No. 4.

REPORTS ON THE MARINE ALGÆ OF CEYLON.

No. I.—ECOLOGICAL AND SYSTEMATIC STUDIES OF THE CEYLON SPECIES OF CAULERPA.

By NILS SVEDELIUS, Ph. D.,
Docent in Botany at the University of Uppsala.

I.—INTRODUCTION.

The investigation of the marine flora of Ceylon, of which this is the first part published, was carried out by myself during the years 1902 and 1903 with the help of a grant from the Regnell Botanical Travelling Scholarship at the University of Uppsala. My stay in the island lasted, with a short interruption, from November, 1902, to August, 1903, and for the greater part of the time I stopped at Galle, on the south coast, which place showed itself to be the most convenient centre for algal studies in Ceylon. Thus, here are to be found close under the ramparts one of the greatest coral reefs in Ceylon, which together with the rocks adjacent offers a rich marine flora living under partly varying external conditions, and at the same time a rich material for studies in various branches of algology. Here, too, I had the great advantage, through the courtesy of the Ceylon Government, of being allowed to carry on my investigations in the newly established Ceylon Marine Laboratory, by which my studies were greatly facilitated. It is with great pleasure that I seize this opportunity of expressing my sincere thanks to Mr. James Hornell, F.L.S., Marine Biologist to the Ceylon Government and Inspector of Pearl Banks, for the never-failing interest he showed and the great assistance he afforded me in the prosecution of all my algal investigations in Ceylon.

After making myself tolerably familiar with the Ceylon marine flora within a limited district, I extended my knowledge of the algal vegetation by journeys along the coast. So I visited Weligama, Matara, Dondra Head, and Tangalla, in the south; Gintota, Ambalangoda, Kosgoda, Bentota, Beruwala, Colombo, and Negombo, in the west. The marine vegetation in the north of Ceylon is known to me by studies at and excursions about Jaffna and by visits to Paumben on the Island of Rameswaram. This little island does not belong to Ceylon, but to India; its situation, however, since it bounds the Gulf of Mannar in the north, justifies it in being included in the Ceylon marine flora district. The vegetation of the east of Ceylon is known to me through a lengthy stay at Trincomalee, on the east coast. Naturally, it was predominantly the littoral flora that was the object of my studies. As far as was possible for me I tried, by dredging, to get to know the sub-littoral vegetation; but my knowledge of it is unfortunately rather fragmentary, since dredging required a much more complicated apparatus than was at my disposal. Dredging, moreover, is exceedingly difficult to carry out on the open Ceylon coasts with their often difficult bottoms, the more so as the outrigger canoes of the natives are too narrow a craft for such work, which requires broader and more roomy boats. At smaller depths one can conveniently make use of native divers, but the yield from this source is invariably poor. My knowledge of the sub-littoral flora is thus rather fragmentary, and the best material I got from deeper water came from the pearl

banks in the Gulf of Mannar, and for that I am also indebted to Mr. HORNELL, who collected it during his official journeys for the study of pearl oysters.

Important sources for studies in the marine flora of Ceylon are the collections of HARVEY and FERGUSON. W. H. HARVEY stayed in Ceylon from September to December, 1853, and visited Trincomalee, Weligama, and Galle. Of his collections, which are preserved in Trinity College, Dublin, there are duplicates in the collections of the Royal Riksmuseum in Stockholm and in the Algal Herbarium of J. G. AGARDH in Lund. The rich collections of marine algæ made by W. FERGUSON are preserved in the British Museum, but duplicates of them are also in the Herbarium at Peradeniya and in the Herbarium of J. G. AGARDH in Lund. Through the courtesy of Dr. J. C. WILLIS, Director of the Botanic Gardens, Ceylon, the FERGUSON collections in the Peradeniya Herbarium were placed at my disposal at Uppsala, and this considerably assisted me in my studies. I am deeply indebted to Dr. WILLIS for this material help. From the Botanical Museum of Copenhagen and from the Botanical Department of the Royal Riksmuseum in Stockholm I was also allowed to borrow rich collections of Caulerpas, which were kindly lent me as material for comparison, and for which I here beg to thank the Directors of those Institutions, Professor E. WARMING and Professor C. A. M. LINDMAN. Finally, I beg to express my thanks to Professors O. NORDSTEDT, B. JÖNSSON, and S. MURBECK in Lund for their kind assistance during my studies in J. G. AGARDH'S valuable Algal Herbarium in the same town.

The extent of my material has forced me to publish my studies in several parts, and if I begin with *Caulerpa* it is because the plants of this genus, interesting from so many different points of view, have hitherto been studied so little in their natural state from an ecological point of view—*i.e.*, their biology. Hence it seemed to me that a real gap in our knowledge of these interesting plants remained to be filled, and that this should be done as soon as possible. It is clear that a study of this nature introduces such difficult questions as the relationship and variation of the species, their geographical distribution, and the like. To try to give an account of the Ceylon Caulerpas from these points of view is the aim of the present essay.

Uppsala, April, 1906.

II.—ON THE MODE OF LIFE OF THE CAULERPAS.

The Relation between Habitat and Organization.—Do Caulerpas show any Examples of Adaptation?

1.—DO ALL CAULERPAS GROW UNDER SIMILAR EXTERNAL CONDITIONS?

Concerning the ecology of the Caulerpas, there are in botanical literature very few, indeed practically no reports. This may be chiefly attributed to the fact that so many of those who have studied the tropical algæ had no opportunity themselves of observing them in nature, but examined them exclusively from material collected by others. Thus, for instance, C. A. AGARDH and J. G. AGARDH, who were the first to give a detailed monographical account of the genus *Caulerpa*, had themselves never collected or even seen any living Caulerpas.

On the other hand also, the algologists who, as HARVEY, had themselves travelled and collected much, only devoted themselves casually to the observation of the habitats of the algæ, of which, as a rule, only short notices were communicated.

Of those who, more recently, have dealt with the Caulerpas monographically, Madame WEBER v. BOSSE and Professor REINKE, only the former had collected her material herself, during travels in the Tropics; but still it is remarkable how entirely her great work, "Monographie des Caulerpes," is lacking in information about the habitats, vertical distribution, &c., of the different species. Hence, too, it is fully explicable that Professor REINKE, in his discussion of the Caulerpas, almost starts *a priori* from the assumption that they all live under practically quite similar circumstances. Thus, in speaking of the problem of the surprising diversity of the organisms ("Ueber Caulerpa," pp. 55, 88), he mentions

precisely the genus *Caulerpa* as an example of a large genus with some 50 species that offer considerable dissimilarities, but which nevertheless live among identical external conditions. The differences between the species are therefore not to be considered as due to adaptations, and in this he finds a support for his theory of exclusively inner causes, "determinants," for the motley multitude of the organisms. As a kind of confirmation of how this conception of the independence of external conditions among the variable Caulerpas prevails in literature, we may mention what Madame WEBER v. BOSSE in a later work ("Etudes sur les Algues de l'Archipel Malaisien," p.128) has uttered in connection with the question about the vegetative propagation of these plants: "La facilité avec laquelle les Caulerpes se multiplient végétativement et *varient sous des influences qui échappent à notre perspicacité** est à mon sens indice de plus qu'une reproduction sexuée ou par spores leur fait défaut."

OLTMANNS however rightly points out (in "Morphologie und Biologie der Algen," I., p. 312) that in this matter we must, for the present, bide our time until the different species have been studied in detail in their natural localities, as well as the external factors that affect them there.

That Caulerpas actually live under very different conditions can already be concluded from various notices in the literature of the group. Thus, for instance, the only European species, *C. prolifera*, which was almost exclusively the form that was the object of detailed investigations and which has therefore been the physiological *Caulerpa par préférence* and has been made the type for the whole genus, is in the Mediterranean apparently a pronounced still-water form, which even if it can occur at the surface (0·5 metre BERTHOLD) yet seems to prefer deeper localities down to a depth of about 15 m.† That it lives under the same conditions in the West Indies follows from COLLINS's note (in "The Algæ of Jamaica," p. 245), that it is not to be found at Jamaica except washed ashore. On the other hand, there are notices in literature about other Caulerpas, which tell us that they live on rocks amongst corals or also in pools; of others, again, that they live in sand and mud, often at no considerable depth (cf. for instance, the above mentioned paper of COLLINS; REINBOLDS; the Marine Algæ in "The Flora of Koh Chang"; A. VICKERS' "Contributions à la Flore algologique des Canaries" and "Liste des Algues marines de la Barbade," &c.).

Therefore, to judge from certain statements in the literature, the Caulerpas do not live under such quite identical external conditions as is commonly supposed. And that the Ceylon species of *Caulerpa* occur to some extent under greatly different external conditions, and that this, in its turn corresponds with evident differences in organization, I hope to show in the following pages.

In examining whether, among a group of plants, the different forms or species really show examples of adaptations to their surroundings, or to employ a term first used by DETTO, they are ecologisms ("Okologismen"), we can proceed in different ways. Since, just as in the following case, direct experiments were out of the question, the comparative method is the only one which analytic ecology can adopt. We can, then, compare either widely different species, *i.e.*, such as have different characters of organization ("Organisations-Merkmale" to use NÄGELI v. WETTSTEIN'S expression), but which still live amid similar surroundings, in order to examine whether, besides these characters, others of similar kind (*i.e.* adaptations to the similar surroundings) occur; or, following DETTO, examine whether they may be examples of ecological convergence (DETTO, *loc. cit.*, p. 146). But we can also go to work in another way; we may compare one species, which occurs very plentifully in one district in many forms and amid different surroundings, in order to study the changes it undergoes in the different situations and endeavour to find out whether these may be considered as adaptations to environment.

Of the some 20 species of *Caulerpa* that I found in Ceylon, some are very rare and to be met with in only few specimens; others, it is true, have very limited distribution, but show abundant local occurrence; some, finally, are very widely distributed, and occur in plentiful closely related forms which are hard to distinguish. To the very rare species which are only found in scanty specimens

* Italicized by the author of the present paper.

† FALKENBERG mentions *C. prolifera* in the Gulf of Naples at a depth of from 2-15m. Cf. also A. VICKERS "Contribution à la Flore algologique es Cdanaries," p. 30.

belong, for instance, *C. scalpelliformis*, *Freycinetii*, *cupressoides*, *Fergusonii*. In abundant individual occurrence, but with very limited distribution, we have *C. verticillata* and *lætevirens*. Lastly, to the commonest and most widely distributed belong *C. clavifera*, *uvifera*, *peltata*, *imbricata*, and others; in a word, all those species belonging to the very critical *racemosa group*, according to WEBER v. BOSSE's definition, a variable group very difficult to define.

If we compare the different situations in which the Ceylon species of *Caulerpa* grow from the point of view of the character of the substratum, we shall find in a preponderating number of cases that it consists of firm rocky or coral ground. But very commonly, too, *Caulerpa* grows on soft bottom, in sand or coarse gravel formed by decomposition products of the reefs, remains of corals and lithothamnia, or again in soft mud carried out to sea by rivers and streams.

2.—DIFFERENT ECOLOGICAL TYPES AS DISTINGUISHED BY VARYING DEVELOPMENTS OF THEIR ROOT-SYSTEM.

(A.) *C. verticillata type.*

Do the Caulerpas show any differences in their organization and mode of growth upon the different bottoms?

Let us first examine *C. verticillata* (fig. 1), which I observed at the mouth of a river on rocks partially and at times, during the south-west monsoon, entirely covered by sand and mud carried out to sea, as was the case at Galle. The tufts grow in very thick masses which all arise from more or less deep growing axes, now horizontally (fig. 1*a*), now obliquely growing upward (fig. 1*b*), and which higher up form side axes which grow out horizontally. Evidently this mode of growth is very favourable to a *Caulerpa* growing in localities exposed to the danger of being covered by sand, and this whole mode of growth is quite analogous with that of the dune grasses or certain bog mosses, which are characterized by a continuous succession of dyings-off in the basal parts in proportion as they sink deeper down. This comparison, first suggested by REINKE, is really very striking, and is strengthened by the fact that down in the mud we find remains of verticil branches which have been killed and buried in the sand.

