

COMMONWEALTH OF AUSTRALIA

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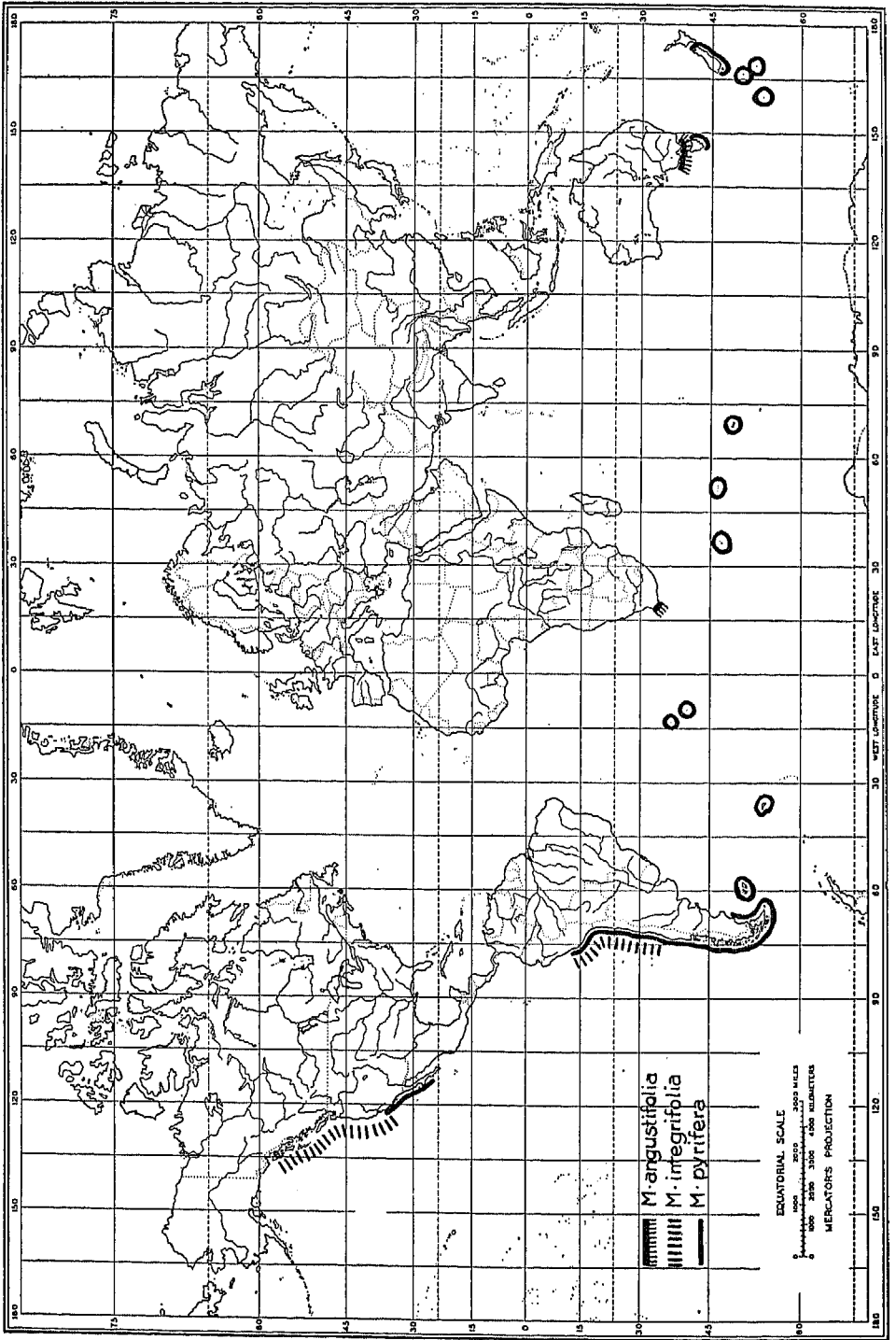
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it is clear that the locality originally given cannot be fixed with any certainty, except so far as it was somewhere in the south Atlantic Ocean. Two aspects can then be considered:

1. The possibility that current systems had carried South African *Macrocyttis* either into the region of the Gulf of Guinea or westward into the South Atlantic, or that such floating masses more likely had originated elsewhere.
2. The course taken by sailing ships of the eighteenth century (the type material was collected about 1770) between Europe and South Africa.

