

# STUDIES IN THE GENUS *FUCUS* L.<sup>1</sup>

## I. *FUCUS DISTICHUS* L. EMEND. POWELL

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(Plates I and II and Text-fig. 1)

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### INTRODUCTION

Apart from the alga currently known as *Fucus spiralis* L. emend. Batt., and certain hermaphrodite hybrid *Fucus* forms that will be discussed in a later paper, several other hermaphrodite forms of the genus *Fucus*<sup>1</sup> occur on the shores of the North Atlantic, the North Pacific and the Arctic oceans. These forms have been described under many different names by many authors; and there has been and still is much confusion, as well as real difference of opinion, concerning their delimitation and taxonomic status.

Thus, many European authors, including Rosenvinge (1893) for Greenland, Børgesen (1902) for the Faerøes, and Jónsson (1903) for Iceland, regard all such forms, occurring in the various parts of the North Atlantic studied in detail by them, as ecological forms of a single species, and have shown that, at least in some parts of this wide area, all possible intermediate forms between the more distinctive extreme forms can be found. The name *F. inflatus* L. has

<sup>1</sup> The full citation of author's names for this genus is *Fucus* L. (1753) pro parte, emend. Dec'ne et Thur. (1845); for most purposes, however, it is sufficient to shorten the citation to *Fucus* L. (The often used citation '*Fucus* (L.) Dec'ne et Thur.' is nomenclaturally incorrect.)

been generally used by recent European phycologists<sup>1</sup> for this complex of forms and several characteristic forms have been widely recognized as follows:

Rosenvinge (Greenland, 1893)	Börgeesen (Faeröes, 1902)	Jónsson (Iceland, 1903)
<i>Fucus inflatus</i> L., M. Vahl	<i>Fucus inflatus</i> L., M. Vahl	<i>Fucus inflatus</i> L., M. Vahl
var. <i>edentatus</i> (De la Pyl.) Rosenv.	f. <i>edentata</i> (De la Pyl.) Rosenv.	f. <i>typica</i> Jónss. (= <i>F. edentatus</i> De la Pyl.)
var. <i>evanescens</i> (C. Ag.) Rosenv.	(only a few specimens found that approached f. <i>evanescens</i> (C. Ag.) Rosenv.)	f. <i>evanescens</i> (C. Ag.) Rosenv.
var. <i>linearis</i> (Oed.) Rosenv. —	f. <i>linearis</i> (Oed.) Rosenv. f. <i>disticha</i> (L.) Börg.	f. <i>linearis</i> (Huds.) f. <i>exposita</i> Jónss. (= f. <i>disticha</i> (L.) Börg.)

The type form, = f. *edentatus* (De la Pyl.), and f. *evanescens* (C. Ag.), of these authors are large plants found on sheltered or semi-exposed shores; f. *linearis* is a smaller, slender plant, usually found in littoral pools; f. *disticha* (L.) Börg., = f. *exposita* Jónss., is a small, narrow, but robust form developed on coasts very exposed to swell and wave-action.

Recent North American authors, on the other hand, interpret certain essentially similar North American Atlantic and Pacific furoids as distinct species, as follows:

- (i) North-east Atlantic coast of North America (Taylor, 1937):  
*F. edentatus* De la Pyl., *F. evanescens* C. Ag., *F. filiformis* Gmel. (in pools),  
*F. miclonensis* De la Pyl.; (also listed are *F. serratus*, *F. vesiculosus* and  
*F. spiralis*).
- (ii) Pacific coast of North America (Gardner, 1922; Setchell & Gardner, 1925):  
*F. edentatus* De la Pyl., with five forms recognized and described. (Species  
based upon a Newfoundland plant.)  
*F. evanescens* C. Ag., with twenty-one forms. (Species based on North  
Pacific material.)  
*F. furcatus* C. Ag., with thirteen forms. (Species based on North Pacific  
material.)  
*F. membranaceus* Gardner, with six forms.  
*F. nitens* Gardner.

These authors reject the name *F. inflatus* L. altogether, on the grounds that Linnaeus's original short description and the fragmentary specimens bearing the name '*inflatus*' in the Linnaean Herbarium are inadequate to delimit any particular species of *Fucus*.

In order to determine the correct names to apply to two forms of '*Fucus inflatus*' found in Britain it has been necessary, therefore, to consider first the following taxonomic and nomenclatural problems: (i) are the furoids

<sup>1</sup> Lund (1949*a, b*) uses the name *Fucus edentatus* De la Pyl. in reporting the recent immigration of this furoid into Danish waters but, in reply to an inquiry, he has informed me that he considers that the Danish plants should be named *Fucus inflatus* L., f. *edentatus* (De la Pyl.) in accordance with the views of Rosenvinge, Börgeesen and others.

listed above sufficiently distinct to be regarded as separate species, or are they best regarded as forms of a single extremely variable species; (ii) if best regarded as a single species, is the use of the disputed specific epithet '*inflatus* L.' justifiable; and (iii) is the particular nomenclature adopted for formae by, for example, Rosenvinge, Børgesen and Jónsson, in best accord with modern taxonomic concepts and nomenclatural rules and procedures?

*Species, subspecies, or formae?*

After full consideration of all that has been published on the autecology and world distribution of these forms, I am in agreement with Børgesen (1902), Jónsson (1903), and other authors, that the numerous forms described are not sufficiently distinctive to warrant separate specific status, but are best interpreted for the present as forms of a single, extremely plastic, highly successful and widely distributed species. Chief weight is given to the fact that, at least near the centres of distribution of the species (e.g. in the Faerøe Islands and Iceland, and probably in northern Europe and on the Pacific coast of North America), whole series of forms (clines) of this fucoid intermediate in character between the extreme forms are very common. The close affinity of the various forms is further emphasized by the occurrence of caecostomata (see p. 418) in varying number in most, and probably all, of them, but not in any other species of *Fucus*.

Near the centres of distribution of the species it is possible to interpret the extreme forms as products of their ecological environment, with the intermediate forms developing under intermediate environmental conditions. Towards the southern and northern limits of distribution, however, the species is often represented by populations of only one or two of the more distinctive (best adapted) forms, confined to restricted habitats and often geographically isolated. Such isolated populations often have a very limited range of form, and several could well be regarded as genetically adapted ecotypes. For these reasons the more distinctive forms are interpreted as *subspecies* in the present paper.

THE CASE FOR REJECTION OF THE NAME  
*FUCUS INFLATUS* L.

The name *F. inflatus* is first used by Linnaeus (1737) in *Flora Laponica*, Ed. 1, p. 351, No. 468, the material being collected (by Linnaeus?) at Rørstad in Nordland, Norway, on his Lapland journey in 1732. It is first described in this way: '*Fucus folio bifido, laciniis ovato-lanceolatis inflatis, ad apicem divisus.*' The diagnosis given by Linnaeus in *Species Plantarum* (1753, p. 1159) is '*Fucus fronde bifida: laciniis ovato-lanceolatis inflatis apice divisus. Fl. lapp. 468, Fl. suec. 1004. Habitat in Oceano Atlantico*'. Finally, in *Systema Naturae* (1766) and *Systema Vegetabilium* (1774), Linnaeus slightly enlarges the diagnosis to read as follows: '*Fronde plana, dichotoma, integerrima, punctata, ovato-*

*lanceolata, inflata, apice diviso*’; this may be translated as ‘frond plane [flat], dichotomously branched, entire [margins], punctate [presumably this refers to the presence of cryptostomata], ovate-lanceolate [see below], inflated [probably refers to the presence of irregular inflations], divided at the apices’. These diagnoses of *F. inflatus* are certainly inadequate to define any particular species as understood to-day; Linnaeus is presumably describing sterile material and the diagnoses could fit, but could not define, forms of *F. ceranoides* L., *F. vesiculosus* L., or *F. edentatus* De la Pyl. (= ‘*F. inflatus* L., M. Vahl’ of authors), all of which may have irregular inflations in the thallus.

‘*Fucus inflatus* L.’ is first illustrated by Martin Vahl (1794) in *Flora Danica* (Vol. 7, fasc. 19, tab. 1127); the caption to tab. 1127 is identical with that quoted above from *Syst. Nat.*, and the reference given is ‘Lin. S.V., p. 966’ (i.e. it is quoted from *Syst. Veg.* of Linnaeus, 1774). However, Vahl adds the following information, presumably from his own knowledge, concerning the distribution of the species: ‘*Vulgaris in praefectura Salten, Senjen et Tromsöen Nordlandiae, in aliis partibus Norvegiae non mihi obvius.*’

However, throughout most of the nineteenth century (until Foslie, 1886) the name *F. inflatus* L. was not used for an independent species but, if used at all, was regarded either as a synonym or else as a form of *F. vesiculosus* L.; and, during this period, several new species of *Fucus* were first described, including *F. evanescens* and *F. furcatus* (C. Agardh, 1820), and *F. edentatus*, *F. fueci* and *F. miclonensis* (De la Pylaie, 1829).

Foslie (1886), in proposing that the name *F. inflatus* L. be revived, in particular for those Norwegian plants referred by other authors to *F. edentatus* De la Pyl., recognized that Linnaeus’s description ‘is no doubt incomplete’ (‘er vistnok ufuldstændig’), but suggested that Vahl’s illustration and further information on distribution be accepted as delimiting the species in a satisfactory manner, and proposed that the species be cited as ‘*F. inflatus* (L.) Fl. Dan.’. Foslie adds that certain other early authors (e.g. Lightfoot, 1777) had mistakenly used the name *F. inflatus* L. for certain forms of *F. vesiculosus* L., but suggests that it is very unlikely that Linnaeus, who correctly listed all the other true fucoids of Scandinavia in *Flora Laponica*, would have set up two species for *F. vesiculosus*.<sup>1</sup> He states that it is highly probable that Linnaeus would have found the species in question at Rørstad; and adds that the epithet *inflatus* doubtless refers to the irregular swellings that are rather common, especially in sterile specimens of this species.