Through the stimulus to upward growth which the over-sanding exercises, this plant can always keep its assimilation branches in the light where they stick up out of the mud and wave to and fro in the swell. Thus *Caulerpa verticillata* seems to show, in its system of shoots, an example of an organization adapted to the surroundings in which it lives. The information about the situations wherein this plant lives in other countries is very scanty. Both JOHS. SCHMIDT ("Flora of Koh Chang," IV., p. 104) and COLLINS ("Algæ of Jamaica" p. 245) only mention that it grows on coral reefs without any further specification.

Mlle. VICKERS ("Liste des Algues marines de la Barbade," p. 57) only says, "Flaques, abritées, à basse mer." Remarkable, on the other hand, is COLLINS's note on the *f. charoides*, which is closely related to the main species, *C. verticillata*. He says of it (*loc. cit.*, p. 245) that it grows "in soft mud near Mangrove swamp," consequently in localities to some extent similar to those where *C. verticillata* occurs at Galle. But if, in other respects, there can be discovered any analogies in the formation of the shoots, cannot of course be determined as far as this form is concerned, any more than is the case with the other related Caulerpas belonging to the *Vaucherioideæ*- and the *Charoideæ*-group, all of which are distinguished by finer and weaker shoot systems than are to be found in other Caulerpas. In *C. verticillata*, therefore, we have found a type of *Caulerpa* which grows in soft, muddy bottom, where the danger of oversanding is present, and I have not seen another *Caulerpa*-species in Ceylon belonging to the same biological group, nor do any other Caulerpas occur together with *C. verticillata* in the localities where it grows.

(B.) *Sand Caulerpas.*

Another type of the Caulerpas that grow in a movable substratum is represented by such species as *C. Freycinetii*, *cupressoides*, *Lessonii*, and *Fergusonii*. The figure of *C. Lessonii* (fig. 11) gives us a good idea of this rhizome type, which seems to be rather common among the Caulerpas and of which

REINKE has figured several, as, for instance, *C. flagelliformis* (REINKE, *loc. cit.*, fig. 10), *prolifera* (fig. 11), *Freycinetii* (fig. 38), *paspaloides* (fig. 52), and others. The characteristic of these species is that the rhizome is rather coarse, sparsely branched, grows more or less deep in the sand, out of which only the assimilation branches stick up in long rows, with small or great intervals between them. Of *C. Freycinetii* we consequently only see as it were ball-shaped bundles of assimilation branches entangled together. In Ceylon this type of *Caulerpa* is only met with in the north, around Adam's Bridge and the islands about Jaffna, where the shore is always sandy. On the coral reefs and rocky shores of the south-west, this type is scarcely to be met with. To judge from certain indications, this *Caulerpa* type consists chiefly of still-water forms, which therefore often prefer somewhat deeply situated habitats. Thus *C. Lessonii* has only been observed on the pearl banks at a depth of several metres. *C. Fergusonii*, too, does not belong to the upper littoral zone, either. *C. Freycinetii* has been collected by me in the upper littoral zone, it is true, but since it only appears there occasionally we are tempted to assume that its main distribution lies deeper down. That this is not a mere chance guess, and that it has some justification is supported by the fact that JOHS. SCHMIDT collected *C. Freycinetii* in the Gulf of Siam at no depth less than 2 metres, and as for *C. cupressoides* we are told that it occurs in such localities as lagoons (BÖRGESEN), which points to its being a still-water form.

Besides being distinguished by its mode of growth—*i.e.*, half hidden in the sand—this type is distinguished also by its root branchlets being very long and especially very closely and finely branched, and between the fine root branches the particles of sand are pressed so tight that large lumps accompany the plant when it is pulled up from the bottom. REINKE has described this type and given several illustrations of it in his paper (*loc. cit.* figs. 20, 38, 42, 52, 73). As ecological adaptations to the conditions of the life of these plants in the sand, we may consider their long-creeping rhizome axis and especially the development of their root system. Such repeated branching in a great number of fine filaments which fasten themselves firmly to the grains of sand may be taken as an excellent anchoring apparatus for a plant living on a sandy bottom. In this type there is no organization of the shoots to neutralize the danger of being oversanded—a danger which is not to be feared in such places as those where this plant is to be found. Approximating to this type are such species as *C. crassifolia*, *C. dichotoma* (fig. 23), *C. uvifera* (fig. 15), and others, which if not invariably, at least most generally, have a mode of growth analogous with that of the sand Caulerpas just described.

(C.) *Rock and Coral Caulerpas.*

The most numerous Caulerpas belong to a group which grows preferably on stones, corals, and in general, fixed substrata. But here the conditions may be of most dissimilar nature, owing to the different degrees of exposure to the swell, to the other local conditions affecting vegetation, to the presence of Actinians and living corals, and so forth.

(*a*) *C. lætevirens type.*

Among these rock Caulerpas, *C. lætevirens f. laxa* (fig. 19) takes a unique position inasmuch as this species grows by preference in exposed localities, where it constitutes the sole vegetation (forming a special *C. lætevirens* association), and covers large areas, as at Galle, on the boulders north of Victoria Park.

C. lætevirens f. laxa there forms a typical algal association of a kind that has been described from northern seas, and that has been called "böljslagsformationer" by GRAN ("wave-beat formations" is the literal rendering), in "Kristianiafjordens algflora," p. 9. Such formations or associations are, for instance, the *Nemalion* formation of the west coast of Sweden (KJELLMAN, "Algenreg.und Algenformationen," p.11), the *Bangia-Urospora* association of the Faeröese coasts (BÖRGESEN, "The Algæ-Vegetation of the Faeröese coasts," p. 719) and the *Gobia-Dictyosiphon* formation from the Baltic (SVEDELIUS, "Ostersjöns Hafsalgflora," p. 29). What characterises all these formations* is that they are very exposed to the swell and hence are in continual movement, waving to and fro, covered one moment, free the next, in never-ceasing alternation.

* This use of the term "formation" is analogous with the sense in which it is employed in Geology.—ED.

Such algæ must, of course, be firmly fixed to their substratum. Whereas the European forms of this type are characterized by smaller or greater adhesive discs, *C. lætevirens* has quite a different method of fastening to the rock. In this we find, as in the other Caulerpas, a creeping rhizome, but here much more developed than in the species in general. The assimilation axes, on the other hand, are few and placed at comparatively long intervals, and hence the root system, since it develops numerous fine root branches that fasten themselves to the smallest crevices, corners, or irregularities in the rock, becomes in these plants, in proportion to the assimilation system, much greater than in the other *Caulerpa* species. To this must be added—and this seems to me by no means the least characteristic feature of this species—that the assimilation branchlets or pinnules have a strong tendency to grow out into root-forming branches (fig. 19), whereby the whole plant is still more firmly fastened to the rock. That assimilating shoot branches change their character, become procumbent and take root, is, as WEBER v. BOSSE has pointed out ("Monographie des Caulerpes," p. 249), not a rare phenomenon. I have given a picture of such a case in *C. Fergusonii* (fig. 51 a, b). But in *C. lætevirens* it is the branchlets or pinnules (fig. 19, f–i) that grow out into haptera-like rhizomes, and this has become very common in this particular species. As for the shoot system in general, we refer to the description of this species in the special section of the present work. That all this organization is highly advantageous to a species exposed to strong swells, and to the resultant danger of coming loose, is evident; and *C. lætevirens f. laxa* must therefore indisputably be considered as an ecological adaptation to such surroundings.

Very remarkable is the changed appearance this plant assumes (figs. 21 and 22) when it grows in somewhat deeper localities not so directly exposed to swells. I have called this biological form *f. cæspitosa*. It becomes tufted owing to the assimilation branches growing very close together. They are moreover shorter, coarser, and especially more rigid (fig. 22), so that they cannot wave to and fro in the water. To this contributes also the fact that this *f. cæspitosa* grows squeezed between other tufted algæ. Its rhizome and root system are normally developed, not stronger than in the other Caulerpas, and the branchlets, moreover, show no tendency to grow out into root-taking branches. The small, short assimilation-branches are not so pliant in *f. cæspitosa* as in *f. laxa*, but more rigid. They are often clavately swollen at the tops, or sometimes flattened. In the last-named case torsion often occurs (fig. 22, b, c), so that the flattened sides are turned up to the light. It is evident that both the clavate form and the torsions of the branchlets produce the same effect, viz., as great a number of chloroplasts as possible are exposed to the light falling from above. It is interesting that this happens only in *f. cæspitosa*, the rigid form with the stiffer branches. The *f. laxa*, on the other hand, in which the branches wave to and fro, thereby receiving the light from every side, shows no such peculiarities in the organization and position of the branchlets. In this, too, both these forms show differences in their organization that are to be looked upon as ecological adaptations.

We shall reach a similar conclusion if we compare *C. lætevirens* with *C. dichotoma* (figs. 23, 24). As will be pointed out in the more detailed description of this species, it is closely allied to *C. lætevirens*, from which it differs chiefly in its broad flattened dichotomous assimilation branches, commonly arranged in two rows along the main axis. This organization means a considerable increase in the assimilating surface, but at the same time it entails a number of disadvantages to an alga exposed to strong swells. *C. dichotoma* is consequently not found in the upper littoral region in places which are so characteristic for *C. lætevirens*, but at Weligama it grows at a depth of about 2 metres on sand. The horizontal axis and the root system also corresponds far more in coarseness with the sand Caulerpas than with the fine creeping axis of *C. lætevirens*.

Also in *C. dichotoma* the easy transition from assimilation-branches to haptera is entirely lacking, the reverse of the case in *C. lætevirens*, wherein this is so closely connected with its mode of growth. Hence, we see that the characters of these related species are undoubtedly in complete correspondence with their mode of growth and with the closely connected surroundings.

It is remarkable that *C. lætevirens* seems to live under similar conditions on the coast of Western Australia as in Ceylon. Thus HARVEY says (in "Phycologia Australica," I., Pl. XXX.) about *C. cylindracea*, SOND. (= *C. lætevirens f. cylindracea* (SOND) WEBER v. BOSSE): "This plant is excessively common on all the reefs at Rottnest Island, growing in shallow, exposed tidepools, as well as in sheltered spots below low-water mark, and it varies much in luxuriance according to the locality."

From these remarks it follows in any case that *C. lætevirens* in Australia forms a special association with its environment, especially in exposed localities, but that it also grows in deeper and more sheltered places. And, just as at Galle, the different forms also seem to be dependent on the different localities. In what way these make their influence felt HARVEY does not mention. He only speaks in a few words of the variation of *C. cylindracea* "in luxuriance according to the locality."

(*b*) *The remaining rock and coral Caulerpas.*

If, now, *C. lætevirens f. laxa* is a pronounced, even though rare, example of a rock *Caulerpa* growing in strongly exposed localities where no other alga happens to occur, on the other hand we find a preponderant number of other species also growing on rocks, but in more sheltered places, where they occur in company with other algæ, and especially with living corals and small Actinians.* I have frequently observed that amongst living corals and Actinians the Caulerpas must be considered as a characteristic occurrence. With their long rhizomes they creep among the Actinians, and only the assimilation branches are visible where they shoot up between the animal colonies. Such is the case with several forms of *C. clavifera*, *nummularia*, &c. Especially noticeable is *C. longistipitata* (fig. 45) with its long rhizomes creeping on rocks and among other algæ, even if it does not occur on such strongly exposed localities as *C. lætevirens f. laxa*. All these have a root system without the very fine branching present in the sand Caulerpas; the root-branches, on the contrary, are fewer but coarser, and often as if flattened at the top where they are fastened to the stones. But that there is no hard and fast difference between such a root system and the one that occurs in the sand Caulerpas is best proved by the fact that the same species has now the one, and now the other, depending on the substratum. REINKE has already pointed this out (*loc. cit.*, p. 58).