1. The current system in the South Atlantic Ocean (Sverdrup *et al.*, 1942, chart 7, and National Geographic Society map of "The World," issued December, 1951) consists of the west-wind drift between latitudes 40°S and 60°S, and the Benguela current (of deepwater origin) which flows northward off the west coast of southern Africa, then swinging back toward Brazil in South America.

The occurrence of *Macrocyttis* in South Africa is relatively small, both in distribution and in the comparatively limited zone it forms in the upper sublittoral, where it is usually protected by an outer bed of another kelp, *Ecklonia maxima* (*E. buccinalis*) (Isaac, 1937b, p. 126). Although offshore winds could possibly blow the plants out to sea where they might join the Benguela current and be carried northward and westward, it seems more likely that the masses of seaweed in the "floating islands" of *Macrocyttis*, referred to in Linnaeus' description, would be more readily derived from large, deepwater beds than from the more limited growth along the South African coast.

On the other hand, it seems possible that Koenig's specimen could have been carried by the west-wind drift from islands such as Tristan da Cunha (where *Macrocyttis pyrifer*^a has been recorded by Baardseth, 1941, p. 32) or Gough Island, or even from as far away as Fuegia or the Falkland Islands. Hooker (1847, p. 465) refers to floating masses of *Macrocyttis* occurring anywhere in the region of the west-wind drift, encircling the southern ocean, and in referring to it in the meridian of the Cape of Good Hope, states "there the Atlantic Ocean specimens are derived from the southern extreme of America and the neighbouring islands." Hooker also refers to the waters of the Agulhas Bank (directly below South Africa) "literally swarming with *Macrocyttis*, which possibly is taken up from the northern edge of the westerly Polar Current."

Isaac (1937a, p. 652) shows that the current flow over the Agulhas Bank is from east to west (i.e., toward the known occurrence of attached *Macrocyttis* in South Africa), though the bulk of the Agulhas current water is deflected back eastward by the Agulhas Bank. Gilchrist (1904, pp. 155-165) indicates the possibility of more local currents closer inshore carrying objects from the southern end of the west coast of the Cape Peninsula to Agulhas.

It seems improbable that the floating *Macrocyttis* of the Agulhas Bank and of the south of South Africa originates from the attached South African plant. More likely it comes from subantarctic islands some distance away.

Macrocyttis apparently can remain in a viable or growing condition for a

^a Baardseth's specimens in the Oslo Museum appear to be *M. pyrifer* as understood in this study.

long time. Hooker believed it could flourish when floating and detached, and Moore (1943, p. 333) has described a free-living form from Stewart Island, New Zealand.

Whether floating seaweed in the west-wind drift could be swept up into the Benguela current and carried northward is also doubtful. Dr. H. F. P. Herdman of the Discovery Expeditions (personal communication) considers it "extremely unlikely that masses of kelp could be swept up from the West Wind Drift into the Benguela current. The effect of the Benguela current stretches far south, but in the region west and south-west of South Africa there is also the influence of the tail-end of the Agulhas current, flowing from east to west, which would inhibit the passage of kelp to the north. We have often been in this area and I cannot recollect reports of floating kelp." A ship's master, for many years on the run from England around South Africa, also stated that he had never seen floating kelp in the region of the Gulf of Guinea southward.

On the whole, a consideration of the currents indicates that it is unlikely that a large floating mass of kelp, originating from the South African habitat, or coming from the west-wind drift, would be found in the region of the Gulf of Guinea.