Foslie certainly presents as good a case as possible for retaining the name *inflatus* L. Later European authors, almost without exception, have accepted his views and so we find this species cited as ‘*Fucus inflatus* L., M. Vahl’ by

<sup>1</sup> Linnaeus, however, does otherwise give two separate specific names to forms of *F. vesiculosus* as at present understood; in *Species Plantarum* (1753) in the section of *Fucus* described as ‘*dichotomi frondescentes*’, we find the following six species: *serratus*, *vesiculosus*, *ceranoides*, *spiralis*, *inflatus* and *divaricatus*. The last-named is merely a form of *F. vesiculosus* (with single vesicles in the axils of all the branches, in the specimens in the Linnaean Herbarium).

Rosenvinge (1893), Börgesen (1902), Jónsson (1903), Kylin (1947) and others up to the present day. However, as the American authors Gardner (1922) and Taylor (1937) have decided that the type specimen of *F. inflatus* L. is a fragment that cannot be associated with any particular species, and use other specific epithets for American fucoids, it is important to resolve this nomenclatural impasse if possible.

For this reason I have been permitted to examine the specimens in the Linnaean Herbarium. The only specimens labelled *F. inflatus* L. in this herbarium are two small pieces of a fucoid mounted side by side on a single sheet (Genus 1274, *Fucus*, Sheet No. 51, in the Catalogue of Savage, 1945), and labelled near the foot of the sheet '5 inflatus' in Linnaeus's handwriting (Pl. I, fig. 1). The pieces of *Fucus* are incomplete (both lack a holdfast) and could well be parts of a single plant; both pieces are completely sterile. The left-hand specimen is 11.7 cm in length with three dichotomies; the lower part of the frond is narrow (3-4 mm) and most of the rest of the frond is less than 10 mm wide, except that midway along the two main branches the frond widens to as much as 17 mm and then becomes narrow again towards the tips. It is suggested that these wider parts are probably the reason for Linnaeus including 'ovato-lanceolata' in his description of the frond. The right-hand specimen is essentially similar, 11.6 cm long, with four dichotomies; and again the rather narrow frond broadens out half-way along its length and then becomes narrower again. The wider parts of both specimens are now pressed flat but some wrinkling of the surface, of the right-hand specimen especially, supports the view that the wider parts were once irregular inflations, such as may be supposed to have occurred in Linnaeus's *F. inflatus* (cf. Gardner, 1922, p. 10). It seems probable that Linnaeus, in preparing his later diagnosis in *Syst. Nat.*, had these particular specimens in mind; thus 'punctata' would seem to refer to the rather frequent cryptostomata that are present in both specimens and which appear as prominent raised white spots on the frond surface of the right-hand specimen (Pl. I, fig. 1). Microscopic examination shows that each white spot consists of an aggregation of salt crystals located round the raised orifice of a cryptostoma. Caecostomata (see p. 418) could not be detected even by sectioning a small part of the frond. The fronds are thin and have a very narrow, sharply defined midrib, strongly marked right to the tips of the branches. Near the tips of the left-hand specimen the margins of the thallus appear to be very slightly serrulate; this appearance is caused by marginal cryptostomata, and one of the Linnaean specimens of *F. vesiculosus* (Sheet 48) also shows traces of this character.

These Linnaean specimens of *F. inflatus* closely resemble forms of both *F. vesiculosus* L. and *F. ceranoides* L. as understood to-day and could be interpreted as either of these species. However, having made a critical examination and comparison of the Linnaean specimens of all three species, the author concludes that the specimens labelled 'inflatus' on Sheet 51 are rather

closer to the specimens of *F. vesiculosus* L. than to that of *F. ceranoides* L. and are best interpreted simply as a form of *F. vesiculosus* L. lacking true vesicles.

In the Linnaean Herbarium there are four pages of notes referring to Herb. Linn. specimens, written by Dawson Turner, and it is interesting that he writes of the above specimens: 'one specimen fragment—only a var. of *vesiculosus*' (see also Turner, 1809, pp. 45-7).

The epithets *vesiculosus* L. and *inflatus* L. are both included in *Species Plantarum* (Linnaeus, 1753) and therefore have equal priority but, because *vesiculosus* L. is represented by good specimens in Herb. Linn. (with true vesicles and with unisexual conceptacles), it is desirable that the name *F. vesiculosus* L. be retained for the plant currently known by that name. Turner (1802, 1809) has already clearly united these two taxa under the name *F. vesiculosus* L. and, in accordance with Article 67 of the International Code of Botanical Nomenclature (Lanjouw *et al.* 1952), his choice of epithet must be followed.

Vahl's diagram of '*F. inflatus* L.' in *Flora Danica* (tab. 1127), on the other hand, is certainly of a plant very different from that of Linnaeus, and probably Vahl meant to illustrate the plant widely known now by the later epithet, *edentatus* De la Pyl.<sup>1</sup> The illustration shows a sturdy plant with a broad and prominent midrib running strongly right up to the base of the receptacles; the latter are terminal, rather elongated (4 to 5 times longer than broad), swollen-looking and distinctly pointed. The thallus has a number of irregular inflations, especially in the upper parts. This illustration, despite the much too conspicuous midrib, could be regarded as the earliest publication of the form later widely known as *F. edentatus* De la Pyl.; but the illustration alone could equally well represent a form of *F. vesiculosus* without vesicles and it is therefore recommended that it be disregarded for purposes of typification.

None of the principal defenders and users of the name *F. inflatus* L. have examined the specimens in the Linnaean Herbarium, although, in view of Linnaeus's inadequate diagnosis, the specimens must be decisive. On the other hand, Gardner (1922) obtained a description and sketch of the specimens, and Taylor (1937) examined the specimens personally, and both concluded that these fragments are not sufficiently distinctive to be associated with any particular species. However, neither of these authors mentions that there does exist in the Linnaean Herbarium a sheet of good specimens of the short, very narrow furoid known as *F. distichus* L. and, since the epithet *inflatus* L. must now be rejected, these specimens assume great importance. If it can be shown that the taxon *F. distichus* L. is taxonomically valid, adequately defined by diagnosis and type specimens, then this name would have priority over all the

<sup>1</sup> See Foslie (1886); also Jónsson (1903) who states in a footnote (p. 184): 'In this connection it may be added that specimens gathered by M. Vahl in Nordland and determined as *F. inflatus* L., fully agreeing with the typical *F. inflatus* L. as it is understood now, are to be found in the Botanical Museum at Copenhagen.'

other names proposed later for the various members of this complex of forms. It will now be shown that the name *F. distichus* L. is valid, but it applies to the very narrow form usually found in littoral pools—the f. ‘*linearis*’ of Rosenvinge, Børgesen and Jónsson—rather than to the short, but more robust, plants developed on very exposed coasts which Børgesen unfortunately and incorrectly named ‘f. *disticha* (L.)’.

#### THE CASE FOR USING THE NAME *FUCUS DISTICHUS* L.

The name *F. distichus*<sup>1</sup> is first used by Linnaeus in *Systema Naturae*, Ed. 12, Tom. 2, p. 716 (1767). The diagnosis given for *F. distichus* is ‘*Fucus fronde plana dichotoma integerrima lineari fructificationibus tuberculatis mucronatis*’; this may be translated as: ‘*Fucus* with fronds plane [flat], dichotomously branched, entire [margins], linear [i.e. very narrow], with fructifications [receptacles] having small rounded humps [i.e. conceptacles probably] and sharply pointed.’

This short diagnosis could not by itself delimit any particular species of *Fucus*, and unfortunately Linnaeus does not state where the plant was found. The most significant parts of the diagnosis are the ‘linear fronds’ and ‘pointed receptacles’; ‘linear’ in the sense used by Linnaeus means very narrow and elongated, and probably also implies uniform breadth.

In the Linnaean Herbarium there are two sheets of *Fucus* specimens labelled ‘*distichus*’; the sheets are numbered ‘1274.56’ and ‘1274.57’, respectively, as stated in the Catalogue of Savage (1945, p. 200).

#### SHEET 56

Sheet 56 has five pieces of plants pasted on, and is labelled ‘*distichus*’ near the foot of the sheet in Linnaeus’s hand (Pl. I, fig. 2, pieces labelled A–E by author). These pieces are the true type specimens of *F. distichus* L. and establish the validity of this taxon with certainty. All five specimens are quite short and extremely narrow; in none of them is the holdfast present; the fronds are all compressed and thin, but tough. Specimens A, B and C measure 14.7, 7.8 and 10.8 cm in length, respectively; they are extremely narrow, < 1–2 mm wide, rather cylindrical at the base (< 1 mm), becoming flat above to reach a maximum of 2 mm wide but usually slightly less; A and C have narrow, pointed, terminal receptacles up to 9 mm long and up to 1.5 mm broad, i.e. up to at least 6 times longer than broad; B is sterile.

Specimens D and E measure 7.9 and 8.6 cm in length, respectively, but appear to be only the terminal parts of plants slightly more robust than specimens A–C. The measured width of D and E is not much greater than A–C (fronds *ca.* 2.0 mm wide throughout, but up to 2.5 mm in parts), but

<sup>1</sup> Greek *διστιχος*, = *distichus*, ‘consisting of two rows’; ‘distichous’ in modern botanical sense, implying branches disposed in two diametrically opposite ranks or rows.

the fronds appear to be rather thicker. The receptacles are very well developed, are bigger than in A-C, being up to 20 mm long  $\times$  1.5 to 2.0 mm broad, i.e. at least 10 times longer than broad, and are rather pointed at the tips.

Parts of receptacles from specimens A and E were removed and soaked, and microscopical examination of some fifteen conceptacles showed that all were hermaphrodite; there were 8 eggs per oogonium.