3.—DIFFERENT ECOLOGICAL TYPES AS DISTINGUISHED BY THE VARYING DEVELOPMENT OF THEIR ASSIMILATION SYSTEM.

If, then, as we have already seen, there is a great difference in the root systems or adhesive organs in general, at least within certain *Caulerpa* groups, the difference is much greater in the assimilation branches and the shoot system. It is really with reference to this difference that REINKE ("Ueber Caulerpa," p. 67) seems to have been led to the opinion that the genus *Caulerpa* offers a special point of interest, because it shows that even under similar external conditions and with essentially similar inner organization, the external form can yet be variable: "Alle Caulerpen sind dem Lichtleben in Wasser angepasst: jede Art ist ein Spezialfall dieser Anpasung, und alle sind verschieden geformt. *Diese Verschiedenheit beruht aber nicht auf besondere Anpassungscharakteren.*† Die Assimilationsarbeit lässt sich bewerkstelligen eben so gut mit gleichartigen feinen Fäden der *C. fastigiata*, wie mit den breiten ungetheilten Blättern der *C. prolifera*, den grossen fiederspaltigen Blättern der *C. taxifolia* und den kleinen einfachen Blättern der *C. racemosa* und *Lycopodium*" . . . . and again we read: "Wer es liebt, auf die Unterscheidung von morphologischen und Anpassungsmerkmalen Werth zu legen, der wird daher die Speziescharaktere von *Caulerpa* sowhol zu den ersteren wie zu den letzteren rechnen müssen." But none the less REINKE has a feeling of the possibility that the Caulerpas may be, for all that, more or less adapted in their main functions to their surroundings, and he adduces as an example how a fine-leafed species—as *C. hypnoides* — has greater possibilities of profiting by and making the fullest use of the light in every situation than for instance a *C. taxifolia* or *C. prolifera*, and these advantages show themselves chiefly in moving water.

* These are chiefly Zoanthids.—ED.

† Italicised by the present author.

If we examine the assimilation system in the Ceylon Caulerpas, we shall find several different types and variations. They may be roughly divided into two groups, viz., such as have the assimilation system very strongly branched (always a system of short shoots, pinnules), and such as in their assimilation organs have a measure of correspondence with, or at least some outward resemblance to, the leaves of the higher plants. To the latter group belong such forms as *C. scalpelliformis* (fig. 2), *crassifolia*, *taxifolia* (figs. 4, 5), &c.; to the former such as *verticillata* (fig. 1), *clavifera* (fig. 13), *uvifera* (fig. 15), *lætevirens* (fig. 19), &c. But a division of this kind is of course incomplete and vague. For it could also be expressed in this way: the one group (the leafy one) is characterized by its assimilation branches being bilateral, the other by its axes being radial. But here it is to be observed that only the main axes are radial, the lateral axes or the short shoots may afterwards assume the most variable shapes. They, too, can be radial, *i. e.*, cylindrical as in *C. lætervirens f. laxa*, cylindrical with spherical point as in *C. loncistipitata* (fig. 45), *crassicaulis* (fig. 47), *clavifera*, *uvifera*, &c.: finally, disciformly flattened, as in *C. nummularia* (figs. 35, 36), *imbricata* (fig. 30), and others. The questions now arise whether in these various leaf and shoot forms we can see any adaptations to their different surroundings; whether one can be considered in any way more perfect than another, or whether they are all equally good for the purpose, and whether really the great variability is only to be ascribed to formative energy in the plant that escapes our direct observation. We will deal with these in that order.

(A).—*The bilateral leaf-like Caulerpas.*

It seems to me indisputable that the leaf-like flat Caulerpas are derived from radial forms as being the more primitive ones: that they are very closely related is shown already by such a species as *C. flagelliformis*, of which there are both radial and flattened forms, very similar to one another and often passing over from the one to the other. Such a fine leaf-like species as *C. prolifera* can even be transformed, as KLEMM has shown, into the cylindrical form, exactly in the same manner as several species of *Opuntia*.

A comparative examination of the assimilation axis of the bilateral species shows moreover that the bilateral axes are often radial at the base, and there form branchlets round the axis. This by no means rare case is illustrated in this work by *C. Lessonii* (fig. 11, the branches to the left of the picture), by *C. taxifolia f. tristichophylla* (fig. 5), and also by *C. dichotoma* (fig. 24, *a*) where some branches at the base show weak indications of radial arrangement. It is evident that by the lateral arrangement a surface increase has been gained, the advantage of which for the work of assimilation is self-evident. So far, as great an increase of surface as possible were desirable, provided no disadvantage were involved. But such is undoubtedly present: the large flattened leaf-like organ, without any special mechanical elements or tissues, runs a great danger of splitting if exposed to too violent a strain, in the form of ground-swell or the like. That *Caulerpa prolifera* is actually very susceptible to this, and cannot withstand a too turbulent sea follows very clearly from JANSE's notes ("Bewegun. d. Protoplasma von *Caulerpa prolifera*," p. 166) on broken Caulerpas in the Gulf of Naples after very stormy weather, which has stirred up even the quiet depths where *C. prolifera* lives. It is evident, therefore, that if such broad-leafed forms are to have any chance of living it must be in sheltered places, and, of course, especially at considerable depths that are not disturbed by heavy seas. In this respect how does the matter stand with the other leaf-like Caulerpas? It has already been pointed out above that *C. prolifera* is by preference a deep water form, both in the Mediterranean and in the West Indies. The same may be asserted of *C. scalpelliformis*. In the littoral zone I only found it once, at Paumben, and for the rest it is wanting in the littoral zone of Ceylon. As, however, it has been noted from the pearl banks in the Gulf of Mannar (E. S. BARTON, "List of Marine Algæ collected . . . . at Ceylon," p. 165), and has moreover been obtained by JOHS. SCHMIDT at as great a depth as 15 metres and more in the Gulf of Siam ("Koh Chang," IV., p. 104), and as it is mentioned by HARVEY ("Phycologia Australica," I., Pl. 17) as growing "a few feet below the low-water mark," we may consider ourselves justified in not counting *C. scalpelliformis* among the typical algæ belonging to the upper littoral zone, but as a Caulerpa which prefers somewhat deeper regions.

The same may be said of *C. crassifolia*. I only found it once in the littoral zone of Ceylon, and then in its deeper parts at a depth of about 2 m. On the other hand it does not seem to be rare on the pearlbanks in the Gulf of Mannar. No detailed information as to locality is present from other places. It is highly probable, by reason of its appearance in Ceylon, that this species also belongs to those which prefer somewhat deeper regions. On the other hand *C. crassifolia* is, even if evidently bilateral and provided with rather broad and flat main axes, so lobed that the danger of splitting is not really serious in this species, even if it grows in exposed places in the upper littoral zone. What is true of *C. crassifolia* is true also of *C. taxifolia* (figs. 4, 5) and its different forms. It avoids exposed localities when it grows in the upper littoral zone, where it is to be met with in pools. On the other hand, it is plentiful on the pearl banks in deeper water. COLLINS only knows this alga from Jamaica as "washed ashore." The deep-water form, *f.asplenioides* (fig. 4), has somewhat broader but shorter pinnules, directed straight outward, the surface form smaller but longer, and sickle formed branches bent upwards. Remarkable is HARVEY'S note on this species ('Phycologia australica,' III., Pl. 178): "There is fully as much difference among my Friendly Island specimens, between those collected in the quiet waters of the lagoon and those from the outer reef, as I find in those from opposite hemispheres."

HARVEY thus remarks in this species variations according to different situations, but without characterizing the nature of the changes.

An examination of the occurrence of *the larger bilateral Caulerpa* forms both in Ceylon and on other coasts, where anything is known of them, consequently shows that in any case they have *not* their main distribution in the littoral zone—even if isolated specimens occur there—but that this *must be located in deeper and quieter regions.*

(B).—*The radial Caulerpas—The Analogy between the C. clavifera-uvifera type and the C. nummularia-peltata type.*

Where do we find, on the other hand, the Caulerpas which have radial structure of their assimilation system in the form of short-branches ?

Of the *Caulerpa* species of Ceylon, besides the *C. verticillata* and *lætevirens* which have already been dealt with, we have in this group *C. longistipitata, sedoides, clavifera, uvifera, peltata, nummularia, parvula, imbricata*, and *Chemnitzia*. It should be observed at once that all these species occur in the littoral region, and several of them belong to the commonest algæ in the upper littoral region. Some species with wide distribution are also to be met with deeper down, and these show very instructive and interesting changes of form. More of this later on. A few species, as *C. longistipitata* and *C. sedoides*, have only been found in relatively very few places; but as JOHS. SCHMIDT ("Flora of Koh Chang," IV., p. 105) also mentions them only from the littoral region, they seem most probably to be at home in this region.

Under what conditions do these forms live, and can we see any adaptations to their surroundings in their organization ?

Let us first examine *C. clavifera* (fig. 13). In the special part the characteristic mode of growth of this species is dealt with. The form which is pictured in fig. 13 is a pronounced surface form, which at low water is often only laved by the waves. Its characteristic is its extended—almost flattened—mode of growth, which depends on the vertical axes being so short and having only a small number of side branchlets. When, at the same time, the root system and the horizontal axes are strongly developed, the whole plant is firmly fixed to the rock, while the small short vertical axis offers few points of attack to the swell. It is to be noted that as a rule no Caulerpas at all—with the possible exception of *lætevirens*—are ever met with in the littoral region in really strongly exposed localities, but *C. clavifera* can sometimes grow in places which, even if the sea there cannot be described as violent, are yet exposed to wear and tear of a kind. In such places we often come across *C. clavifera* and others with similar construction, as *C. nummularia* and others. It is rather remarkable that these Caulerpas are so often to be found among small living corals and small colony-forming Actinians. The horizontal axes creep amongst the Actinians

and fasten on to them. *C. clavifera* then often gets somewhat longer vertical axes, and the whole plant assumes an appearance more closely resembling TURNER's *Fucus clavifer*, Pl. 57, vol. I., and WEBER v. BOSSE's, fig. 4, Pl. XXXIII.

If it grows directly on the rock and more isolated, it appears as in fig. 13. That for such a pronounced littoral alga, which grows squeezed in between Actinians and corals, such a mode of growth offers certain advantages, seems evident to me. Partly because, as mentioned above, the surface exposed to the waves is relatively small compared with the well-developed adhesive system, partly because the exposure of the assimilation system—and this, I think, is worthy of special note—becomes under such circumstances the most favourable, since it is practically spread out in one level and thereby as many branchlets as possible are exposed to the light. That, for instance, the taller vertical axis with pronounced uviform shape, as *C. uvifera* (fig. 15), cannot be a suitable form amongst corals will easily be understood, for if these vertical axes are squeezed in between equally high corals, only the uppermost branchlets, that is the points alone, can be exposed. Therefore short axes with few side branchlets must be considered as especially suitable shapes for such habitats. The reduction in the assimilation system that results from the diminished number of branchlets is compensated by their being larger and coarser. It is also in such localities that we meet with forms with very large ball-shaped branchlets, KÜTZING's *Chauvinia macrophysa*.

These observations of mine concerning the occurrence and mode of growth of *C. clavifera* in Ceylon, correspond with Madame WEBER v. BOSSE's note on *C. clavifera f. macrophysa* ("Monographie des Caulerpes," p.362) where we read : "J'ai recueilli la plante sur des recifs de corail : la fronde de la *v. clavifera* était enclavée entre des morceaux de corail, les ramules s'étaient par conséquent tournés du côté de la lumière, s'étaient rapprochés du côté frontal de la fronde et en meme temps agrandis." This seems to indicate that the assimilation branches were all as in a level at the same time as they were enlarged.