2. Papefuss (1940, p. 7), believing that "Oceanus Aethiopicus" applied to that part of the Atlantic which lies opposite Africa from the coast of Guinea southward, considered that the type specimen of *M. pyriferus* came from this area. However, the sailing ships of the eighteenth century, going from Europe to India and Australia, always followed the trade winds over to South America, and then struck south to pick up the westerlies. Tristan da Cunha was a favorite landfall in checking their position on this southward leg.³ With the trade winds blowing from the southeast toward the equator, it would be most unlikely for any sailing ship to be in the region of the Gulf of Guinea southward on its outward voyage from Europe.

There is, however, no direct evidence available that the material was collected on the outward voyage from Europe, and not on the homeward voyage. The only indication is that Linnaeus' original description gives a Koenig number of 42, which might indicate that it was collected relatively early on the trip.

If the type specimen were collected on the outward voyage, it probably came from somewhere in the south Atlantic Ocean, very possibly in the region of Tristan da Cunha, rather than from South Africa.

The type locality of *Fucus pyriferus* would not be of such importance if, as many authors have held, there is only one species in the genus, or if the South African and subantarctic plants were the same. In recent years, however, two species have been recognized on holdfast characters and, as will be shown below, a third seemingly distinct species occurs.

It now appears that the mature holdfasts are the only sound basis for specific segregation in *Macrocystis*, since all frond characters are extremely variable. Yet the type (?) specimen of *F. pyriferus*, in the Linnaean Herbarium,⁴ consists only of a small part of a frond, both terminal blade and holdfast being completely

³ I am indebted to Dr. Herdman for information on this matter. The route of sailing ships is also indicated on old globes in the British Museum.

⁴ There is only one specimen of *Fucus pyriferus* in the Linnaean Herbarium, London, with nothing on it to indicate that it is the original specimen of Koenig.

absent. Thus the type specimen can fit equally well any of the three species of the genus, unless future detailed anatomical studies show differences in the internal structure of the fronds. At present this seems unlikely.

Several monographs on *Macrocystis* (Skottsberg, 1907; Setchell, 1932) have clarified concepts of the plant usually called *M. pyrifera* (L.) Agardh. Further, it is now evident that the South African plant (there seems to be no evidence that there is more than one species growing on South African coasts) is not the same as the usually held concept of *M. pyrifera*, but is identical with the southern Australian plant called by Bory, *M. angustifolius*.

If the South African plant were accepted as representative of *M. pyrifera*, the concept of this species would have to be changed, and the American and subantarctic plants would have to be referred to by a different name, probably *M. humboldtii* (Bonpl.) Kunth. Because of the uncertainty about the source of the type specimen, which might equally well have come from a subantarctic island (where *M. pyrifera*, as usually accepted, grows), it seems best to retain the established concept of *M. pyrifera*, and to refer the South African plant to *M. angustifolia*. This also obviates a name change of a species that is frequently referred to in papers on its economic and chemical aspects.

SPECIES OF MACROCYSTIS

Since the original description of *Fucus pyriferus* in 1771, numerous other species of *Macrocystis* have been described. C. A. Agardh (1839, pp. 283-316) in the first monograph on the genus, recognized six species. Nearly all the early species were based on herbarium material only, and not until the thorough report of Hooker (1847, p. 461) had the plant ever been adequately described from field observations. Hooker referred some ten previously described species to *M. pyrifera*, regarding them as forms of one species. Later Skottsberg (1907, pp. 80-136), in his morphological and anatomical monograph on the genus, also recognized only one species, referring to it some 22 specific names. In view of these papers of Hooker, Skottsberg, and of Setchell (1932), a detailed review of the history of the genus is unnecessary, but it is significant that up to the publication of Howe's (1914) paper on the marine algae of Peru, scarcely any attention had been given to the nature of the holdfasts. This was largely owing, no doubt, to their absence in herbarium collections and the difficulty of obtaining them from deep water. Skottsberg (1907, fig. 132) figured the distinctive rhizome of *M. integrifolia* (as *M. pyrifera* f. *angustifolia*), but did not consider it constituted a difference of specific rank. Howe (1914, pp. 60-66), following the views of Areschoug (1883, p. 22), considered that two distinct species occur on the Peruvian coast, *M. pyrifera* (L.) Ag. and *M. integrifolia* Bory. His distinction was based very largely on the holdfast and was later followed and elaborated by Setchell (1932), who showed that the two South American species occur also on the west coast of North America. Setchell considered that only *M. integrifolia* occurred above Point Conception, and only *M. pyrifera* south of this point.