The midrib is rather indistinct in all five specimens, but sections of part of the narrow thallus of A showed that the midrib occupies up to about one-third of the width. Cryptostomata are few and well spaced out in A-C, but rather more frequent in D and E; in D the location of cryptostomata is again indicated by white spots on the frond surface (see p. 411). Caecostomata were quite frequent in A but could be detected only by sectioning the thallus.

Specimens A and C bore frequent calcareous tubes of the worm *Spirorbis borealis* Daudin along most of the length of the specimens; A had a few filaments of a *Ceramium* sp. entangled on the lower part of the lower left-hand branch (see Pl. I, fig. 2); and one small specimen of *Mytilus edulis* L. was found on each of specimens A and D. The delicate habit, and the associated species, of plants A-C in particular, suggest that they may well have been growing in a rock-pool.

The following items are also on Sheet 56: a small label with 'No. 25' written on it (by J. G. Koenig?); and the writing 'linearis Huds. ex syn. Gmel.' and (against the word 'distichus') 'Syst. Nat. [ed.] 12.' in pencil by Sir J. E. Smith.

A comprehensive description of *Fucus distichus* L., accompanied by a very accurate illustration of the Linnaean type specimen (Pl. I, fig. 2 A) is given in Turner (1808, pp. 7-8, and pl. 4), and this is the earliest illustration of the type form of this species that can be accepted without question. Turner describes and illustrates the receptacles and 'tubercles' (= conceptacles) in a detail that is remarkable for his time: 'Fructification situated in the apices of the frond, which are then lengthened to half an inch or more, and become receptacles, containing globular tubercles, placed immediately under their surface, perforated with a small pore, and furnished with a few oblong brown seeds surrounded with a pellucid limbus.' It is clear from his plate 4 (figs. c, d, and e) that the 'oblong brown seeds' are in fact undivided oogonia; his drawings of transverse section conceptacle are not sufficiently detailed to show antheridia, but it should be remembered that antheridia were not properly recognized and described in any species of the genus until much later (Decaisne & Thuret, 1845).

It is practically certain that all five specimens on Sheet 56 are of the same species, and it is quite certain that this is a plant distinct from all known forms of the *Fucus* spp. currently named *F. serratus*, *F. vesiculosus*, *F. spiralis* and *F. ceranoides*; in fact it is *F. distichus* L.



## SHEET 57

Sheet 57 of the Linnaean Herbarium is labelled '*Fucus distichus*' in Linnaeus's handwriting. The word '*distichus*' has been crossed out later and alongside is written '*membranaceus* of Stackhouse, D. Turner' in Sir J. E. Smith's handwriting (see Savage, 1945); apparently Smith is quoting Dawson Turner's opinion. Also, in the four pages of notes written by Turner in Herb. Linn., we read: '*F. linearis*,<sup>1</sup> 5 specimens on one paper' (i.e. Sheet 56) 'all the same and right, one on another paper' (Sheet 57) 'a very large specimen of *F. membranaceus*, it was from this latter that Linnaeus was induced to add to his descriptions "Frons nervo medio, textura herbacea".' Following this up, we read as follows in Turner (1808, p. 8, under '*Fucus distichus*')—'It appears by Linnaeus's Herbarium, that he had himself confounded it with *F. membranaceus* of Stackhouse, and this accounts for the observation in *Systema Plantarum* [1779] that the texture is herbaceous.'

'*Fucus membranaceus* of Stackhouse' is the brown alga now known as *Dictyopteris membranacea* (Stackh.) Batt. (= *Haliseris polypodioides* C. Ag.) and it can superficially resemble a plant of *Fucus*. The alga on Sheet 57 is 23 cm long, profusely branched and has thin textured, rather narrow fronds (mostly 2–4 mm broad, but swelling to ca. 6 mm when soaked. The author has made a critical examination of this specimen and has found that it is definitely a plant of the genus *Dictyopteris* Lamour., with abundant characteristic male sori; the species could well be *D. membranacea*, although the specimen is much more branched than is usual in this species. The existence of this plant in the Linnaean Herbarium, and the addition to the diagnosis in *Syst. Plant.* (Linnaeus, 1779), could be held to imply that Linnaeus did not have a very clear conception of the delimitation of his *Fucus distichus*. This indeed is very likely and is scarcely surprising. However, this does not alter the fact that his *F. distichus* as originally defined, and particularly as represented by the specimens on Sheet 56 in his herbarium, corresponds precisely to a narrow form of *Fucus* that is widely recognized but which passes under various names today—e.g. *F. inflatus* f. *linearis* (Oed.) Rosenv.; *F. inflatus* f. *linearis* (Huds.) Rosenv.; and *F. filiformis* Gmel. (used by Taylor, 1937). From the taxonomic point of view, it is immaterial that Linnaeus later thought that a plant we know as *Dictyopteris membranacea* should be included in *Fucus distichus* L.; we now place these algae in distinct genera, and the point is covered taxonomically simply by quoting the species as follows: *Fucus distichus* L., *Syst. Nat.*, Tom. 2, p. 716 (1767); syntypes on Sheet 56 in Herb. Linn. (non Sheet 57 which plant is certainly *Dictyopteris* and probably *D. membranacea* (Stackh.) Batt.).

Having thus established that the name *Fucus distichus* L. applies to a

<sup>1</sup> In these early (but undated) notes Turner was doubtless thinking of *F. linearis* Oeder (*excl. syn. Hudson*) which he later regarded as a synonym of *F. distichus* L. (see also p. 416).

particular and distinctive furoid, it remains to confirm that it is either taxonomically distinct from, or else has nomenclatural priority over, several other early names for narrow forms of *Fucus* that have been revived more recently: (i) *F. linearis* Hudson (1762, *Fl. Angl.*, p. 467); (ii) *F. linearis* Oeder (1767, *Fl. Dan.*, tab. 351); and (iii) *F. filiformis* Gmelin (1768, *Hist. Fuc.*, p. 72).

*Fucus linearis* Hudson (1762, p. 467)

'*Fucus dichotomus planus linearis vesiculis ovatis sparsis. Anglis, narrow-leaved Fucus, or Sea-Thongs.*' (No illustration).

I fully agree with Turner (1802, p. 128; 1809, p. 45) that *F. linearis* Huds. is a narrow form of *F. vesiculosus* L., with (few or) no vesicles and with elongated receptacles, corresponding to the plant currently known in Britain as *F. vesiculosus* f. *evesiculosus* auctt. In Kew Herbarium there is a sheet of furoids, originally part of Turner's herbarium, which includes two small pieces of a furoid labelled '*Fucus linearis* Huds.—from himself—H.D. I divide with you an indifferent specimen'. This is material given by Hudson himself to the Rev. H. Davies who, to quote Turner (1802, p. 128), 'was kind enough to divide with me [Turner] an original specimen'. The present author has made a critical examination of this most interesting specimen and confirms that it is indeed a (male) plant of *F. vesiculosus* 'f. *evesiculosus*', without vesicles. In view of this finding, it is clear that the name '*f. evesiculosus*' is nomenclaturally superfluous, and the narrow, reduced form of *F. vesiculosus*, with few or no vesicles, found on exposed and semi-exposed coasts, should properly be named *F. vesiculosus* L., f. *linearis* (Huds.).<sup>1</sup>

*Fucus linearis* Oeder (1767)

Tab. 351 in *Flora Danica* (Vol. 2, fasc. 6, 1767, edited by G. C. Oeder) shows a rather idealized drawing of a furoid certainly very similar to *F. distichus* L. The caption referring to the plate (on p. 9) states:

'*Fucus marinus secundus. Dod. Pemt. 479. Fucus, linearis, dichotomus planus linearis acutus, vesiculis ovatis sparsis. Huds. Angl. 467. Locus. In fundo oceani Islandici.*'

Oeder is thus using Hudson's name *linearis* and quotes Hudson's diagnosis, but gives Iceland as the locality. The name *linearis* Huds. has just been shown to refer to a plant taxonomically quite distinct from *F. distichus* L., but if Oeder's sketch is indeed of a plant from Iceland then it could well be of true *F. distichus* L. I am inclined to agree with Turner (1808), Lyngbye (1819) and Hornemann (1827) that the sketch (only) of *F. linearis* in *Flora Danica* can be accepted as an illustration of *F. distichus* L. and may be cited in this respect in the following manner (= '*F. linearis*' *Flor. Dan.*, tab. 351, *excl. syn.* Hudson).

<sup>1</sup> Batters (1902, p. 50) is therefore in error in supposing *F. linearis* Huds. to be the curious, very narrow form of *F. ceranoides* L. apparently recorded in Britain only from Loch Stenness, Orkney Islands, where it grows in rather unusual environmental conditions (for recent information on the flora and physical conditions in Loch Stenness, Orkney, see Dunn, 1937, and Nichol, 1938). I have seen authentic specimens of this form of *F. ceranoides* from Loch Stenness in the Greville Herbarium (University of Edinburgh) and there is no doubt that it really is a form of *F. ceranoides*, with extremely thin, narrow fronds, and with the midrib very distinct and fine; the receptacles are elongated (but not markedly so) and the plants are dioecious. Lightfoot's (1777, p. 912) record of '*F. distichus* L.' from 'Loch Stennis, Orkney' also almost certainly refers to this same narrow form of *F. ceranoides*.

