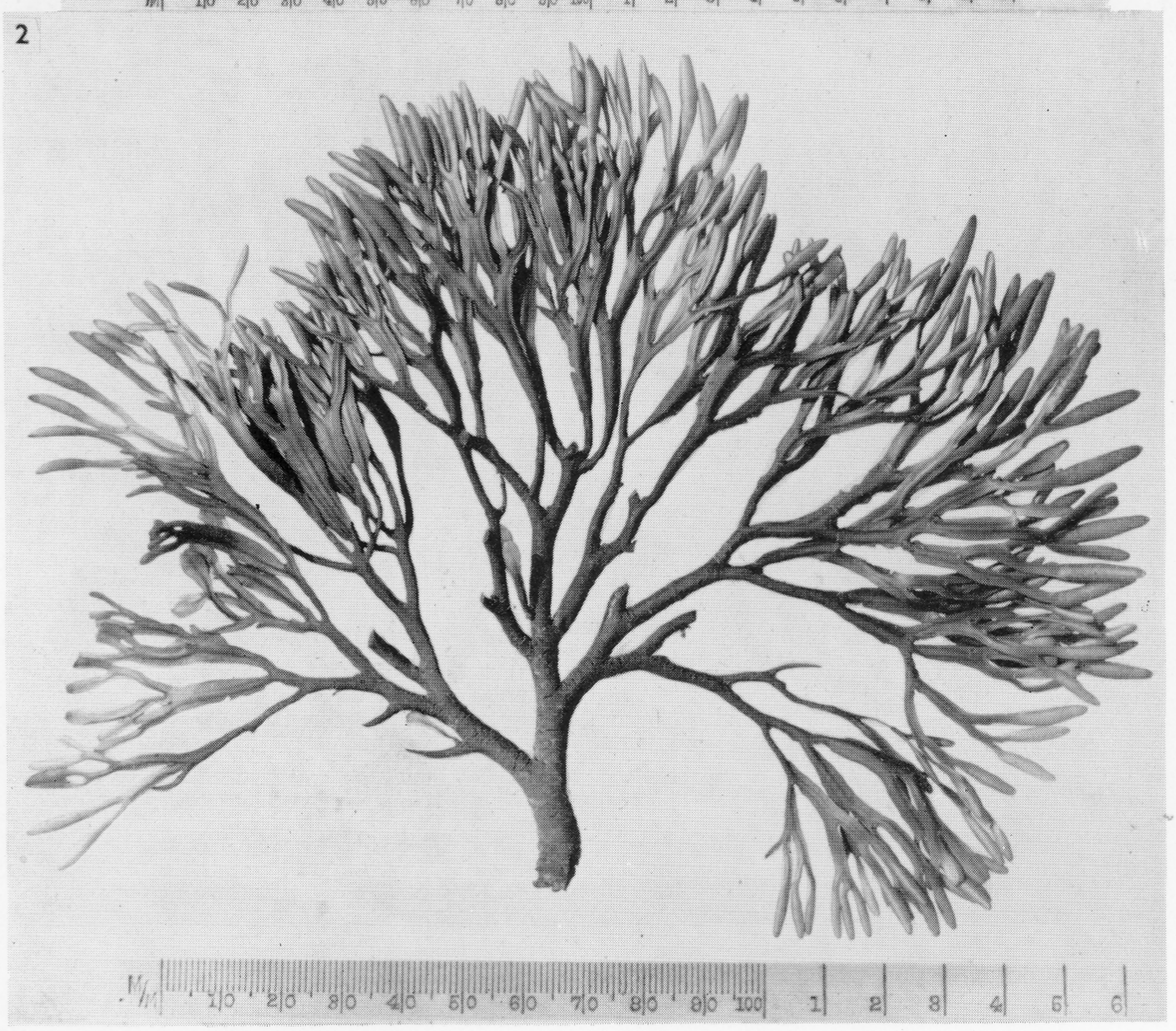
(*Facing p.* 694)



1

2


1
M/M
1|0 2|0 3|0 4|0 5|0 6|0 7|0 8|0 9|0 100
1 2 3 4 5 6 7 8 9 10


2
M/M
1|0 2|0 3|0 4|0 5|0 6|0 7|0 8|0 9|0 100
1 2 3 4 5 6

1

2