Smith (1942, p. 647) considered that besides differing in the nature of the holdfasts, *Macrocystis pyrifera* and *M. integrifolia* on the Monterey Peninsula also differ in the form of the terminal growing blade, the former having a broadly

falcate blade with 12–20 young splitting blades, whereas the latter has an elongated blade with 2–6 young blades still attached. Both Setchell and Smith recognized ecological differences between the two species, *M. pyrifer* forming offshore beds in deep water (20–60 ft.) and *M. integrifolia* growing from low-water level to about 20 feet below. *M. pyrifer* is also usually a much larger plant than *M. integrifolia*.

Scagel (1947, p. 7), however, reports that on Vancouver Island, British Columbia, *Macrocystis* grows from 3 feet above zero low water (tidal rise about 20 ft.) to 20 feet below. All the holdfasts have the typical flattened and broad rhizomatous branches of *M. integrifolia*, with haptera arising along the two margins, but the terminal blades are very variable, mostly conforming to Smith's description of terminal blades of *M. pyrifer*. Scagel regards these plants as *M. integrifolia*, considering the holdfast as the only sound diagnostic character. It seems that although the terminal blade may be useful in distinguishing the two species in restricted regions, such as the Monterey Peninsula, it is of little use over long stretches of coastline. Scagel's specimens and the wide range of material in the Herbarium of the University of California emphasize the great variation in any character associated with the fronds and terminal blades.

The type specimen of *Macrocystis integrifolia* (see Bory, 1826b, pl. 6) has almost entire smooth blades and presents a somewhat unusual appearance in this respect. Similar specimens from Chile and Peru have been seen in several herbaria, some with the characteristic holdfast of *M. integrifolia*; several other specimens showing intermediate frond characters between this smooth, entire type and the rugose, spiny type on the California coast have been seen. Thus specimens in the University of California Herbarium and information from Dr. J. Proskauer, who has seen *Macrocystis* in Peru, show that the *M. integrifolia* as known in California does occur in South America, and that this species in California may have some smooth, almost entire blades when young.

Another unusual variant found in South America and New Zealand is what has been called *Macrocystis Orbigniana* Montagne, with extremely long, slender vesicles (to 20 cm. long and 1 cm. wide). Vesicles of similar dimensions also occur on plants at Robe in South Australia, with the more normal pyriform ones on the same plants, and these clearly represent only ecological variations.

Skottsberg (1907, and personal communication) considered that environmental factors—such as degree of roughness and strength of currents through the beds—cause the great frond and vesicle variation. Possibly plants growing in relatively calm, still water develop almost spherical vesicles, whereas in wind-affected places or in strong currents between islands the pyriform or elongate vesicles are developed. The degree of wave action on fronds at the surface is likely to cause considerable variation in the shape of the terminal blade and the number of incompletely split segments. It is perhaps significant that *Macrocystis* growing in denser beds (*M. pyrifer*, and the *M. integrifolia* along the coast of British Columbia) seems to have a broader blade with more segments than *M. angustifolia* and *M. integrifolia* growing where the fronds are more exposed to broken water. The form of the terminal blade on one plant may also vary with depth below the surface. The observations of Smith (1942, p. 649) were limited to fronds lying on the surface, and might not apply to terminal blades below the surface.

On southern Australian coasts, two species of *Macrocyrtis* can be distinguished by holdfast characters. One species (pls. 1, 3, and 4) occurring on the south and southeast coasts of Tasmania, agrees well with the conceptions of Setchell, Smith, and others, of *M. pyrifer*, and certainly appears to be identical with plants of this species cast up on La Jolla beach, southern California. The other species (pls. 2, 5, and 6), found abundantly at Robe in South Australia, and probably growing in the upper sublittoral around much of the Victorian coast, is strikingly different in holdfast characters from *M. pyrifer*. The conical holdfast consists of a number of rhizomatous branches, only slightly flattened if at all, which emit haptera on all sides, though more so from the edges if slightly flattened. The name *M. angustifolia* Bory was first given to this Australian plant, and although no authentic holdfast occurs with the type specimen, there can be little doubt about the application of this name.