*Fucus filiformis* Gmelin (1768)

This name has been revived by Taylor (1937) for a narrow fucoid found in littoral pools in North-east America. However, again we find that Gmelin (p. 72) is merely quoting a name used for the first time by Hudson (1762, p. 472), who gives the following diagnosis for this plant: '*F. filiformis dichotomus planus. Anglis, flat Fucus. Habitat in littore Lancastriensi*' [Lancashire coast]. In the second edition of *Flora Anglica*, however, Hudson (1778, p. 585) gives an expanded diagnosis and additional information about '*F. filiformis*', as follows: '*Fucus fronde cartilaginea filiformis compressa dichotoma acuta. Anglis, filiform Fucus. Habitat in rupibus et saxis prope insula Walney in comitatu Lancastriensi. Desc. Frons semipedalis, cartilaginea, filiformis, compressa, dichotoma, diaphana, rubescens.*' This almost certainly refers to a red alga, and probably to a form of *Chondrus crispus* (L.) Stackh. Gmelin (1768) repeats Hudson's (1762) earlier diagnosis verbatim and adds some further description; for location he states '*Oceanus septentrionalis*' [northern Ocean] and he also gives a drawing of his conception of this plant (1768, tab. 1A, fig. 1). Other authors (e.g. Turner, 1808, though with some doubts) have quoted this illustration (but without the diagnosis and reference to Hudson) as a further possible illustration of *Fucus distichus* L. However, I think that the drawing is not accurate enough to be cited in this connexion; in particular, Gmelin's figure shows the midrib altogether too narrow and well defined, and clearly distinct all the way to the tips of all the branches (including running along the length of what are presumably rather flat-looking receptacles, a phenomenon that I have otherwise seen only in a few young receptacular apices of British *F. ceranoides*).

Thus the name *F. filiformis* (Hudson, 1762, 1778, Gmelin, 1768) has been used with different meanings and cannot now be associated with any particular type; it should therefore be rejected (Lanjouw *et al.*, 1952, Article 73). On the other hand, Taylor's (1937) own description and illustration of North-eastern American plants correspond precisely with the plants of *F. distichus* L. in Herb. Linn. and I have no doubt that they should be so named. (The nomenclature of North American fucoids will be discussed further on a later occasion.)

*FUCUS DISTICHUS* L. EMEND. POWELL

It has been shown above that the name *F. distichus* L. applies to a distinctive narrow fucoid that can be regarded as a good species. It is now proposed that the specific limits of *F. distichus* L. be amended to include the various hermaphrodite fucoids reduced to synonymy below. In the present treatment four of the many described forms are considered as subspecies. Each subspecies is fairly distinct from the others, at least in some parts of the species range. Near the centres of distribution, however, all possible intermediate forms between the four main subspecies may be found.

## GENERAL CHARACTERS OF THE SPECIES AS A WHOLE

The species as a whole is extremely plastic and, in response to varying environmental conditions and in different parts of its very wide geographical range, develops into a great variety of forms, the over-all range of form being indicated in the descriptions of subspecies below. Two particular characters, however, are fundamental to the present conception of the species: (i) the

conceptacles of all forms are invariably hermaphrodite; (ii) closed cavities, termed 'caecostomata', are found in variable number in the fronds of most forms of the species, but not in any other species of the genus *Fucus*. The author cannot yet state that caecostomata are invariably present in all forms, but they have been detected (sometimes only in very small numbers) in all specimens so far examined for this character. In view of their taxonomic importance in a group (*Fucus* spp.) in which diagnostic characters are few, caecostomata are dealt with in detail.

### *Caecostomata*

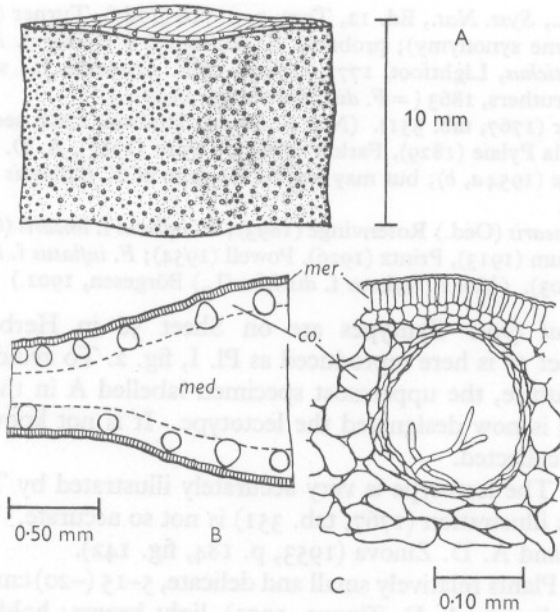
The descriptive term caecostomata was apparently first suggested by Prof. W. A. Setchell, and first used in print by Gardner (1922), for small completely closed cavities found in the fronds of certain Pacific coast fucoids referred by Gardner to the species '*F. furcatus* Ag.' (and '*F. edentatus* De la Pyl.'). Caecostomata are mentioned otherwise only by Setchell & Gardner (1925), Smith (1944), Fritsch (1945, p. 368, quoting Gardner, 1922), and Doty (1947)—all referring to Pacific coast material. However, Gardner (*loc. cit.*, p. 9) suspects that J. Agardh (1868, p. 38) may have been referring to them under '*Cryptostomata immersa saepe numerosa, plurima diu clausa*' [immersed (sunken) cryptostomata often numerous, most long since enclosed] with reference to his (J. Agardh's) conception of *F. filiformis* Gmelin, *F. linearis* Flor. Dan. and *F. miclonensis* De la Pyl.; this may be so, and J. Agardh repeats the above description (p. 40) with reference to the following fucoids: *F. edentatus* De la Pyl., *F. furcatus* C. Ag. and *F. evanescens* C. Ag. (De Toni, 1895, repeats the J. Agardh description for these same fucoids). Gardner also states (p. 18), very significantly, that he found 'a large number of caecostomata' in some of Børgesen's specimens of '*F. inflatus* f. *edentata*' from the Faeröes.

I have found caecostomata in all of the North Atlantic forms of *F. distichus* L. emend. Powell, and disagree with the taxonomic conception of Gardner (1922) that the presence of caecostomata can be used as a 'fundamental distinguishing character' of his *F. furcatus* Ag. emend.

In British material of *F. distichus* subsp. *edentatus* the presence of caecostomata may readily be detected (in both fresh and herbarium material) simply by holding a frond up to a light, when the internal cavities appear as small, lighter coloured (less dense), rounded spots in the frond, and, when the caecostomata are very numerous, the frond appears to be stippled with small light-coloured dots. Also, the meristoderm and cortex form a slight hump above each cavity, so that the frond surface appears to be covered with low, rounded, miniature pimples and has the appearance of a very fine-grained morocco-leather. The caecostomata (Text-fig. 1) are, in general, both more numerous and smaller near the thallus margins. The cavities are lined with flattened cells, are located at first mostly in the cortex (later extending a little deeper, into the outer medulla), and vary a good deal both in shape and size: the shape is most often pyriform, or rounded, or sometimes a rather flattened pear-shape; the size of the cavities is usually (50–) 100–200 (–250)  $\mu$  greatest diameter. Gardner (1922) states that 'no paraphyses develop' in the caecostomata he examined, but investigation of British material has shown that reduced, colourless paraphyses may develop to a small extent in some few of the caecostomata (Text-fig. 1 C), although the paraphyses are sometimes more numerous than shown in the figure. The paraphyses may be slightly branched.

The development of caecostomata has been investigated, by sectioning and squashing thallus apices, and my observations confirm those of Gardner that caecostomata

originate in the same way as do the conceptacles and ordinary cryptostomata in *Fucus* spp. (see Fritsch, 1945, for a review of the literature relating to the origin and development of these structures; Fritsch refers to cryptostomata as 'cryptoblasts'). All three structures originate just behind the growing point from a single initial cell. This soon becomes lodged at the base of a deep and narrow cavity owing to rapid growth and division of the surrounding cells. The cavity then enlarges and becomes lined with several layers of flattened cells, which delimit these structures from the compact cortical tissue and loose medullary tissue.



Text-fig. 1. Caecostomata in *Fucus distichus* subsp. *edentatus* (plant from Lerwick harbour, Shetland Islands). (A) Surface view of part of thallus; the circles represent (internal) caecostomata. (B) Transverse section of part of thallus, showing caecostomata situated mostly in the cortex. (C) Enlarged diagram of a single caecostoma, containing two colourless paraphyses. *co.*, cortex; *med.*, medulla; *mer.*, meristoderm.

From this point onwards, the development of caecostomata differs from that of cryptostomata and conceptacles. The pores communicating with the exterior become blocked by cell-division of the meristoderm very close behind the apex (within the first few mm), and the cavities soon become completely roofed over. In the older parts of the thallus the cavities are seen to have become very much larger, and to be roofed over by slight mounds of tissue (consisting of flattened limiting cells, a few layers of cortical cells, and meristoderm), and appearing as small mounds on the surface of the frond.

It would seem best to interpret the caecostomata as small, reduced, closed cryptostomata, although cryptostomata never occur (in any species of *Fucus*) at anything like the density that caecostomata may achieve.

In British *F. distichus* subsp. *edentatus*, caecostomata are often extremely abundant (up to a maximum density of 500 per cm<sup>2</sup>), and cryptostomata few or absent; while in

the Linnaean type of *F. distichus* subsp. *distichus*, and generally in *F. distichus* subsp. *anceps* (both with very reduced fronds), both caecostomata and cryptostomata occur only in small numbers and the caecostomata often can be detected only by sectioning the frond.

#### DESCRIPTION AND GENERAL DISTRIBUTION OF SUBSPECIES

##### Subsp. *distichus*. (Pl. I, fig. 2)

- Fucus distichus* L., *Syst. Nat.*, Ed. 12, Tom. 2, p. 716 (1767), Turner (1808, pp. 7-8, but excl. some synonymy); probably *F. distichus* f. *b tenuior* J. Agardh (1868). [Non *F. distichus*, Lightfoot, 1777 (= form of *F. ceranoides* L., see footnote on p. 416), Carruthers, 1863 (= *F. distichus* subsp. *anceps*).]
- F. linearis*, Oeder (1767, tab. 351). (Non *F. linearis* Hudson, 1762, see p. 416.)
- F. filiformis*, De la Pylaie (1829), Farlow (1881), Taylor (1937), A. D. Zinova (1953), E. S. Zinova (1954*a, b*); but may not be the type of *F. filiformis* Gmelin (1768) (see p. 417).
- F. inflatus* var. *linearis* (Oed.) Rosenvinge (1893); *F. inflatus* f. *linearis* (Oed.) Börgesen (1902), Norum (1913), Printz (1926), Powell (1954); *F. inflatus* f. *linearis* (Huds.) Jönsson (1903). (Non *F. inflatus* f. *disticha* (L.) Börgesen, 1902.)