I have therefore come to the conclusion, as a result both of my own observations and of such notices in botanical literature as the above, that *C. clavifera* may be characterized as the coral reef Caulerpa *par préférence*.

The changes *C. clavifera* undergoes when it grows deeper down can in general be characterized by the vertical axis, as well as the cylindrical parts of the assimilation branchlets, being lengthened. The *f. remota* (fig. 14), described by myself, is such a pronounced form from a deep pool. Its vertical axes are very lengthy, are not recumbent, nor root-taking. Between this and the surface form intermediate forms can be found. The *f. remota* as a form living in deep pools is never exposed to the tearing influence of the swell to the same extent as the main form. Its root system is relatively weaker, but the assimilation branchlets are longer, slenderer, and more pliable, so that when they wave to and fro they also can derive every benefit from the light.

That these various forms arise directly through the influence of light, so that, for instance, obscuration favours the lengthening of the axes, while bright or intense light causes shortening of the axis system, seems very probable. But this can only be determined by direct experiments. A comparative examination shows, in any case, that the one type is almost exclusively at home in the upper littoral region, the other in somewhat deeper localities. For analytical ecology, however, it is sufficient to state that both kinds of forms in this organization have certain advantages suitable to the different surroundings amid which they live, and can therefore with good cause be considered as adaptations or ecologisms.

This *C. clavifera* organization shows itself still more closely an ecological adaptation if we compare it with *C. uvifera*. In the special section I have dealt in more detail with the differences which exist in Ceylon between these two species. In this place I may call special attention to the fact that *C. uvifera* will be looked for in vain on the coral reefs of the south-west of Ceylon. It is this species however that seems to be the commonest in the north. At the present time I do not venture to decide whether this different distribution of the two forms is to be exclusively attributed to the different nature of the shores ; viz., that on the south-west and south coasts there occur only cliffs and rocks, which are favourable

to the growth of *clavifera*, whereas such formations are rare in the north. There the shores are more sandy, with very scanty vegetation in the upper parts of the littoral region, and with algal life beginning only a little further down. That *C. uvifera* is closely allied to the sand Caulerpas, I have already pointed out. Though it is chiefly the rhizomes and the root system in which this appears, yet even the assimilation axes point to its being predominantly a deep form. For the assimilation axes are much longer than in *C. clavifera*, and especially very thickly covered with branchlets, which show a firm cluster-shaped formation (fig. 15). That such an organization is very unsuited to exist amongst corals and Actinians has already been pointed out above; it would be equally unsuited to strongly exposed localities. Deeper down in sandy bottom, however, it has a more suitable habitat, and the long vertical axes wave to and fro in the currents so that the whole axis gets exposed to the light from every side. As JOHS. SCHMIDT (*loc. cit.*, IV., p. 105) also only found *uvifera* at a depth of from "1-2 fathoms water (coral sand)," the opinion I formed about this plant in Ceylon is strengthened: the opinion, namely, that it is a sand Caulerpa from somewhat deeper regions.

With respect to the variations of *C. uvifera* and their ecology I need not take up much space, since I have only collected *f. planiuscula* myself. It differs only in that its upper branches show a tendency to flattening out (fig. 16), while the vertical axes at the base have rather few side branchlets. This change seems to be favourable to the reception of light coming directly from above, but about the special habitats of this plant my notes unfortunately do not afford me any help. It occurs only in the north of Ceylon, with about the same distribution as the main species.

C. longistipitata (fig. 45) and *C. sedoides f. crassicaulis* (fig. 47) have a similar organization to that of *C. uvifera*. As far as *C. sedoides* is concerned, at least, the resemblance seems to apply also to its mode of growth, for at Weligama it grew inside the reef at a depth at low-water of about 2 metres together with *C. taxifolia* and *sertularioides*, anyhow not in the upper exposed part of the littoral region. At Matara it occurred in rock pools. It also seems capable of variation in the length of its shoot axis, some branches being very short (fig. 47), analogous with those in *C. clavifera*.

C. longistipitata, on the other hand, seems to show some analogies with *C. lætevirens* in its lengthy root system that creeps along the stones, and its long, slender, and weak assimilation branches. It occurs at Paumben in the upper littoral region, but not in any exposed places. Seeing that I only observed it in that place, I will not venture to express any opinion as to where this form is really at home, but JOHS. SCHMIDT (*loc. cit.*, IV., p. 105) also informs us that he only found it in the littoral region.

Of the remaining species that occur in the littoral region, *C. peltata*, *nummularia*, *parvula*, *imbricata*, and also *Chemnitzia* may be considered as a very uniform and closely related group, distinguished by all their short branchlets being more or less pronouncedly disciformly flattened.

Of these species *C. nummularia* (figs. 35, 36) occurs in about the same localities as *C. clavifera*, *i.e.*, in the upper littoral region, not rarely together with corals. The organization of the shoots is also quite analogous with that of *C. clavifera*. The branches are all recumbent, root-taking, and creep among corals and on stones. These branches are dorsi-ventral and form disciform assimilation branchlets on the upper side only. The whole plant resembles a matty tuft (fig. 36) with the assimilation system in one level. Thus we here find an organization quite analogous with the one we have already described in *C. clavifera* (fig. 13), and which is characterized by the relatively strongly developed root system in comparison with the shoot system, and by the shortening of the shoot axis, whereby the assimilation system is flattened out so that it receives the whole light vertically from above. *C. clavifera* and *C. nummularia* are both pronounced light algæ from the upper littoral region, growing in localities with frequent changes of water and often somewhat exposed to the swell. These analogies in the outward conditions of life correspond to pronounced resemblances in mode of growth. Therefore, too, these forms might with reason be characterized as ecological adaptations; they are, as DETTO says ("The orieder direkten Anpassung," p. 146) *examples of ecological convergence*.

What is true of *C. nummularia* is also true of *C. parvula* (fig. 43), which in its mode of growth and occurrence is quite analogous with *C. nummularia.*

In the same way as in the series with the ball-shaped branchlets, *C. clavifera* is a surface form, and the more long-branched *uvifera* is a deep form ; similarly, in the series with disciform assimilation branchlets, the surface form *C. nummularia* (fig. 36) has an analogous form in the relatively deep form *peltata* (figs. 31, 32, 33). The changes in form in the *nummularia-peltata* series are also quite analogous with those in the *clavifera-uvifera* series. *C. peltata* has long vertical branches with the side branchlets placed all round and their flattened assimilation discs obliquely directed upwards (figs. 31, 32, 33), whereas *C. nummularia* has recumbent axes with assimilation discs on the upper side only (fig. 35). It is evident that with this position the exposure of these branchlets to the light is the most favourable one for vertical axes when they have branchlets all round them, for horizontal ones when they have them dorsiventrally developed. That some transition forms with both radial and dorsiventral axes can be found (fig. 32) will be pointed out by me in the description of the different species.

Just as *uvifera* was predominantly a deep form, so too this *C. peltata* is only to be met with deeper down in rock pools and other places not too strongly exposed.

What applies to the different types of the *clavifera-uvifera* series as far as their advantages and disadvantages are concerned, applies also, of course, to the *nummularia-peltata* series. *Thus we see that between C. peltata* and *C. uvifera there is a similar ecological convergency to that between C. nummularia and C. clavifera.*

Finally, with regard to *C. imbricata* and *C. Chemnitzia*, the latter, in its organization, mode of growth and occurrence, corresponds exactly with *C. uvifera.* The differences are only of a morphological nature, and only apply to the form of the branchlets, *i. e., C. Chemnitzia* (fig. 27) has quite cylindrical branchlets at the base of the vertical axis. *C. Chemnitzia* is also, in accordance with its organization, a form which occurs by preference in still water deeper down often together with *C. uvifera.*

C. imbricata (figs. 37—42), on the other hand, is a species which seems to prefer the upper littoral region. It is as a rule closely tufted (fig. 37), which gives it a certain likeness to *C. nummularia.* It might be characterized as a *C. peltata* in which the branches have contracted, so that the vertical axes are very short as are also the branchlets, while they are almost pressed together, thus forming an almost continuous assimilation surface. The detailed description of the species will also show that there are certain transition forms between *C. imbricata* and *C. parvula.*

This *C. imbricata* grows on coral reefs together with *C. clavifera* and *C. nummularia*, but is far less frequent, and does not occur on strongly exposed parts. So, on the reef at Galle, this species was only to be met with on the more sheltered rocks below the Clippenberg Bastion and the Neptune Bastion. It is evident that the form points to a surface enlargement of the assimilation system, if we compare it with *C. nummularia* and *parvula*, since isolated branches grow up vertically and become covered with assimilation discs (figs. 41, 42). But this also involves greater danger of laceration, as the strain is increased. It seems, therefore, as if *C. imbricata* may be conceived as a variant of the *nummularia* type that has increased its assimilation system, and that occurs where the external circumstances do not stand in its way.

(C).—*C. sertularioides type.*

It follows from what has been said above that the bilateral *Caulerpa* forms in common are to be met with in deeper regions, whereas the radiate forms in general have their main distribution in the littoral region. Certain of the radiate species are replaced in the uppermost littoral zone by more or less dorsiventral species.

It is to be noted, however, that in the Ceylon marine flora a typically bilateral Caulerpa also occurs in the uppermost parts of the littoral region, viz., *C. sertularioides* (figs. 7-10). I have already pointed out above the advantages and disadvantages which are connected with the bilateral shoot form in general, which may be shortly characterized as follows :—the assimilation surface is extended, but this, on the other hand, is accompanied by an increased risk of laceration. As a matter of fact, all the bilateral

Ceylon *Caulerpa* forms are more or less lobed, even the deep water forms. Furthest in this respect goes *C. sertularioides*, which has very fine branchlets, whereby the whole shoot axis has the appearance of a feather (fig. 10), to which it owes its former name of "*plumaris*." Strictly speaking *C. sertularioides* is closely allied to the radiate forms in that its branchlets are cylindrical and subulate, and it need only develop these radially as in *f. Farlowi* or *C. Selago*, for the organization to be perfectly radial.

C. sertularioides occurs on the shores of Ceylon in a number of different forms. It is very common in the uppermost exposed littoral region on coral reefs and rocks in the south-west. It is often of low growth with the branches at the top as if chopped off sharp (*f. brevipes*, fig. 7). The branches are now very fine, now somewhat coarser and with coarser rhizomes. The latter seems to be the case especially on sandy bottom as at Jaffna. Sometimes it also seems able to form small tufts (fig. 8). It often grows, as we have said, in very exposed places, and the feather-like axes wave to and fro in the swell. It is clear that such fine subulate branches are very well adapted to a species with such a mode of growth. In this respect *C. sertularioides* corresponds with *C. lætevirens f. cylindracea*, of which it also reminds us in its mode of growth, even if it does not occur in such exposed places as the latter.

C. sertularioides also occurs in the deeper parts of the littoral region, as for instance at Weligama, from a depth of about 3 metres. Johs. Schmidt has also collected this species in 1-2 fathoms of water. In this case it has a somewhat different appearance (*f. longiseta*). It is longer, weaker, and not chopped off sharp at the top (fig. 10). I observed quite similar forms in dark cavities in coral masses on the reef at Galle, so that it seems very probable, in my opinion, that this lengthening of the axis in dark localities and its shortening in intensely bright must be attributed to the influence of light.

4.—On the Difference between Morphological and Adaptational Characters in Caulerpas.

It should follow from what has been said above that *Caulerpa* can scarcely, in contrast to other plants, lay claim to be able to show a multitude of variable types in which no correspondence can be traced between the outer form and the surroundings, which Reinke has presumed. As I think I have shown, several *Caulerpa* species, *e.g.*, *lætevirens*, are as evident ecologisms as one could wish, and different localities are characterized by different *Caulerpa* types.