Macrocyrtis angustifolia in southern Australia is similar to *M. integrifolia* on the west coast of North and South America in its habitat and in the general nature of the holdfast. In both species the holdfast is formed of rhizomatous branches, but whereas these are terete or only slightly flattened (4–10 mm. wide) in *M. angustifolia*, they are strikingly flattened and 10–25 mm. wide in *M. integrifolia*. (Occasionally they may be only slightly flattened when young, but the haptera are still confined to two sides.) Living holdfasts of these two species are quite distinct, and no herbarium material showing intermediate stages has been seen. The rhizomatous branches originate by the base of the stipe becoming prostrate, and the dichotomies are produced by splitting of the young blades into two; the rhizomatous branches themselves probably do not branch, but only produce the dichotomous haptera.

In Australia, *Macrocyrtis pyrifer* and *M. angustifolia* can usually be distinguished by the form of the terminal blade (pls. 1 and 2). This difference is much the same as that reported by Smith between *M. pyrifer* and *M. integrifolia* on the Monterey Peninsula. The blades of *M. angustifolia* are usually narrower and more linear than those of *M. pyrifer*. However, in view of the known variation in the frond characters in the genus, separation of the Australian species on the terminal blade probably breaks down in some localities, and holdfasts remain the only character that can be used safely.

The type specimens of *Macrocyrtis angustifolia* and *M. integrifolia* have no holdfasts, and the latter is a poor specimen with no terminal blade. Thus the concept of these two species used in this paper is established on association rather than on objective fact. However, the concept of *M. integrifolia* as a plant with broad, flattened, ligulate rhizomatous holdfasts has been well established by Howe, Setchell, Smith, and others, and the fronds of the type specimen, from Valparaiso, are very similar to numerous other specimens from this locality. (I have seen good holdfasts from this locality in various herbaria.) Similarly it seems reasonable to associate *M. angustifolia* with the Australian plant, with relatively narrow fronds and a narrowly falcate terminal blade, since *M. pyrifer* from Tasmania usually has much broader fronds and a broadly falcate terminal blade. However, the variation and unreliability of frond characters has been emphasized elsewhere in this study.

Since holdfasts are lacking in the majority of herbarium specimens, these cannot

be determined specifically unless they come from an area where it is known that only one species occurs, or unless other characters have been shown to hold good in that locality (e.g., terminal blade form on Monterey Peninsula and perhaps in southern Australia). Therefore, no attempt is made here to place many of the old names as synonyms of the three species.

The geographical distribution of each species is summarized under the taxonomic descriptions, but may well have to be modified in the future as more attention is given to holdfast characters.

Extremely few specimens have been seen in the herbaria visited which do not agree well with the specific concepts expressed below. The only doubtful cases consist of very young and immature holdfasts, and as such cannot be relied upon. Annotation labels have been placed on many specimens in various herbaria by the writer, but here the known distribution of the species is summarized rather than attempting to list all specimens examined.

KEY TO SPECIES OF MACROCYSTIS C. A. AGARDH

1. Mature holdfast consisting of a central, terete, erect axis (the base of the stipe) from which dichotomous haptera arise on all sides.....*M. pyrifer*
1. Mature holdfast consisting of rhizomatous branches, one to many in each holdfast, slightly to prominently flattened, producing dichotomous haptera on all sides or from the edges..... 2
 2. Rhizomatous branches terete or slightly flattened, 4-8(-10) mm. across, producing haptera on all sides or sometimes mainly from the sides.....*M. angustifolia*
 2. Rhizomatous branches usually strongly flattened, (10-)12-25 mm. broad, producing haptera only from the edges.....*M. integrifolia*

Macrocystis pyrifer (Linnaeus) C. A. Agardh

(Pls. 1, 3, and 4)

Macrocystis pyrifer (Linnaeus) C. A. Agardh, 1820, p. 47. Skottsberg, 1907, pp. 80-136. Howe, 1914, p. 64, pls. 14B, 23, and 24. Setchell, 1932, pp. 445-461, pls. 39-47. Setchell and Gardner, 1925, p. 627, pls. 64, 65.