*Nomenclatural type.* Syntypes are on Sheet 56 in Herb. Linn. (non Sheet 57); Sheet 56 is here reproduced as Pl. I, fig. 2. To avoid any possible ambiguity in future, the uppermost specimen labelled A in the photograph (Pl. I, fig. 2A) is now designated the lectotype. It is not known where the syntypes were collected.

*Illustrations.* The lectotype is very accurately illustrated by Turner (1808, pl. 4). Oeder's illustration (1767, tab. 351) is not so accurate. Taylor (1937, pl. 23, fig. 2); and A. D. Zinova (1953, p. 184, fig. 142).

*Description.* Plants relatively small and delicate, 5-15 (-20) cm in length (up to 40 cm according to A. D. Zinova, 1953), light brown; holdfast relatively small; stipe very thin, lax, round or oval in section; branching dichotomous and usually distichous, the axils rather acute; branches with entire margins, evesiculate, narrow, linear, 1.5-3 (-4) mm wide, thin; principal branches with a definite but not very prominent midrib and narrow lateral alae; in the lower parts of the plant the midrib becomes a little narrower but somewhat thicker, forming the thin stipe, while towards the tips of the branches the midrib usually becomes indistinct; cryptostomata and caecostomata both usually present, but few, small and obscure. Receptacles apical, narrowly cylindrical to fusiform, generally inflated, broader than the distal parts of the fronds which bear them, 0.5-3 cm long and 1-4 mm broad, unbranched or once-forked; conceptacles hermaphrodite.

*Distribution.* Kara Sea (A. D. Zinova, 1953); Barents Sea; White Sea; N. and W. Norway; Iceland; Faerøe Islands; Greenland; Atlantic coast of Canada and U.S.A.; Sea of Okhotsk and Gulf of Tartary (E. S. Zinova, 1954*a, b*). Not recorded (and probably absent) from British Isles. This plant largely occurs in rock-pools (but may occur also on open rock in some northern

parts of its range) in the upper part of the littoral zone, at both exposed and sheltered sites.

*Authentic specimens examined.*<sup>1</sup> The syntypes in Herb. Linn. (LINN) have been examined in detail; it is not known when, where, or by whom, the specimens were collected. **N.W. Russia.** 'Terra parva Samojedorum: Cap Barmin, August, Dr [F.] Ruprecht' [as '*F. vesiculosus* L. (f. *nana*)'] (K, ex Herb. Hooker). **WHITE SEA:** *F. Ruprecht* (K, same sheet). (Also on this sheet in Herb. Kew are some authentic specimens of subsp. *distichus* labelled '*Fucus distichus* ex herb. Linn.; Mr. Stackhouse from M. Der Fontaine 1802'.) **Norway.** **FINMARK:** Vardöhus (TCD); (also in Herb. Harvey, TCD, is another sheet of authentic material labelled '*F. distichus* L., ex Herb. Agardh'—presumably these are the 'authentic specimens' sent to W. H. Harvey by J. Agardh—see Carruthers, 1864); Gjesvaer, 1880, *M. Foslie* (BM, ex Herb. Holmes); 'Norv. arct., Mehavn,' May 1882, *F. R. Kjellman* (BM, ex Herb. Batters); 'West Finmarken, Maaröe' (?), July 1867, *Th. M. Fries* (BM, ex Herb. Batters). **LOFOTEN:** Reine, May 1952, *E. Baardseth* (MILL). **NORDMÖRE:** Bud, July 1955, in pools, *E. Conway* (GL). **Iceland.** Sept. 1897, *H. Jónsson* (K, *Plantae islandicae*). **Faeröe Islands.** **SYDERÖ:** Famien, May 1896, *F. Börgesen* (BM, *Algae marinae Faeroenses*, Nr 501 a, two sheets—one ex Herb. Batters, the other ex Herb. Holmes). **Canada.** **NOVA SCOTIA:** Peggy Cove (near Halifax), Aug.–Sept. 1948, *T. A. & A. Stephenson* (Herb. M.S. Doty, No. NSP. 14, two sheets).

Subsp. *anceps* (Harv. et Ward ex Carruthers) Powell, *n.comb.*  
(Pl. II, fig. 1)

*Fucus anceps* Harv. & Ward, Carruthers (1864), Gray (1867), Batters (1902), Newton (1931); *F. anceps* Ward & Harv., Harvey (1864); *F. anceps* 'Wood & Harv.', J. Agardh (1868); *F. anceps* 'Harv. et Wood', Areschoug (1868).  
*F. distichus*, Carruthers (1863, excl. synonymy and distribution), Du Rietz (1947), A. D. Zinova (1953); probably *F. distichus* f. *a robustior* J. Agardh (1868).  
*F. inflatus*, Arwidsson (1937), Parke (1953); *F. inflatus* f. *disticha* (L.) Börgesen (1902, but excluding some of his synonyms), Norum (1913), Printz (1926), Hygen & Jorde (1935), Levring (1937); *F. inflatus* f. *distichus* (L.) Börg., Powell & Lewis (1952), Gauld *et al.* (1953), Burrows *et al.* (1954), Lewis (1954); *F. inflatus* f. *exposita* Jónsson (1903), Powell (1954).

The name *Fucus anceps* Harv. & Ward ex Carruthers refers to a small form of *Fucus* found growing on the very exposed face of Duggerna Rock, Kilkee, West Ireland, by Prof. W. H. Harvey and Mr N. B. Ward on 19 July 1863. The plant was first briefly reported as '*F. furcatus* Ag.' (Anon., 1863), then as '*F. distichus* L.' (Carruthers, 1863, who described and illustrated the plant

<sup>1</sup> The abbreviations used for herbaria are as follows: (BM) British Museum; (E) Royal Botanic Garden, Edinburgh; (GL) University of Glasgow; (K) Royal Botanic Gardens, Kew; (LINN) Linnaean Society of London; (MILL) Scottish Marine Biological Association, Millport; (TCD) Trinity College, Dublin.

in detail). However, after examining authentic specimens of *F. distichus* L. sent to him by J. Agardh, Harvey finally decided that the Irish plant was 'a distinct and hitherto undescribed species' for which (in a letter to Carruthers) he proposed the name *F. anceps* Harv. & Ward (see Carruthers, 1864)<sup>1</sup>; the Latin word *anceps*, means 'two-headed', or 'two-fold' and was considered appropriate by Harvey (1864) because 'this *Fucus* seems to combine the characters of the ribbed and ribless species'. Additional details relating to the original discovery of *F. anceps* at Kilkee are given in notes and correspondence published in *Trans. bot. Soc. Edinb.*, Vol. 8, 1866 (pp. 52, 53, 111). I propose to revive the name *anceps* for this plant of very exposed coasts because the good description and figures of *F. anceps* quoted above are the earliest really certain account of this very distinctive subspecies.

*Nomenclatural type.* The description of this plant given in Carruthers (1863) is based on a series of syntypes from Kilkee, now lodged in the Herbarium of the British Museum. One specimen is closely similar to the principal illustration in Carruthers (1863, tab. 12, fig. 1) and I select this specimen as the lectotype, even though it is sterile.

*Illustrations.* Carruthers (1863, tab. 12, figs. 1-9); Børgesen (1902, p. 471, fig. 93, this illustration is reproduced by A. D. Zinova, 1953, p. 191, fig. 146); Printz (1926, p. 210, fig. 25); present work, Pl. II, fig. 1.

*Description.* Plants relatively small but very sturdy, usually (4-) 6-10 (-15) cm in length; yellowish brown to dark brown; holdfast well developed, up to 2 cm diam., giving very firm attachment; stipe short, relatively very thick, almost terete and stands erect, while the more lax distal branches arch over very characteristically; branching distichous, and usually dichotomous but may be unilateral in part; the angle between older branches is often rather wide and between youngest branches very acute, so that the young terminal branches are closely crowded and run almost parallel; branches with entire margins, evesiculate, alate above but narrow, seldom more and usually less than 4 mm wide, thicker than in subsp. *distichus* and consisting mainly of a stout midrib, with very narrow lateral alae on each side; towards the tips the branches become narrower, the midrib and alae are less distinct and the frond becomes more nearly oval in section; on older branches the alae are usually absent; a small number of cryptostomata present, often as a single row on each side of midrib in the younger thalli; in older branches, the hairs of the cryptostomata are often worn down to the level of ostiole; caecostomata present in small numbers in all specimens examined, but often their presence can only be detected by sectioning. Receptacles apical, elongated, narrowly cylindrical and often slightly curved (continuation of arching of frond), generally inflated, always broader than the distal parts of the frond

<sup>1</sup> In another letter reporting the new name, Harvey (1864) cites the authorities in reverse order, i.e. as 'Ward & Harvey'. I propose to retain the order of authorities given in Carruthers (1864).



which bear them, usually 1.5–3 cm long and 2–3 mm wide, but occasionally up to 4 cm long and 4 mm broad, unbranched or once-forked, apices bluntly pointed and often sterile, and continued vegetative growth beyond the receptacle is often seen; conceptacles invariably hermaphrodite. Often all the apices of a frond are fertile at the same time. Occasionally irregular areas of fertile tissue (often occupying only half the width of the frond, or less) may be found some way back from the apex; this character was first noticed by Carruthers (1863, p. 354, and tab. 12, fig. 7) and described as an ‘inferior lateral receptacle’ (cf. description of subsp. *edentatus* below).