The different localities are characterized by differences in the bottom (sandy bottom or rock), by different degrees of exposure to the swell, by different depths, and by different intensities of light—and all these differences in environment correspond with differences in organization. Thus, the sand Caulerpas (*C. Freycinetii*, *cupressoides*, *Lessonii*, *Fergusonii*, and others) are distinguished by their long creeping rhizomes with finely branched roots, whereas the coral and rock Caulerpas (*C. clavifera*, *nummularia*) are often far less elongated, and their root system consists of adhesive roots with rather few and short branches. Then we find that in more exposed localities—besides that the adhesive organs are more strongly developed—the assimilation axes approach the cylindrical, at the same time being very narrow, *i.e.*, offer the least possible opposition to the tearing power of the waves (*C. verticillata*, *lætevirens*, *f. laxa*, *sertularioides*). On the other hand, the branchlets are numerous and cylindrically arranged so that complete exposure is favoured by the continuous movements in the swell. The different depths at which the Caulerpa lives is reflected in the organization; the deep forms are often leaf-like and reach the highest dimensions (*C. scalpelliformis*, *pinnata*, *taxifolia*): the surface forms have a shortened axis system, while at the same time the whole assimilation system is extended at the sides in one level (*C. clavifera*, *nummularia*, *parvula*), whereby also the assimilation discs themselves strive, as it were, to extend horizontally (*C. nummularia*).

Reinke, as is well known, is of the opinion that in Caulerpas there is no difference between so-called "morphologischen und Anpassungsmerkmale," so that "Wer es liebt, auf die Unterscheidung von morphologischer und Anpassungsmerkmale Werth zu legen der wird daher die Speziescharaktere von *Caulerpa* sowohl zu den ersteren wie zu den letzteren rechnen müssen." ("Ueber Caulerpa," p. 68.)

But in this connection we need only refer to the parallel between *C. clavifera*, *C. uvifera*, and their forms on the one side, and *C. nummularia*, *peltata*, and *parvula* on the other, to prove that REINKE's assertion cannot be justified, for the "Spezies-character" in the former group is the *ball-shape* of the small assimilation branches, in the latter their more or less *disciform* shape. But the "Anpassungs-charactere," on the other hand, are the different lengths of the rhizomes and axes which form the analogy between *C. clavifera-nummularia* and *C. uvifera-peltata*. And between them as a transition form, or rather as a primary form common to both, stands *C. Chemnitzia*, which in its organization shows a faculty to develop in the one or the other direction, thus less markedly differentiated or adapted than the other two groups.

If what REINKE says about *Caulerpa* were really a fact, it would be most remarkable and would alone justify these algæ in taking an exceptional place in the vegetable kingdom. For the opinion of the biologists of our day is inclined to recognize that it is justifiable to distinguish between organization characters and adaptational characters. So, for instance, Professor GOEBEL said in his lecture at the Congress of Arts and Sciences in St. Louis, 1904, "The Fundamental Problems of Present Day Plant Morphology" ('Science' N. S., Vol. XXII. No. 550, 1905): "In reality it seems to me that morphological comparison as well as experiment shows that the distinction between organization and adaptational characters is justified." This principle may be said to hold good, as I have tried to show, also of the many changing forms of the genus *Caulerpa*.

III.—ON THE DIFFERENT KINDS OF VARIATION IN CAULERPA.

1. CONTINUOUS VARIATIONS IN SHOOT BRANCHLETS (PINNULES) FROM BASE TO POINT

The variations often point to a surface increase.—Comparison with the heterophylly of the higher plants.

In the foregoing I have shown the differences in the organization and structure in the shoots of *Caulerpa*, which are to be looked upon as adaptations to different modes of life. Thus we have seen that the shoot systems of many surface living Caulerpas are closely connected with the conditions of the light and the exposure to sea and wind that exist in the littoral region, and that when the Caulerpas grow in deeper and calmer water they assume other larger and more branched and taller forms. In all these cases the relation between organization and locality is evident.

But in this genus there is another kind of variation in the shoots, between the forms of which and the external conditions of the plant no such direct relation can be traced. It is the multitude of these variations that seems to have caused the difficulties in determining the definitions and limitations of the species in this genus. That Madame WEBER v. BOSSE has kept in sight these different variation types can be seen from what she says on p. 245 in the "Monographie des Caulerpas:" "La question sur la valeur des espéces.....est d'autant plus difficile à resoudre puisque le thalle à structure continue de ces algues, subit une grande influence du milieu où il pousse, et que la même plante adopte en outre des formes très diverses, sans qu'on puisse trouver une raison quelconque pour expliquer l'apparition de formes si variées au même stolon." It is precisely this variation that has been so sharply accentuated, both by Madame WEBER v. BOSSE and by Professor REINKE, that the variations according to localities have been almost entirely overlooked.

The variations that are not directly dependent on locality are mentioned by Madame WEBER v. BOSSE on p. 246, and are either characterized by the branchlets or pinnules of an assimilator being of a different form at the base than at the point, or there shoot out from the same horizontal axis dissimilar assimilators, in that some have exclusively one kind, other exclusively another kind of branchlets. Lastly the variation can also consist in the branchlets being arranged in a varying number of rows, though the branchlets be similar among themselves.

Here it may happen either that assimilators with a different number of branchlets shoot up from the same horizontal axis, or that one and the same assimilator may have branchlets with a number of rows varying at the top and at the base.

For a discussion of these different variations and their nature it is perhaps advisable to begin by describing some special cases. Let us, therefore, examine some Ceylon Caulerpas which show a variation of this kind.

Among other forms of *C. uvifera* from the islands around Jaffna I observed one which I have described under the name *f. planiuscula* (fig. 16). It shows a series of transitions in its branchlets. At the base they are all ball-shaped, without exception, but a little higher up they begin to grow more and more flattened, at first hardly noticeable, afterwards very evident. At the top of the assimilators the greater number of the branchlets are more or less flattened, whereas at the base no such branchlets at all are to be seen.

An analogous variation of the branchlets is to be observed in *C. corynephora f. complanata* (fig. 18). The main axis is flat, with the branchlets in two rows. At the base these are of the same width, but higher up they swell out at the points, so that they have the appearance of being somewhat constricted. The transition between the different kinds of branchlets is gradual, without sharp contrasts.

To some extent of the same kind is the variation in *C. dichotoma* (figs. 23, 24), in that in this species too the basal branchlets are simple and the dichotomous ones only begin higher up, but in this species we have, besides this, to note that the branchlets at the base are arranged radially around the axis, whereas the bifurcated branchlets higher up are arranged predominantly in two opposite rows, whereby the whole assimilator becomes bilateral. Moreover it sometimes happens that some assimilators have only simple radially arranged branchlets. *C. dichotoma* thus shows an example of different kinds of variation of branchlets.

C. peltata (figs. 31-33), on the other hand, shows somewhat different kinds of variation ; either an exclusive increase in the assimilation discs, the intervals being then longer, at the same time as the branchlets only develop from the upper side of the side branches, which thus become dorsi-ventral (fig. 32), or some branchlets develop in the direction of the spherical form, showing a tendency to swell up (fig. 33). The larger assimilation discs in the former variety, as well as the swollen ones in the latter, occur at the tops of the shoots, whereas the base is surrounded by the more numerous but smaller assimilation branchlets.

Of about the same kind is the metamorphosis of the branchlets or pinnules in *C. Chemnitzia* (fig. 26–30). At the base they are more or less pronouncedly cylindrical (fig. 27), of about the same shape as in *C. lætevirens* ; higher up they become trumpet-shaped at the top and as if abruptly cut short. At the very top the branchlets are either disciform in certain varieties (fig. 29), which have a tendency in the *peltata* direction, or spherically swollen in others which thus approach the *racemosa-uvifera* series (fig. 30).

In all the forms of variation in the branchlets described above it is a common feature that the variation proceeds more or less regularly, step by step, and furthermore that a tendency to surface increase is apparent, though it is effected in different ways ; for it is evidently shown in *C. corynephora f. complanata* (fig. 18), *dichotoma* (figs. 23, 24), *peltata* (fig. 32), *Chemnitzia* (fig. 27), and also to some extent in *uvifera f. planiuscula* (fig. 16).

Reinke, in his treatment of the variations of *Caulerpa* (*loc. cit.* p. 87), has distinguished between such as pass over " allmählich " and such as pass over " sprungweise," *i.e.*, " gradually " or by " leaps and bounds." The variations in question are apparently identical with those Reinke has characterized as " allmählich."

It is indisputable that this metamorphosis of the branchlets reminds one in many respects of the heterophylly of the higher plants. It can, however, be of an essentially different kind, in that the difference between the younger and older leaves is bound up with different conditions of life during different phases

in the life of the plant, or else such different conditions do not occur, but the heterophylly depends on the first developed leaves being arrestment stages (" Hemmungsstadien ") of the fully developed ones.

Are they then arrestment stages of the same kind as the primary leaves, as for instance the simple leaves of Leguminoseæ with otherwise normal compound leaves? Yes, to a certain extent they are quite analogous with them. Thus, the basal branchlets of *C. dichotoma* (figs. 23, 24) are undoubtedly much simpler than the later dichotomous ones, and there is nothing that debars our considering these simple branchlets as arrested stages of the other ones. The same may be said to apply to *C. corynephora f. complanata* (fig. 18) and *C. Chemnitzia* (figs. 24, 29) and other species with simpler branchlets at the base.

But, on the other hand, certain reasons offer definite testimony against our explaining all the differences in the development between base and top as arrestment phenomena. So, for instance, *C. Lessonii* offers an example (fig. 11) of the branchlets at the base being arranged in many rows, *i.e.*, are more numerous at the base than higher up. The same is also the case with the *f. tristichophylla* of *C. axifolia* (fig. 5) and several *cupressoides* forms. For in these *more* rows of branchlets are developed at the base than higher up, and this can scarcely be characterized as an arrestment, but rather the reverse. Every case, therefore, mentioned above must not be looked upon as an arrestment stage.

But cannot the different forms of branchlets at base and point be explained phylogenetically ? That is, a *Caulerpa* rhizome, which for some cause or other has entered on a new course of development as far as the form of the assimilation branches is concerned, has returned to the more primitive branch form. But by reason of the exclusive propagation of *Caulerpa* by the formation of shoots, the difference between phylogeny and ontogeny is practically *nil*, provided the latter term is not meant to express the history of the limited development of each assimilation axis (= assimilator, REINKE).

There is scarcely any reason to consider indisputable arrestments as reminiscences of phylogenetic evolution. GOEBEL, in his work " Vergleichende Entwicklungsgeschichte der Pflanzenorgane " in SCHENK'S ' Handbuch der Botanik ' (III., 1), has pronounced against such an opinion. Thus on p. 261 he says : " Derartige Erscheinungen (=Hemmungsstadien der Laubblätter) phylogenetisch aufzufassen, dazu liegen glaube ich, kein Grund vor, ich sehe in jenen einfachen Primärblättern nur Hemmungsbildungen, deren Ursachen in Eigenthümlichkeiten des Wachstums oder der Zusammensetzung embryonaler Sposse liegt." In the cases where no objection can be raised against considering the different branches as simply arrestment forms—and such cases exist, as we observed above, also in Caulerpas—there is no valid reason for the hypothesis that phylogenetic phenomena has played a part, but both cases are so similar and analogous that what is the cause of the one kind may well be supposed to be the cause of the other. Experiments alone can decide the point.