Fucus pyriferus Linnaeus, 1771, p. 311.

Plant (sporophyte) to 60 m. or more long. Holdfast conical, to 80 cm. high and as much across, composed of long, densely entangled, dichotomous haptera, arising on all sides from the base of the terete stipe. Stipe 3-6 times dichotomously divided shortly above the holdfast, branches terete to somewhat flattened. Terminal blade of each branch usually broadly falcate, with 8-20 young lateral blades in progressive stages of differentiation by splitting from base to apex, but with considerable variation. Length of terminal blade (including all partly split segments) 1-5 times its breadth. Mature lateral blades lanceolate, smooth to rugose, with denticulate margins, up to 100 cm. long and 15 cm. (or more) wide. Base of blades stipitate, with an elongate to pyriform or even spherical vesicle. Blade and vesicle characters very variable on the same plant and among different plants.

Habitat.—Usually forming extensive beds in deep water (20-120 or even 200 ft. deep). Drifting plants common in ocean currents of the cold temperate and subantarctic regions. The Tasmanian plants are somewhat unusual in that on the shoreward side of the beds they are attached in only a few feet of water.

Geographical distribution.—Circum-subantarctic, on most subantarctic islands, between latitudes 40°S and 60°S. In South America, extending up the west coast to about Callao, Peru, under the influence of the cold Humboldt current; on the east coast, not known attached farther north than about latitude 50°S, but drifting specimens occur as far north as the Río de la Plata. In North America, from about Magdalena Bay on the west coast of Baja California to the Monterey

Peninsula. In Australia, on the east and southeast coasts of Tasmania, possibly elsewhere on Tasmania. In New Zealand, mainly on the east and south coasts of the South Island and near Wellington in the North Island.

Macrocyttis pyrifera grows within a wide temperature range, from close to zero in the subantarctic in winter to about 18°C in California in summer.

Macrocyttis angustifolia Bory

(Pls. 2, 5, and 6)

Macrocyttis angustifolia Bory, 1826a, p. 10; 1826b, pl. 8.

Plant (sporophyte) to 6 (-10) m. long. Holdfast to 30 cm. high and as much across, composed of terete or slightly flattened, irregular, rhizomatous branches 4-8 (-10) mm. across with dichotomous haptera arising on all sides but more so along the lateral margins. Haptera and rhizomatous branches forming a compact, intertangled, conical mass, with the rhizomatous branches in the upper part. Stipes with 1-3 dichotomies, several arising from each holdfast. Terminal blade usually narrowly falcate, with 2-8 young segments in progressive stages of differentiation. Length of terminal blade 6-10 times its breadth. Mature lateral blades linear-lanceolate, rugose, with denticulate margins, up to 50 cm. long and 2-5 cm. broad, with a basal, pyriform to very elongate (4 cm. long and 3 cm. wide to 20 cm. long and 1 cm. wide) vesicle.

Habitat.—From just above extreme low water to about 20 feet below, usually forming a belt along the coast, occasionally forming small beds in shallow water.

Geographical distribution.—In Australia, from Robe in South Australia eastward to Walkerville in Victoria; possibly slightly east and west of this range and in Tasmania. In South Africa, on the southwestern coast of the Cape Province, from Olifants River (?) in the north to Cape Point in the south.

Bory (1826, p. 10) recorded *Macrocyttis angustifolia* from Valparaiso, but his specimens probably did not possess holdfasts. Areschoug (1883, p. 22) also recorded it from Valparaiso, but Setchell in unpublished notes in the Herbarium of the University of California, states that specimens of Areschoug "from Valparaiso are exactly the same as our specimens from shore pools at Pacific Grove—with broad rhizomes etc."—that is, they are *M. integrifolia*. Postels and Ruprecht (1840, pl. 5) also figure a Chilean plant as *M. angustifolia*, but the rhizome and general appearance of the plant in their figure appear fairly typical of *M. integrifolia*. It seems likely that *M. angustifolia* does not occur in South America.