*Distribution.* North-west Russia (Barents Sea and White Sea) according to A. D. Zinova (1953, p. 191) who describes the plant under the name *F. distichus*; North, West and South Norway; Iceland; Faerøe Islands; British Isles (North and West Scotland and Ireland only). This plant is found only on very exposed coasts, subjected to considerable swell and wave-action, in the upper part of the littoral zone.

*Authentic specimens examined.* **Norway.** NORDMÖRE: Bud, July 1955, E. Conway (GL), G. G. Smith (MILL). **Faerøe Islands** (all specimens collected and distributed by F. Børgesen). MYGGENAES HOLM: July 1902 (BM, *Algae marinae Faeroenses*, ex Herb. Holmes; K, *Alg. mar. Faer.*, ex Herb. Børgesen). STORE DIMON HOLM: June 1896 [BM, *Alg. mar. Faer.*, two sheets—one (No. 895) ex Herb. Batters, the other ex Herb. Holmes]. SYDERÖ: Vaags Ejde, June (K, *Kryptogamae Exsicc.*, No. 1746); Sumbö Holm, July 1899 (BM, *Alg. mar. Faer.*, No. 1617a, ex Herb. Holmes; K, *Alg. mar. Faer.*). **Scotland.** SHETLAND ISLANDS: Fair Isle: (i) North Gavel, (ii) reefs S.W. of South Lighthouse, June 1952, H. T. Powell (MILL, GL). ORKNEY ISLANDS: Sandwick, Mainland: (i) Hole o’Rowe, Oct. 1938, and (ii) near Garson, May 1939, J. Sinclair (Herb. J. Sinclair, Sheets No. 445 and 511, respectively). CAITHNESS: North coast: (i) near Crosskirk, (ii) Lower Dounreay, (iii) near Sandside Head, etc., July 1951, H. T. Powell (MILL, BM, K). OUTER HEBRIDES: Island of Lewis: (i) ‘Butt of Lewis’ [?], April 1909, W. J. Gibson (K), (ii) Buaille na Faing (half-mile N. of Port of Ness), July 1954, H. T. Powell (MILL); St Kilda Islands: Glen Bay, Hirta, July 1952 and July 1956, T. B. Bagenal (MILL). **Ireland.** DONEGAL: Malin Head, July 1953, J. R. Lewis (MILL). CLARE: Duggerna Rock, Kilkee, (i) July 1863, W. H. Harvey & N. B. Ward [BM (syntypes and lectotype), E, K, TCD], (ii) July 1953, H. T. Powell (MILL); Kilkee, (i) J. Cook (BM, ex Herb. Holmes), (ii) Sept. 1897, E. George [BM, K, etc., a large collection of sterile plants widely circulated as Holmes’s *Algae Britannicae Rariores Exsiccatae*, Fasc. X, No. 240]; also from (i) Donegal Point, (ii) George’s Head, (iii) reefs just N. of Goleen Bay, and (iv) four sites just N. of Ross Bay, July 1953, H. T. Powell (MILL). KERRY: Kerry Head, June 1953, J. R. Lewis (MILL).

Subsp. *edentatus* (De la Pyl.) Powell, *n.comb.*

(Plate II, fig. 2)

- Fucus edentatus* De la Pylaie (1829, p. 84, *excl. syn.*), J. Agardh (1868), Gardner (1922), Setchell & Gardner (1925), Taylor (1937), Lund (1949*a, b*), A. D. Zinova (1953, 1954); *F. edentatus f. typica* Kjellman (1883).
- F. inflatus*, probably Vahl (1794, tab. 1127), Foslie (1886), Kjellman (1890), Printz (1926), Kylin (1947), Sundene (1953); *F. inflatus f. typica* Jónsson (1903); *F. inflatus var. a edentatus* (De la Pyl.) Rosenvinge (1893); *F. inflatus f. edentata* (De la Pyl.) Børgesen (1902, 1903); *F. inflatus f. edentatus*, Burrows *et al.* (1954). (*Non F. inflatus* L., see pp. 409–12.)
- F. furcatus* C. Agardh (1820, 1821), J. Agardh (1868), Kleen (1874), Farlow (1881), Gardner (1922, in part), Setchell & Gardner (1925, in part); (= *F. Gardneri* Silva, 1953)<sup>1</sup>.
- F. evanescens*, Gardner (1922, in part), Setchell & Gardner (1925, in part).
- F. nitens* Gardner (1922), Setchell & Gardner (1925).

*Nomenclatural type.* Not seen by the present author. According to De la Pylaie (1829, p. 84) type material from Newfoundland (De la Pylaie, Herb. Terre-Neuve) was deposited in the Herbarium of the Paris Museum. Gardner (1922, p. 11) confirmed this and published a photograph (his plate 60, fig. 1) of the 'type specimen', which is presumably the holotype.

*Illustrations.* Kützing (1860, tab. 17 11); Børgesen (1902, pp. 467–9, figs. 90–92; 1905, p. 747, fig. 158), (1904, p. 56, fig. 7); Gardner (1922, pl. 60, fig. 1, also pls. 4, 10, 13, 18–23, 25, 54); Hylmö (1933, p. 383, fig. 4, uppermost plant); Taylor (1937, pl. 23, fig. 3); Levring (1946, fig. on p. 192); Kylin (1947, taf. 16, fig. 2); Lund (1949*a*, p. 233, fig. 1); A. D. Zinova (1953, p. 186, fig. 144); present paper, Pl. II, fig. 2. (The illustrations referred to by De la Pylaie, 1829, were unfortunately never published.)

*Description.* Plants typically large and sturdy, 20–45 (–60; and exceptionally –90, Taylor, 1937) cm in length; dark brown; branching regularly dichotomous and usually distichous, axils generally acute; branches with entire margins, evесiculate, leathery and more or less flaccid, alate above, but rather narrow for a furoid of this size, (5–) 9–15 (–20) mm broad but a little broader just below the dichotomies, relatively quite thick, midrib very distinct below but may become very indistinct above (especially immediately below the receptacles); irregular inflations may occur in the lateral alae especially in distal segments; towards the base the midrib is denuded of alae and forms a firm stipe; holdfast a broad conical disk; cryptostomata typically few but can be quite numerous, usually rather small and inconspicuous in older branches; caecostomata usually present, from few to very abundant (up to 500 per cm<sup>2</sup>). Receptacles apical, typically elongated and swollen, cylindrical

<sup>1</sup> Silva (1953) proposed the new name *F. Gardneri* for *F. furcatus* C. Ag., because the latter name is a homonym of *F. furcatus* Esper [1800, p. 178 (138 by error), plate 95] and is therefore nomenclaturally illegitimate; according to Silva, 'Esper's *Fucus furcatus* was based on a plant from the Adriatic Sea...most likely referable to the alga currently known as *Fauchea repens* (C. Ag.) Mont.'

or somewhat flattened, 2-10 (-22, Gardner, 1922, p. 50) cm long, 5-15 (-25, Gardner, 1922) mm broad below, often tapering to acute (sterile) tips, usually divided 1-3 times into antler-like subdivisions, often not very sharply demarcated from sterile tissue below; vegetative growth beyond the receptacle may often occur (see Pl. II, fig. 2); conceptacles invariably hermaphrodite. Occasionally irregular areas of fertile tissue (often occupying only half the width of the frond, or less) may be found some way back from the apex (*cf.* subsp. *anceps*). When dried, the plants become very dark brown or black in colour and the receptacles of herbarium specimens are usually pressed quite flat; the midrib may appear more prominent in dried specimens than in living plants.

*Distribution.* North-west Russia (Barents Sea and White Sea) according to A. D. Zinova (1953, p. 185); North and West Norway, Oslofjord, West Sweden, Copenhagen; Iceland; Faeröe Islands; British Isles (only in Shetland Islands and Fair Isle); Greenland; Atlantic coast of Canada and U.S.A.; Pacific coast of Canada and U.S.A.; Kamchatka; North Japan. This plant is typically a good deal larger than the two preceding subspecies, and it grows best at sheltered or semi-exposed sites, in the sublittoral fringe and lower mid-littoral zones. It may be found, however, at any level from the upper mid-littoral zone down into the sublittoral zone; the plants growing at high levels or in more exposed situations are generally shorter and narrower.

*Authentic specimens examined.* **Norway.** TROMS: Tromsö, June 1887, M. Foslie (K, *Hauck et Richter Phykotheke universalis*, No. 164). LOFOTEN: Reine, May 1952, E. Baardseth (MILL). S. TRÖNDELAG: Trondheimsfjord, July 1955, H. Blackler (GL). AKERSHUS: Oslofjord, May 1953, O. Sundene (MILL). **Iceland.** 1897, H. Jónsson (K, *Plantae islandicae*). Skalaness, Aug. 1952 (GL). **Denmark.** Copenhagen harbour, May 1951, S. Lund (MILL). **Faeröe Islands.** STRÖMÖ: (i) Thorshavn, June 1895 (No. 224), (ii) near Kalbakfjord, June 1898, F. Børgesen (BM, *Algae marinae Faeroenses*, ex Herb. Batters). **Scotland.** SHETLAND ISLANDS: Mainland: Lerwick, (i) '16. 6. 1902', F. Børgesen (K), (ii) June 1908, W. A. Russell (BM, K, Holmes's *Algae Britannicae Rariores Exsiccatae*, Fasc. XII, No. 288), (iii) June-July 1952, H. T. Powell (MILL, GL); Scalloway harbour, July 1952, H. T. Powell (MILL). Fair Isle: North Haven, June-July 1952, H. T. Powell (MILL, GL). **Canada.** NOVA SCOTIA (all specimens collected Aug.-Sept. 1948, by T. A. & A. Stephenson, and now in Herb. M. S. Doty): (i) Halifax harbour (Herb. No. NSH. 13, one of three sheets labelled *F. evanescens*); (ii) Peggy Cove (Herb. No. NSP. 14, two sheets); (iii) Hall's Harbour, Minas Channel, Bay of Fundy (Herb. No. NSBF. 5, two sheets). BRITISH COLUMBIA: Vancouver Island: Beacon Hill, Victoria, June 1908, J. Macoun (BM, ex Herb. Geological Survey of Canada). **U.S.A.** MAINE: Eagle Island, Penobscot Bay, July 1896, F. S. Collins (BM, *Phycotheca Boreali-Americana*, Collins, Holden & Setchell, XIII). MASSACHUSETTS: Nahant (BM, ex Herb. F. S. Collins).