But as for the shoots in which the basal branchlets are so far from being arrested that the very opposite is the case, it seems that there is no other explanation possible than phylogeny. It cannot be denied that the resemblance between the basal branchlets of *C. dichotoma* (fig. 23) and the branchlets of *C. lætevirens* (fig. 19) is perfect. The same holds good to almost the same extent of the corresponding branchlets of *C. Chemnitzia* (figs. 26, 27, 28, 29) and *C. lætevirens*. And the basal branchlets of *C. uvifera f. planiuscula* (fig. 16) are typical *uvifera* branchlets, just as basal branchlets of *C. taxifolia f. tristichophylla* (fig. 5) are *C. falcifolia* branchlets, and the basal branchlets of *C. Lessonii* (fig. 11) are *C. cupressoides* branchlets. Examples of the same thing are not uncommon among the Caulerpas in general. Thus *C. plumaris f. Farlowi* (WEBER v. BOSSE, "Monographie," p.295, Pl. XXIV., 4–6) is a form with branchlets running in every direction and is to *C. plumaris* as *C. falcifolia* is to *taxifolia*.

In this respect *C. mamillosa*, regarded by Madame WEBER v. BOSSE as a variety of *C. cupressoides*, is especially remarkable (WEBER v. BOSSE, *loc. cit.* p. 332, fig. 6, Pl. XXVIII.). Its base is surrounded by globular branchlets, which forcibly remind one of certain forms of the *pedicellatæ* group (for instance, *C. lentillifera*, compare fig. 6, Pl. XXVIII. and fig. 2, Pl. XXXIV. in WEBER v. BOSSE, *loc. cit.*). Similar examples could be multiplied. These examples show clearly how the development of the branchlets may

be conceived as having taken place. Whatever the factors were that produced them, the changes (metamorphoses) proceed precisely as in other plants, in that these factors must be considered to have exercised a transforming influence upon the embryonal substance in the growing point itself, and this results in a successive transformation of the branchlets in some direction which then is either a direct surface increase of the assimilation system (*C. dichotoma*, figs. 23, 24) or a transition of the assimilation from several branchlets placed in many rows round a cylindrical axis to only a few but opposite rows of branchlets on a flattened but broader main axis. It follows then that a study of the metamorphosis of the branchlets can give us some serviceable hints for the solution of the question of the evolution of the different *Caulerpa* species, and hence of the system and phylogeny of the whole genus.

Thus, for instance, it seems to me that such a form as *C. lætevirens*—at least as far as its assimilation branchlets are concerned—is a very primitive type, because this form of branchlets reappears at the base of so many other forms, as *C. dichotoma*, *Chemnitzia*, and several of WEBER v. BOSSE'S *uvifera* and *clavifera* forms, which must thus be considered as younger than and derived from *lætevirens*. (Cf. figs. 3, 8, 18, &c., Pl. XXXIII., WEBER v. BOSSE, *loc. cit.*). In the same way forms with the branchlets radially arranged around cylindrical axes must be considered as more primitive than the bilateral forms, because one often meets with axes with the branchlets at the base radially arranged, higher up bilaterally, but not the other way about. Also some Caulerpas with articulated base, but for the rest with very varying and different shape, show, in my opinion, that the articulation is a very old and primitive character, while their form otherwise must be considered as something that has arisen in relatively recent times. In any case they are undoubtedly younger than the truly articulated species of *Caulerpa*.

In general, the earlier stages phylogenetically are very strongly pronounced in such plants as have been developed under extreme conditions, very different in nature when compared with those under which their ancestors lived. So Xerophytes, Hydrophytes, and climbing plants are often characterized by a pronounced heterophylly, the explanation of which must be looked for in their phylogenetic evolution, even if the plant's present mode of growth can be an explanation for its being so differently organized at different periods of its life.

As for the Caulerpas, it seems that no such sharply pronounced difference exists, with respect to their external conditions of life, as may explain the cause of the different development at base and point. But, in the foregoing, we have seen that the localities of the species of *Caulerpa* can vary not inconsiderably. So *C. lætevirens* is confined to strongly exposed localities where its position is not threatened by any other *Caulerpa*, and we have seen that its organization is an adaptation to precisely such surroundings. It is highly probable that this or some similar form under altered conditions of life has given origin to forms, such as *dichotoma*, and *Chemnitzia*, both of which could be derived from *lætevirens*. In both these species in the upper branchlets an increase of the assimilation surface takes place, but it is produced in different ways : in *dichotoma* (figs. 23, 24) by the cylindrical branchlets being flattened out and becoming leaf-like and, finally, bifurcated at the top; in *Chemnitzia* (figs. 27, 29) by the branchlets expanding trumpet-like, being more sharply cut short at the top, and finally being perfectly disciform. In both cases very similar results are produced, but in different ways. To this we must add that both these forms, *C. dichotoma* and *Chemnitzia*, are still-water forms in comparison with *C. lætevirens* and the gradual metamorphosis of the branchlets can thus be seen in connection with the changed conditions of life, which allow a surface increase of the branchlets that in *C. lætevirens* is perhaps made impossible by its mode of life, *i.e.*, by the external conditions in which it grows. Therefore, of course, the external conditions can very well be considered in this genus too as the factors that produce a transforming influence on the growing-point by irritation, and through that the whole organization of the plant. Why the development in the one case takes the direction of flattened leaf forms, and in the other of trumpet-like ones, is a question that cannot, of course, be answered by deductions from the above facts. Now, at the base of the branches in the derived species, branchlets are still developed of the more primitive kind which entirely covered the axis system of the parent form, in the same way as *Acacia* seedlings *in their youth* develop

primary leaves like those in other species of *Acacia* and only develop phyllodes later on. It, therefore, seems that, also in Caulerpas, the base of the shoot has retained most of the character of the parent form.

The differences in the formation of the shoots, which I have just dealt with, are characterized by the different kinds of shoots originating successively in the same main axis ("allmählich erfolgend," REINKE) or, in other words, they are an example of differences in organogenesis at different stages of development in the life of the shoot, *ergo*, analogous with the early forms ("Jugendformen").

Closely allied are the cases in which, from the same horizontal axis, vertical axes shoot out, each with its several special kind of branchlets (a "sprungweise erfolgende" variation, REINKE); for, usually, the different vertical axes are to some extent individualized, so that the branchlets in different axes are transformed at unequal rates. Thus, for instance, we can see one axis in which the primitive form of the branchlets covers the axis rather high up, another in which they only occur at the base and abruptly pass over into the definitive form (Cf. fig. 11 of *C. Lessonii*, the branchlets to the left).

If, now, the case occurs that in one axis the primitive forms are very few, or even entirely wanting, and that the opposite is found in another, that is to say, that there is nothing but primitive forms, it results that from one and the same horizontal axis quite different vertical axes may derive. In this form of variation, however, there are always transition forms, which show how the different axes may have arisen. The same is the case when the difference between the vertical axes only consists in their branchlets having developed in a dissimilar number of rows (Cf. fig. 45 *a*, *b*, of *C. longistipitata*). It is precisely these differences that REINKE has kept in view in distinguishing the variations in the two kinds "allmähliche" and "sprungweise" (*loc. cit.*, p. 87), and he characterizes the difference thus, that in the one we have to deal with a little, in the other with a big bound ("sprung"). According to him, there is no other difference.

It is one very characteristic trait in all the shoot variations we have been speaking of that they occur successively, *i.e.*, with transitions that may be more or less pronounced; another that they may to some extent be connected with changes in the mode of life, to which they can be conceived as adaptations or "ecologisms." The more primitive forms of branchlets at the base may be explained by the base of the shoot having kept more of its primitive character, a character more closely allied to that of the ancestral form. Therefore they must be explained phylogenetically.

(2) *Discontinuous Variations—Atavistic reversions or mutations?*

Quite different from all the other kinds of variations are those that occur in *C. Lessonii f. uticorinensis* (fig. 12). Here we have three different kinds of branches, narrow ones with two-sided and three-sided branchlets, like those in *C. cupressoides*, and furthermore, and this is the most noticeable point, considerably broader ones whose very presence shows their affinity with *C. Lessonii*. The last-named kind occurs abruptly without any intermediary transition form, and corresponds in this respect, as REINKE has pointed out ("Ueber Caulerpa," p. 85) in a striking way with the bud variations we know in such higher plants—especially trees—as can be referred to under the name of "sporting plants" (DARWIN).

Another example of the same phenomenon is the plant I have called *C. sedoides f. mixta* (figs. 49, 50). The branchlets are, as a rule, ball-shaped with or without stalk, but among them shoots out occasionally a perfectly cylindrical branchlet, three or four times as long as the others, and without any transition at all. *C. sedoides f. mixta* thus shows an example of an abrupt variation of branchlets or pinnules, whereas *C. Lessonii* shows an example of similar variation but of long branches or whole assimilators. That these variations are of quite a different kind to all the others I have dealt with in the foregoing chapter is evident, and the difference lies not only in the abrupt transition, but rather in that no correspondence with any external conditions at all, no adaptations, can be traced in this metamorphosis.

Bud variations (DARWIN) or the so-called vegetative mutations have been dealt with at length in DE VRIES' "Mutations-theorie" (Band, II., p. 670). According to him, these can be divided into three

different groups : bud variations due to the vegetative cleavage (" Spaltung ") of bastards ; bud variations due to vegetative atavism in so-called middle races (" Mittelrassen") ; thirdly, the real bud variations, which again may be of two kinds, viz., such as are of atavistic nature and such as are not of atavistic nature but are progressive mutations (vegetative mutations).

As no other propagation than by shoot formation occurs in the Caulerpas every kind of variation due to bastard formation is, of course, absolutely out of the question. There remain, consequently, bud atavism and real mutation. If, now, it is of the former kind, the changes that take place in the appearance of the shoot must therefore correspond with those of ancestral forms. Since no absolute certainty can be arrived at in this matter, we must content ourselves with examining whether possibly any now living species normally possesses branches of a kind which in another species appears as bud variation. If so, it would support the supposition that atavistic phenomena are present.

If we now examine *C. sedoides f. mixta* (fig. 50) which afforded us an example of such a bud variation, it will appear that its elongated or irregular branchlets have the very same form or, at least, are very similar to those in *C. ambigua*, which belongs to the same group as *C. sedoides* (Cf. my fig. 50 and Pl. I., figs. 4, 6, 7, 14 in Okamura, " On the Alg. of the Ogasawara-jima " (Bonin Islands).

It thus seems by no means improbable that *C. sedoides* is derived from a species which has been very closely allied with or similar to *C. ambigua*. That cylindrical branchlets (= pinnules) are more primitive than spherical ones I have already tried to show in the foregoing, while dealing with the question of relationship between *C. racemosa*, *lætevirens*, and *Chemnitzia*. In complete analogy with this is, too, that such species as *C. ambigua* must be considered as more primitive than *sedoides f. crassicaulis*. Everything, therefore, points to the conclusion that the bud-variation in *C. sedoides f. mixta* should be regarded as an atavistic reversion.

Whether the same is the case with *C. Lessonii f. tuticorinensis* is somewhat more difficult to decide. The form which I have indicated as the main species of *Lessonii* (fig. 11) shows at the base branches with three-sided branchlets ; thus, in conformity with the opinion I have attempted to vindicate, it s derived from a species with three-sided branchlets, *i.e.*, from one of the *cupressoides* forms. *C. Lessonii f. tuticorinensis* (fig. 12) also has the prevalent number of branches of the common *cupressoides* form ; two-sided as well as three-sided, and the great majority of the branches never have a different appearance. But amidst these branches the broad flattened ones with their two-sided branchlets are formed just as bud variations. These are from the very beginning two-sided, and not, as often in *Lessonii*, three-sided at the base. It is therefore impossible to say that the broad flat branches in *C. Lessonii f. tuticorinensis* are reversions to *Lessonii*, for that would mean that *Lessonii*, that is the broad flat leaf form, were more primitive than the *cupressoides* branches. But this is contradicted by *C. Lessonii* itself, in which the development shows the exact contrary (fig. 11). This does not seem to support the atavistic nature of these shoots ; yet it seems impossible to look for any definite solution of this problem at the present time. It may be possible for *Lessonii* and *C. Lessonii f. tuticorinensis* to be in the nature of parallel forms of equal rank, both deriving from a *cupressoides* form and with a tendency to form flat bilateral branches. But in the one (*Lessonii*) this tendency is the predominant, and has so to speak become the normal one, while in the other one (*tuticorinensis*) this tendency is more latent and only rarely reveals itself. This is of course a pure speculation, and for the solution of this, as of so many similar questions touching variation in *Caulerpa*, experiments and cultures are necessary which the traveller in the Tropics has difficulty in arranging.