The South African material I have seen consists of 6 or 7 fully mature holdfasts in the collection of Professor Papenfuss, odd specimens in various herbaria, and several preserved fragments of holdfasts sent by Professor W. E. Isaac. All this material is very similar to the Australian *Macrocyttis angustifolia* and quite distinct from *M. integrifolia* as seen on the California coast and in various herbaria. Professor Isaac, however, in a personal communication, states that "in a limited amount of material definite, broader, flattened, more or less strap-like rhizomatous branches have been found, very definitely recalling *M. integrifolia*." These may cause modification of our concept of *M. angustifolia*, but the bulk of the South African species both agrees well with the Australian and is quite distinct from American *M. integrifolia*. Professor Isaac's forthcoming paper on South African *Macrocyttis* should clarify the matter.

Macrocyttis angustifolia occurs within a temperature range of 8°-14°C in Australia and 12°-16°C in South Africa (monthly averages).

Macrocystis integrifolia Bory

(Pls. 7 and 8)

Macrocystis integrifolia Bory, 1826a, p. 10; 1826b, pl. 6. Howe, 1914, p. 60, pl. 18B, 19-22. Setchell and Gardner, 1925, p. 628, pl. 62. Setchell, 1932, pp. 445-461, pls. 33-38.

Plant (sporophyte) to 10 (-25) m. tall. Holdfast composed of one or more flattened, often creeping, subligulate, irregularly dichotomous rhizomatous branches, (10-) 12-20 (-25) mm. across, with numerous dichotomous haptera arising along both lateral margins. The stipe with one to several dichotomies. Terminal blades varying from narrowly falcate with 3-6 differentiating blades to broadly falcate with up to 20 differentiating blades. Mature lateral blades lanceolate, smooth to rugose, with entire to denticulate margins, to 80 cm. long and 2-10 (-16) cm. broad. Vesicles narrowly to broadly pyriform.

Habitat.—From just above low water to 20 feet below, usually as a relatively narrow belt along the coast, but forming extensive beds around Vancouver Island and possibly elsewhere.

Geographical distribution.—In South America, from Callao (Peru) southward to Valparaiso (southern limit doubtful). In North America, from the Monterey Peninsula northward to Alaska.

Field observations on *Macrocystis integrifolia* in South America are needed. A few young plants of the Coker collection described by Howe (1914, p. 62), seen in the New York Botanical Garden Herbarium, are unusual in having rhizomatous holdfasts less flattened than is usual, approaching *M. angustifolia*.

Macrocystis integrifolia grows within a temperature range of about 15-19°C (possibly lower) in South America and 5-15°C in North America.

SUMMARY

Three species of *Macrocystis* can be distinguished by the nature of the holdfasts in the mature plants. Frond characters, however, appear to be so variable as to be useless for specific segregation. In *M. pyrifer* (L.) Agardh, the holdfast consists of dichotomous haptera arising from all sides of the base of the erect stipe. In other species, the holdfast is composed of rhizomatous branches emitting haptera; *M. integrifolia* Bory (from the west coasts of North and South America) has strongly flattened rhizomatous branches, whereas those in *M. angustifolia* Bory (from southern Australia and South Africa) are terete or only slightly flattened. Because of the uncertainty as to the source of the type specimen of *M. pyrifer*, and the inadequacy of the type specimen (since it has no holdfast), the generally held concept of *M. pyrifer* is retained. Therefore the South African plant should probably be referred to *M. angustifolia* Bory, since it possesses the type of holdfast that seems to be characteristic of this species, and not to *M. pyrifer* as has been the custom previously.

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Terminal blade of *Macrocyctis pyrifera* from Port Arthur, Tasmania.
Approximately $\frac{2}{3}$ natural size.



Terminal blade of *Macroeystis angustifolia* from Robe, South Australia.
Approximately $\frac{1}{3}$ natural size.