Subsp. *evanescens* (C. Ag.) Powell, *n.comb.*

*Fucus evanescens* C. Agardh (1820, 1821), J. Agardh (1868), Kjellman (1883), Yendo (1907), Gardner (1922, in part), Setchell & Gardner (1925, in part), Taylor (1937), E. S. Zinova (1933, 1954*a, b, c*), A. D. Zinova (1953).  
*F. inflatus* var. *evanescens* (C. Ag.) Rosenvinge (1893); *F. inflatus* f. *evanescens* (C. Ag.) Jónsson (1903).

*Nomenclatural type.* Gardner (1922, p. 12) states: 'according to Setchell, the type specimen is in the herbarium of J. G. Agardh, under No. 00299, with a query.' I have not seen this (apparently doubtful) specimen and, for the present, temporarily designate as the type C. Agardh's description (1820, pp. 92-3) and illustration (1821, plate 13). C. Agardh's illustration is very well reproduced, photographically, by Gardner (1922, plate 1, fig. 2). For location, Agardh (1820) writes: 'Ad Sachalien, Tilesius; ad Kamtschatka, Chamisso; unde specimina communicaverunt' (whence specimens have been communicated); and the locality of the specimen illustrated by Agardh (1821, plate 13) is also stated to be Kamtschatka. E. S. Zinova (1933, 1954*c*) also records this alga from Kamchatka.

*Illustrations.* C. Agardh (1821, plate 13); Gardner (1922, plate 1, fig. 2; also plates 11, 11*a*, 35, 36, 45, 46, 47, 48, 52, 56, 58, 59); Taylor (1937, plate 23, fig. 4; plate 24, fig. 2); A. D. Zinova (1953, fig. 147).

*Description.* This subspecies is the most variable and therefore the most difficult to define of the four subspecies recognized in the present paper. The principal features of *F. evanescens*, as originally defined and drawn by C. Agardh (1820, 1821), were: plant large, fronds broad; receptacles flattened, not markedly elongated, relatively broad; midrib indistinct in the apical parts of the plant. Some authors (e.g. Rosenvinge, 1893; Jónsson, 1903; Taylor, 1937) have applied the name to large, relatively broad, plants usually found in the lower part of the littoral zone (and in sheltered situations) in some of the more southerly parts of the over-all range of the subspecies; these large plants typically have fronds wider and receptacles shorter than subsp. *edentatus*, and correspond most nearly to the type illustration. Other authors (e.g. Kjellman, 1883; Gardner, 1922; A. D. Zinova, 1953) have applied the name to a number of relatively small and often rather narrow plants found on Arctic and other northern shores. As in subsp. *edentatus*, characters such as the midrib becoming indistinct above, and the numbers of cryptostomata and caecostomata, are in fact very variable; and, if we include the narrow Arctic forms, even the relative width of the frond varies widely. Indeed, the only characteristic morphological features of subsp. *evanescens*, throughout its geographical range, relate to the shape of the receptacles—relatively short and broad, rather flattened, and fairly distinctly delimited from the rest of the frond (*cf.* subsp. *edentatus*). From several Arctic areas, only plants with such receptacles have been reported (it is apparently the only

subspecies that is circumpolar in distribution) and such plants also are not found so far south as, for example, subsp. *edentatus*; it is therefore convenient to recognize subsp. *evanescens* as the subspecies best adapted to Arctic conditions, even though the morphological distinction from forms of subsp. *edentatus* is somewhat arbitrary, and despite the fact that the small distinctions between these two subspecies are obscured in some parts of the world by the presence of all possible intermediate forms, with receptacles intermediate in shape sometimes even on the same plant.

According to Inoh (1935), material of '*F. evanescens* Ag.' collected near Muroran, Hokkaido, Japan, has a haploid chromosome number of 32; this is the number usually reported for *Fucus* spp.

*Distribution.* Arctic and subarctic, circumpolar. Siberian Polar Sea, N.W. Russia, Novaya Zemlya, Svalbard, Jan Mayen, Bear Island; Greenland, Iceland; American Polar Sea, Atlantic Canada, Atlantic U.S.A.; Pacific Canada, Pacific U.S.A., Bering Sea, Aleutian Islands, Kamchatka, Sea of Okhotsk, Kurile islands, North Japan. *F. distichus* subsp. *evanescens* has not been found in Britain; the nearest locality is probably Iceland (Jónsson, 1903), although Börgesen (1902, p. 471) mentions finding a few plants possibly referable to subsp. *evanescens* at Thorshavn (Faeröes). The larger forms of this subspecies are found near or below low tide level at sheltered or semi-exposed sites. The smaller forms are found under more rigorous environmental conditions, such as, at more exposed sites, at higher tidal levels, or under Arctic conditions.

*Authentic specimens examined:* **West Greenland.** Godthaab, July 1886, K. Rosenvinge (BM, *Plantae groenlandicae*, No. 211, ex Herb. Holmes). **Canada.** NOVA SCOTIA: Halifax harbour, Aug.-Sept. 1948, T. A. & A. Stephenson (Herb. M. S. Doty, No. NSH. 13). BRITISH COLUMBIA: Vancouver Island: Esquimalt, Jan. 1860, probably *F. S. Collins* (BM, ex Herb. Holmes, two sheets). **U.S.A.** MASSACHUSETTS: Nahant, Aug. 1884, *F. S. Collins* (BM, ex Herb. Holmes).

#### OTHER DESCRIBED FORMS

Apart from the forms reduced to synonymy in the foregoing treatment, certain other described forms have been regarded as distinct species by some recent authors, as follows:

*Fucus fueci* De la Pyl. (A. D. Zinova, 1953).

*Fucus miclonensis* De la Pyl. (Taylor, 1937; A. D. Zinova, 1953).

*Fucus membranaceus* Gardner (1922; Setchell & Gardner, 1925).

These forms are regarded by the author as further forms of *F. distichus* L. emend. Powell, but they do not appear to be sufficiently distinctive to warrant subspecific status.

## ACKNOWLEDGEMENTS

I am grateful to the Botanical Curator of the Linnaean Society of London (Mr N. Y. Sandwith) for permission to make a detailed examination of some 14 sheets of algae from the Linnaean Herbarium, and to the Council of the Linnaean Society for permission to publish the photographs of Linnaean type specimens reproduced as Pl. I, figs. 1 and 2. I wish to thank also: Miss C. I. Dickinson (K), Mrs Linda Irvine (BM) and Miss Yvonne Chamberlain (BM) for assistance in tracing herbarium specimens and references; Dr Mary Parke and Dr A. P. Orr for helpful criticism of the manuscript of the present paper; and the directors and curators of the following herbaria for the loan of specimens: British Museum; Royal Botanic Gardens, Kew; University of Birmingham. The following colleagues have very kindly provided me with either liquid-preserved or herbarium specimens collected at the places indicated: Dr E. Baardseth, Dr E. Conway, Mr G. G. Smith and Dr O. Sundene (Norway); Dr S. Lund (Copenhagen); Mr T. B. Bagenal (St Kilda), and Dr J. R. Lewis (Ireland). Also, Mr J. Sinclair (Orkney Islands) and Prof. T. A. Stephenson (Nova Scotia) have kindly let me examine specimens collected by them. I am further obliged to Dr J. R. Lewis and Mr J. Sinclair for permission to include their unpublished records in the present paper.

In conclusion, the author would be grateful to receive or borrow specimens of this difficult group of plants from colleagues in any part of the world, and especially from colleagues who may not agree with the taxonomic treatment proposed above.

## SUMMARY

The taxonomic status and nomenclature of the hermaphrodite forms of *Fucus* (other than the alga currently known as *F. spiralis* L. and certain hybrid forms) usually included under the name *Fucus inflatus* L. by European authors, but under several specific names by N. American and some other authors, is discussed. It is considered that the numerous forms described are best interpreted for the present as forms of a single, extremely plastic and widely distributed species.

In order to determine the correct names to apply to two forms of '*F. inflatus* L.' found in Britain, a critical study has been made of the type specimens of *Fucus* spp. in the Linnaean Herbarium. It is concluded that the two small sterile specimens labelled '*F. inflatus*' in Herb. Linn. are most probably plants of *F. vesiculosus* L.; the original diagnosis of *F. inflatus* L. is also inadequate and it is proposed that this name be regarded as a synonym of *F. vesiculosus* L.

However, the taxon *F. distichus* L. (*Syst. Nat.*, Ed. 12, 1767) is shown to be valid, based on good specimens in Herb. Linn., and this is re-established as the earliest acceptable name for the group of forms in question. The principal characters of the species as a whole are: (i) hermaphrodite conceptacles, and (ii) the frequent presence, in all forms, of closed cavities in the frond—the caecostomata. Caecostomata are described for European material (including the Linnaean type) for the first time.

Near the centres of distribution of this species whole series of forms

(clines) intermediate in character between the various extreme forms may be found; in such places the extreme forms can often be interpreted as ecological forms and it may be that in some places they have evolved into true ecotypes (genetically better adapted forms). At the limits of geographical range, on the other hand, intermediate forms are often absent and only one or two of the principal forms may persist, often as populations isolated both geographically and ecologically; it is even more likely that these isolated populations are genetically distinct ecotypes, but this could only be proved by experimentation.