That both these forms go together seems to me indisputable, and I have wished to give expression to this by calling one form the *f. tuticorinensis* of the other, *Lessonii*. But with this I do not imply that *Lessonii* is necessarily more primitive, for here, as in so many other cases, the first form to be distinguished becomes the main species, the later ones the variations, though with equally good reason the reverse might have taken place.

3. *Dwarf Forms.*

Stunted dwarf forms are often looked upon as a special kind of variation. These, too, are not rare among Caulerpas. Dwarf forms in general are produced by poor nourishment, and it is to be assumed that this has also in some way occasioned the *Caulerpa* dwarfs. And it seems to be clearly the case in *C. taxifolia f. interrupta* (fig. 6), in which stunting has perhaps been produced by lack of light, owing to the great depth, for *Caulerpa*, at which it grows (more than 10 m.). In the other cases there are, on the other hand, no directly apparent external circumstances which could justify our calling the cause poor nourishment. On this point, however, it is impossible to pronounce with any degree of certainty, since our knowledge of the requirements in nourishment of the algæ is still so fragmentary. If, now, it is some deficiency or other in the nourishment that has caused them, this type of variation must, according to present day opinion, be classed under fluctuating variability among the different kinds of branchlets, and deserves then to be distinguished at the most as local forms. If, on the contrary, these dwarf forms occur not simply isolated among the normally developed ones, but show a certain constancy within a given district, it is more probable that we have to do with special races. For it is evident that, since we do not know what influence the different external conditions and especially those of nourishment exert, and since we have no opportunity of conducting cultural experiments, it is absolutely impossible to determine objectively whether we have to do with individual variations or with races with constant character. In such cases it must often be a matter of taste for the taxomonist if the plant in question is to be classed as a race or only as a local form.

The dwarf forms that I observed in Ceylon were : *C. taxifolia, f. interrupta* (fig. 6), *C. plumaris, f. umbellata* (fig. 9), *C. lætevirens f. depauperata* (fig. 20) and *C. parvula* (figs. 43, 44). Of these it seems to me that some doubt arises only in the case of *C. parvula* (fig. 44), *i.e.*, whether it is not rather to be regarded as a distinct species, since, at Beruwala, where I collected it, it occurred in several places and seemed to be a more or less constant species. I have, therefore, classed it as a separate species. As for the others, they showed all the signs of being mere accidental varieties, which diverge so much, however, that I think we are justified in distinguishing them as special forms.

4. *Summary.*

In the preceding we have thus got to know different kinds of shoot variations which can occur in one and the same *Caulerpa*. And we have seen that these are of the following kinds :—

1. Variations which depend on the locality, and which are to be considered as adaptations or ecologisms.
2. Variations which cannot be considered as ecologisms, but which are the result of fluctuating variability amongst the different branchlets (= pinnules).
3. Variations which can be considered as phylogenetic stages of evolution (for instance, that the basal branchlets or pinnules are of more primitive form than the upper branchlets).
4. Bud variations of atavistic origin (*C. crassicaulis f. mixta?*).
5. Dwarf forms.
6. The variations which do not fall under any of the above categories may, lastly, be bud variations without atavistic origin (= mutations).

As Reinke has pointed out, it is to be noted especially about *Caulerpa* that no sharp line can be drawn between individual variations and bud variations owing to their characteristic mode of propagation, since all the *Caulerpa* individuals originate as buds on a common horizontal axis, and thus all variations are bud variations in the widest sense of the term. (Cf. the relation between ontogeny and phylogeny in *Caulerpa*, p. 16.)

All these factors again work together and cause the multifarious diversity of *Caulerpa*. And here it is to be noted—as several writers have already pointed out—that all this diversity and all these variations

depend exclusively on changes in the purely vegetative sphere, for no organs of fructification nor spores of any kind are to be found in these plants, and REINKE has, therefore, hit the mark when he says *that the somatic plasma is the medium in and through which the variations of the Caulerpas originate.*

IV.—TAXONOMY OF THE CAULERPAS.—DEFINITION OF THE SPECIES.

It is clear that, as long as we have no firm basis for determining the factors which cause the formation of a species, we can have no real objective principles by which we can determine its limitations. It is for this reason that the conception of the specific character of a species varies more than anything else in the different works on Caulerpas. While some authors prefer small but often less sharply distinguishable species, others prefer wider species, under which are classified a huge number of sub-species, varieties, and forms, often without it being possible for the reader to explain why a certain form should be called there "variety," now only "form."

In this respect also the Caulerpas have been subjected to various fates. LAMOUROUX, the founder of the genus *Caulerpa*, knew 10 species in 1809. Since then new species have been described, one by one, and KUTZING could enumerate 41 species in 1849, divided by him into several genera. The first really valuable monograph on the genus *Caulerpa* was published by J. G. AGARDH in 1872, and he could then distinguish no less than 64 species divided into 13 groups. In 1898 Madame WEBER v. BOSSE, in her monograph, reduced the number of the species to 54, but these species have numerous sub-species and varieties of different rank. It is undoubtedly a great merit in her work that thereby the unity, the great affinity between the various forms, is so strongly accentuated. But, as REINKE so felicitously points out, it is not necessary to group together different species even if transition forms can be found between them. For besides the practical difficulties that accompany such a taxonomy—for one is forced to use as many as four different names (species, sub-species, variety, form) to make quite clear what one is refering to—so too from a purely theoretical point of view one must note that one might just as well reduce the whole genus to one, or a few species, dependent on whether one assumes a monophyletic or polyphyletic origin. But systematic botany ought to lay stress not only upon unity but also upon diversity, and from this point of view it seems more satisfactory to me to employ a more limited species definition, as the older authors did. The genetic relationship of the different species is then not confused, at any rate.

If we apply this to the Ceylon species of *Caulerpa* it is really only the group *clavifera-uvifera-lætevirens-Chemnitzia-peltata* that makes difficulties; for in this group the diversity is greatest. While some *Caulerpa*-species, as *verticillata*, *crassifolia*, *sertularioides*, are less variable, the *racemosa* group (WEBER v. BOSSE) on the other hand, as observed above, is especially rich in forms. It is evident that the genus *Caulerpa*, as so many other genera of plants, shows types of different constancy. While some species vary but little, in other groups the variety is very great and probably new forms are now originating. It is thus probable that in Ceylon this is the case with forms belonging to *clavifera*, *uvifera*, *Chemnitzia*, *peltata*, *nummularia*, and others. In this connection it must be observed that geographical distribution in some cases quite clearly shows that the different groups of forms have in part a tendency to have a distribution which excludes other groups; so, for instance, *C. Chemnitzia*, *uvifera*, and their forms occur especially in the north of Ceylon, whereas *C. clavifera* and *nummularia*, have more predominantly southern distribution. This may possibly be bound up with the conditions of life being so different in different parts of the Island, coral-reefs and rocks in the south, sand in the north.

But with respect to the geographical distribution of these algæ in Ceylon and its causes, this problem, until I have had an opportunity of studying all the algæ of the island, can only be dealt with by me cursorily

V.—ON THE GEOGRAPHICAL DISTRIBUTION OF THE CAULERPAS.

1. The Distribution of the Caulerpas in Ceylon.

Different Species in the North and in the South.

The Relationship between the different External Conditions in the North and in the South.

In this chapter, finally, we shall deal with the occurrence and geographical distribution of the Ceylon species of *Caulerpa*.

The first question we have to answer is, How are the Ceylon Caulerpas distributed in Ceylon? Here, of course, it is to be noted that of the twenty odd *Caulerpa* species in Ceylon, only relatively few, about a third, occur so abundantly that they leave their stamp on the vegetation as a whole. The others occur only sparsely and scattered about, and cannot be classed as plants characteristic of the marine flora of Ceylon, even if they sometimes may occur quite locally in such numbers that they form real associations of their own (*C. verticillata*, *C. lætevirens*.)

Species which occur more or less abundantly and which—in large districts, at least—are very characteristic elements in the Ceylon algal flora, are *C. clavifera*, *uvifera*, *Chemnitzia*, *peltata*, *nummularia*, *imbricata*, and possibly even *sertularioides*. Of these *C. sertularioides* occurs scattered along the whole coast, never in great masses, but always rather isolated, hemmed in between other algæ. The others, on the contrary, occur in great quantities, and contribute in many places to give the algal vegetation as a whole its stamp. Here it should be observed that *C. clavifera*, *nummularia*, and *imbricata* occur especially in the south-west and in the south (Colombo–Tangalla), while *C. uvifera*, *peltata*, *Chemnitzia*, have a more pronounced northern distribution (Gulf of Mannar, Jaffna, Trincomalee). These groups, it seems to me, confine themselves to provinces of their own to a certain extent. Here, again, it is to be observed that the species that have a main distribution in common are also characterized by a certain resemblance in organization. So for instance, *C. clavifera*, *nummularia*, and even *imbricata* are characterized by relatively short vertical axes, which gives rise to a more mat-like mode of growth so that the whole assimilation system is on the same level. On the other hand, both *uvifera* and *peltata*, as also *Chemnitzia*, have lengthy vertical axes that wave in the swell, and thus they form quite a different type of organization.

These differences in organization and distribution of the different species are concurrent with the external conditions of algal life being so different in north and south. In southern Ceylon the coast is partly rocky and the rocks there are often fringed by splendid coral-reefs; whereas, in the north around the islands at Jaffna and at Adam's Bridge, the shores are shallow sand beaches with loose bottom where fringing coral reefs rising to about the level of the sea are lacking.

I have already dealt above with the differences in organization that usually accompany these different external conditions, and it is very remarkable that the short-axed *clavifera*, the most common *Caulerpa* on the coral reefs of south-west Ceylon, is replaced in the north by the closely related long-axed *uvifera*, in the same way as *C. nummularia* and *imbricata* in the south are replaced by the allied *peltata* and *Chemnitzia* in the north. All these species, as is known, are very closely related, and have also been classed by Weber v. Bosse as one single broad species, *C. racemosa*, *sens. ampl.* ("Monographie des Caulerpas," p. 356) with a great number of sub-species, varieties, and forms. For practical as well as scientific reasons I have deemed it advisable to prefer a more narrow definition of the species, but this does not affect the fact that all these species and forms are genetically very closely related. With respect to the form of the pinnules, *C. clavifera* is allied to *uvifera* just as *nummularia* is allied to *peltata*; but from the point of view of organization in general we must group them differently, since then *clavifera* and *nummularia* show themselves to be representatives for one type, *uvifera-peltata* for another. I have already in the preceding given these plants as examples of the fact that also in the genus *Caulerpa* there is—as against what Reinke tries to prove—a difference between morphological and adaptational

characters. And now we see that this difference in adaptational character most closely corresponds with the distribution of the species, so that similarly organized species have a common centre of distribution. This clearly follows from what has been stated above, *i.e.*, that especially *clavifera* and *nummularia* have quite another distribution than *uvifera-peltata*. And since the characters which separate these two groups are to be regarded as adaptations to the external conditions within the respective distribution districts, these closely related species, their organization and distribution, may be given as examples of the principle (WETTSTEIN, "Grundzuge d. geogr.-morphol. Methode d. Pflanzensystematik," p. 30) that forms or species which are adaptations to external conditions with a limited distribution also themselves have a distribution which coincides with that of the conditions in question.