The taxonomic limits of *F. distichus* L. are revised to include the following four principal subspecies: subsp. *distichus*; subsp. *anceps* (Harv. et Ward ex Carruthers) Powell, *n.comb.*; subsp. *edentatus* (De la Pyl.) Powell, *n.comb.*; and subsp. *evanescens* (C. Ag.) Powell, *n.comb.* Of these, only subsp. *anceps* and *edentatus* have been found in Britain.

For each subspecies the following information is given: important synonymy, nomenclatural type, principal illustrations, description, geographical distribution, and a list of authentic specimens examined. The illustrations include photographs of the type specimens of *F. inflatus* L. and *F. distichus* L.

It is shown, incidentally, that the plant currently known in Britain as *F. vesiculosus* f. *evesiculosus*, should more properly be named *F. vesiculosus* f. *linearis* (Huds.).

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## EXPLANATION OF PLATES

## PLATE I

Fig. 1. *Fucus inflatus* L. Photograph of the type specimens (Sheet 1274: 51 in the Linnaean Herbarium).

Fig. 2. *F. distichus* L. emend. Powell, subsp. *distichus*. Photograph of the type specimens (Sheet 1274: 56 in the Linnaean Herbarium). Specimen A is the lectotype.

## PLATE II

Fig. 1. *F. distichus* L. emend. Powell, subsp. *anceps* (Harv. et Ward ex Carruthers) Powell. Photograph of a pressed specimen, 11.5 cm greatest length: Kilkee, Ireland, *J. Cook* (BM, ex Herb. Holmes, no date).  $\times 0.55$ .

Fig. 2. *F. distichus* L. emend. Powell, subsp. *edentatus* (De la Pyl.) Powell. Photograph of a pressed specimen, 25 cm greatest length: Lerwick, Shetland Islands, July 1952, *H. T. Powell* (MILL).  $\times 0.35$ . *r.*, elongated receptacles; *c.*, continued vegetative growth beyond the receptacles. The receptacles are not usually so much elongated as in this specimen.

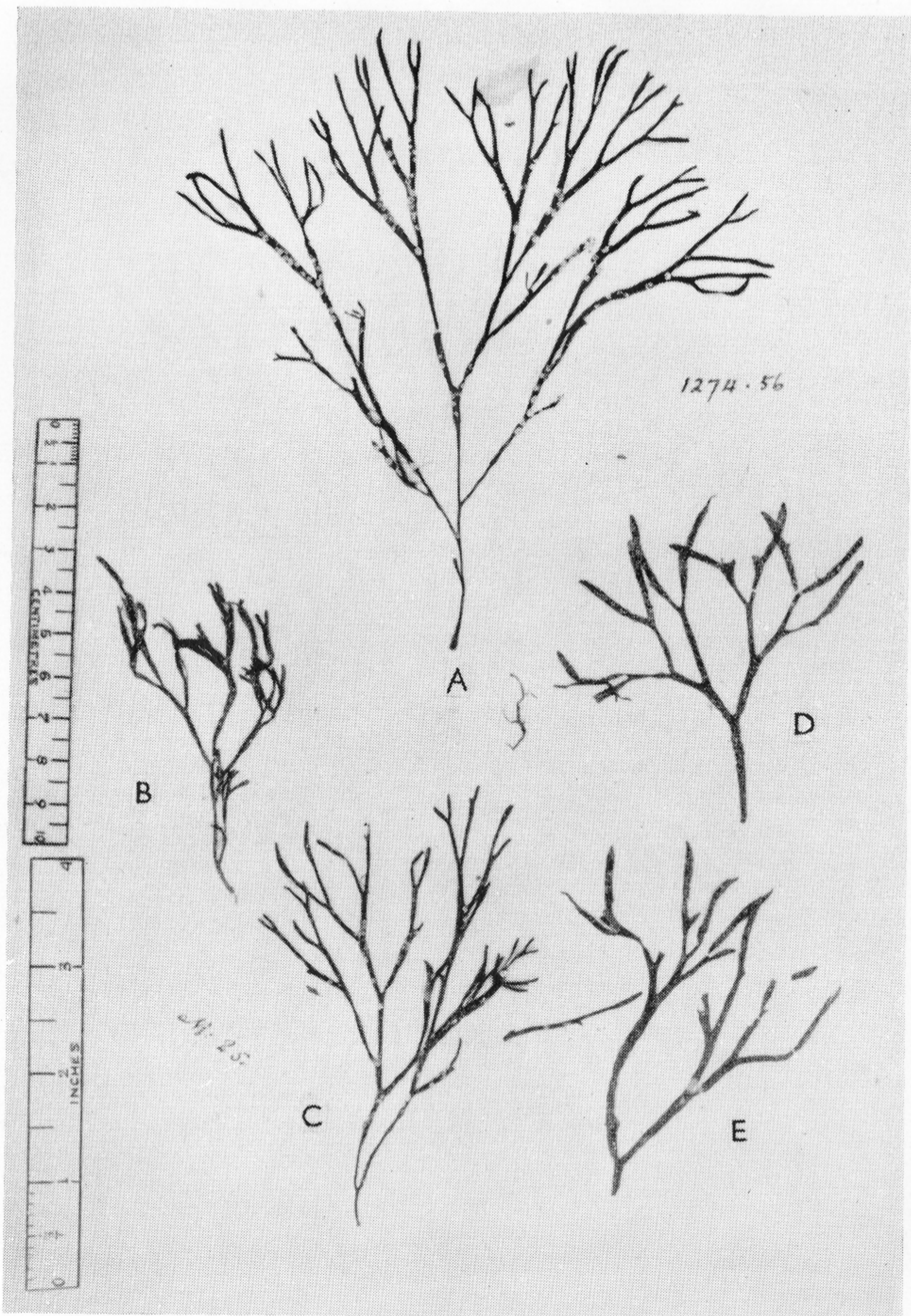


Fig. 2

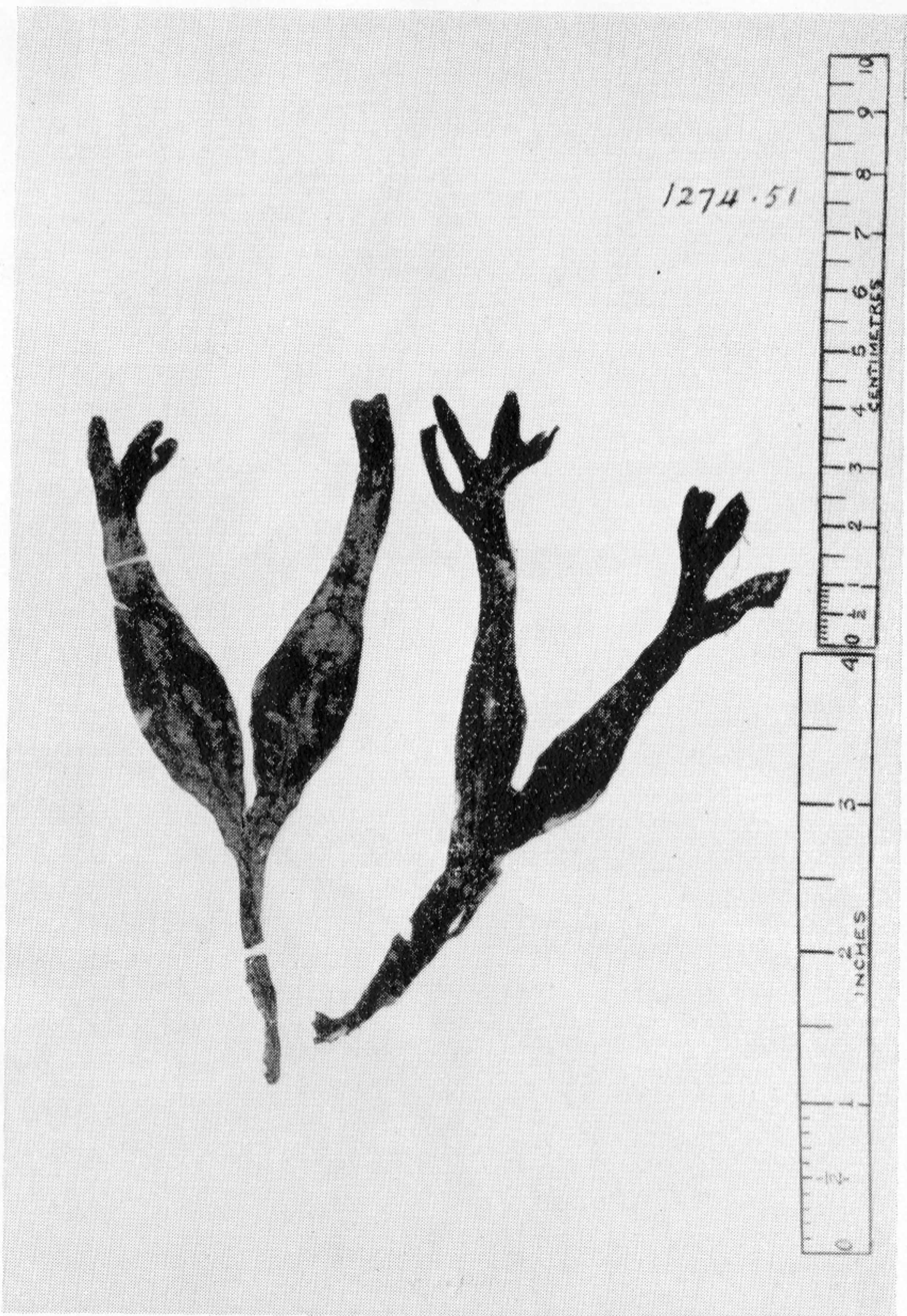


Fig. 1

(Facing p. 432)