To the less common forms of *Caulerpa* that occur in Ceylon belong the following species :—

C. verticillata	*C. corynephora*
C. scalpelliformis	*C. lætevirens*
C. crassifolia	*C. dichotoma*
C. taxifolia	*C. parvula*
C. Freycinetii	*C. longistipitata*
C. cupressoides	*C. sedoides*
C. Lessonii	*C. Fergusonii*

Of these *C. verticillata* has only been observed at Galle, Colombo, and at Tuticorin in South India ; at the first-named place locally but abundantly and forming a special association. The species is not noted from the east coast, nor from the islands and banks which form Adam's Bridge. It is thus predominantly of a western distribution in Ceylon.

C. scalpelliformis, which is probably a deep water form, is only known from the Gulf of Mannar (Pearl banks, Paumben, Tuticorin).

C. crassifolia and *taxifolia* have similar distribution ; the former is the rarer and has been observed from Weligama in the south to as far as the north end of the Gulf of Mannar (Pearl banks and Paumben) ; the latter at several places within the same district.

Several species have only been observed in solitary specimens, as rarities. Of these—

C. Freycinettii (Jaffna)	*C. corynephora* (Tuticorin)
C. cupressoides (Paumben)	*C. longistipitata* (Paumben)
C. Lessonii (Pearlbanks, Tuticorin)	*C. Fergusonii* (Paumben)

have only been observed in the north from the Pearl banks, Paumben, Tuticorin, Jaffna, but are absent from the south-west coast, which has, nevertheless, been the most closely investigated.

On the other hand there are some species with very singular and isolated occurrence, which are only known from the south coast, viz. :—*C. lætevirens* (Galle, Weligama) ; *C. dichotoma* (Weligama) ; *C. sedoides* (Dondra Head, Matara, Weligama) ;* also *C. parvula* is only known from some isolated places (Beruwala in the south-west and Paumben in the north).

If we examine these different species from the point of view of their organization and mode of life, it is remarkable that several of the northern forms prove to be pronounced sand Caulerpas with coarse, horizontal axes, and richly and finely branched roots, *e.g.*, *C. Freycinetii*, *cupressoides*, *Lessonii* *Fergusonii*, besides which *crassifolia*, *taxifolia*, and also *scalpelliformis* join them.

On the other hand it is to be noted that such species as *C. lætevirens*, *sedoides*, and possibly *dichoma*, which have only been observed in the south, are pronounced rock Caulerpas. The species that have been observed especially in the north are, moreover, often deep water Caulerpas—for instance, *C. scalpelliformis*, *C. crassifolia*, *C. cupressoides*, *C. Lessonii*, *C. Fergusonii*—whereas those that have been found only in the south are surface Caulerpas.

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* Note that *f. mixta* has also been observed at Paumben !

From what has been said above it follows that the difference in organization that prevails among the predominating *Caulerpa* species in the north and in the south, and which depends on the difference in the external conditions of life, can also be traced in such *Caulerpa* species as are rather to be considered as being more accidental ingredients in the flora. Here, too, thinning, owing to external influences, makes itself felt, so that, for instance, the rocks and reefs in the south harbour species that in their organization show themselves more fitted for these.

It is remarkable that the north-east coast of Ceylon, as far as we know, has no *Caulerpa* that is not known in other parts of the Island. It is striking, for instance, how at Trincomalee, where the rocks seem to be excellent localities for algae, the marine flora is apparently scanty and, in richness of species and luxuriance in general, very inferior to that on the rocks in the south-west. This fact seems already to have made itself clear to HARVEY, to judge by his disappointment at Trincomalee. (See "Memoir of W. H. HARVEY," London, 1869, p. 251).

2.—THE DISTRIBUTION OF THE CEYLON CAULERPAS IN OTHER PLACES.

Having dealt with the distribution of the Ceylon Caulerpas in Ceylon, we will investigate their geographical distribution elsewhere. But, first, we must remark that the following species are hitherto only known from Ceylon :—

C. imbricata	*C. parvula*
C. dichotoma	*C. Fergusonii*

These, then, must, for the present at least, be regarded as endemic species.

Among the remainder we find that, of the species which make up the main mass of the Ceylon Caulerpa vegetation, the majority are species with very wide distribution—from the Red Sea in the west to the eastern islands in the Pacific, and also in the West Indies. Such species are—

C. clavifera	*C. Chemnitzia*
C. uvifera	*C. peltata*
C. sertularioides	

C. nummularia is not reported from a more western point than Ceylon, and seems to have its main distribution in the Indian Archipelago and tropical Australia. In this connection it must, of course, be borne in mind that such statements about distribution must be taken with some reserve as far as the definition of the species is concerned, as different authors have different interpretations for the various species. Dealing with the distribution of the species, one has therefore always to reckon with the wider sense of the name in question. The restricted species and forms are, of course, much more limited in their distribution.

Of the *Caulerpa*-species that are comparatively rare in Ceylon, the two following have also the same extended distribution (Red Sea, Pacific, West Indies) : *C. crassifolia* and *C. Freycinetii*.

On the other hand, there are several of the rarer species for which Ceylon and the peninsula of India form the western limit of their distribution, as far as we know. Such are :—

C. verticillata	*C. Lessonii*
C. taxifolia	*C. corynephora*
C. cupressoides	*C. sedoides*

and possibly *C. longistipitata.*

The last-named is, be it noted, only found beyond Ceylon in the Gulf of Siam, and has thus its west limit in Ceylon ; but, on the other hand, the closely related *lentillifera* has a still more pronounced west distribution, since it occurs in the western parts of the Indian Ocean (Madagascar).

While, comparatively speaking, so many species have their western limit in Ceylon, *i.e.*, they themselves have a more easterly centre of distribution, it is very striking that Ceylon is not the east limit for hardly more than one species, viz., *C. scalpelliformis*, which together with closely allied forms occurs from the Red Sea to Ceylon in the north and has also a wide distribution on especially the west and

south-west coast of Australia and Tasmania. It is very remarkable that this species is not known from the Pacific, but, on the other hand, it has been collected on the west coast of Africa (Angola), that is, in the Atlantic.

Lastly, Ceylon is the north, or perhaps better the north-west limit for two species, the central distribution of which seems to be Australia, even if they also occur in the West Indies—*i.e.*, *C. laetevirens* and *C. sedoides*. For the former, the central distribution of which seems to be North and West Australia, southern Ceylon is certainly the north limit. *C. sedoides* has similarly its central distribution in Australia, but occurs also in the Gulf of Siam ; it is also found in the West Indies. In any case, Ceylon forms its north-west limit, and it occurs there only on the south coast, not in the north at all.

We find, therefore, that the main mass of the Ceylon Caulerpa vegetation consists of many species with extensive distribution (from the Red Sea in the west across the Indian Ocean to the Pacific Islands in the east, together with the West Indies), but also of several species with a more easterly main distribution for which Ceylon and India form the western limit.

Finally, the Ceylon Caulerpa flora harbours some Australian elements and one species with a pronounced western distribution and, of course, the endemic species mentioned above.

(3) The Geographical Distribution of Caulerpa in General.

In this last chapter we will deal with the question of the geographical distribution of the *Caulerpa*-species in general. They belong almost exclusively to the true tropical flora, and have their main distribution in the tropical and sub-tropical coasts of the Red Sea, the Indian Ocean, and the Pacific, and also in the tropical Atlantic (to which must be added the Mediterranean), especially the West Indies.

But it must be noted in this connection that the Indian Ocean and the Pacific harbour far more species than the Atlantic. Of the 50 to 60 *Caulerpa*-species known, the majority belong to the ocean area of the Indian and Pacific Oceans, which too is considerably more extensive than the tropical Atlantic (including the Mediterranean), which does not harbour as many *Caulerpa*-species. Many of the species belonging to the former area have a wide distribution, from the Red Sea and the east coast of Africa in the West to the easterly Pacific Islands in the East. Others, however, have a considerably more limited distribution.

Thus, especially southern Australia, including Tasmania, is the home of several characteristic and closely related species forming some very natural groups within the genus, namely, J. G. Agardh's groups, *Hippuroideæ*, *Lycopodioideæ*, *Sedoideæ pedicellatæ*, and *Opuntioideæ*, of which only an occasional species occurs exceptionally beyond the Australian coasts.

Of the species that occur in the tropical Atlantic (and Mediterranean) the majority are common also to the Pacific and Indian Oceans, and there are but half a dozen *Caulerpa*-species at the most that occur exclusively in the Atlantic, whereas the Indian-Pacific Ocean has many (30 to 40) species that do not occur in the tropical Atlantic.

It seems from this that it may be asserted that the genus *Caulerpa*, at least at the present time, has its main distribution within the Indian-Pacific Ocean area.

Very remarkable is the distribution of the species, reaching a number of about 12, which the tropical Atlantic has in common with the Indian-Pacific Ocean. Of the *Caulerpa*-species occurring in Ceylon the following also occur in the West Indies :—

C. verticillata
C. crassifolia
C. taxifolia
C. sertularioides
C. Freycinetii
C. cupressoides
C. clavifera
C. uvifera
C. lætevirens
C. Chemnitzia
C. sedoides

i.e., about half the number of the sum total of the Ceylon *Caulerpa*-species. These are entirely lacking along the southern coasts of South America, which, of course, fall in part outside the tropical zone, and in general do not harbour any *Caulerpa* at all. The flora of the Cape is also very poor in Caulerpas; only five are known, and among the species common to the Atlantic and Pacific only two, *clavifera* and *Chemnitzia*, are included in this number and they are, moreover, *exclusively* found in Natal and on the east side of South Africa, which is washed by the warm Mozambique stream, but not on the west side, which has a much less tropical character owing to cold antarctic currents. It is, therefore, a remarkable fact that the centres of distribution which the species have in common, the Atlantic Ocean on the one hand, and the Indian-Pacific Ocean on the other, are at the present time separated from each other, so that there is no communication between the two different districts for the different species. MURRAY, who has closely studied the problem of the distribution of the tropical algae, has pointed this out with reference to all the marine flora that the Atlantic and the Indian Oceans have much in common. To explain this fact MURRAY has suggested that the two rather similar tropical floras in the Atlantic and the Indian Oceans, which now communicate only *viâ* the Cape, must probably "have been periodically mingled at the epochs of warmer climate at the Cape."

This is perhaps not beyond the bounds of possibility, but it seems to me not improbable that the resemblance between the flora districts of the tropical Atlantic and of the Pacific-Indian Ocean may be explained naturally in another way, namely, that it (the resemblance) must be regarded in combination with the geological data which argue in favour of a pre-historic direct communication between the Pacific and the Atlantic, either across the Isthmus of Panama or further south. That such a communication existed even as late as in the Tertiary Age is beyond all doubt (Compare P. M. DUNCAN "On the Fossil Corals of the West Indian Islands"; R.T. HILL, "The Geological History of the Isthmus of Panama and portions of Costa Rica"; A.E.ORTMANN, "Tertiary Invertebrates"), though opinions differ when the question arises *where* the communication took place, some geologists assuming a more southerly connection than across the Isthmus of Panama.

It is very remarkable that the tropical algal district in the Atlantic is almost confined to the West Indies. This probably depends on the eastern coast of South America, just as the western coast of Africa—as MURRAY points out, not offering suitable habitats for algal growth. But then one can scarcely assume that, even if warmer water washed the south coasts of South America and especially of Africa, a more luxuriant algal vegetation should have been harboured then than is the case to-day, seeing how little suited they are said to be for algal growths of any kind. I therefore think that the communication and the relationship between the floral districts of the Indian-Pacific Ocean and the West Indies can be more naturally explained in another way, *i. e.*, that these districts once had direct communication over the districts where now the Central or South American continent separates the two great oceans.

If we examine the geographical distribution of other marine organisms, we cannot fail often to notice a greater resemblance between the West Indies and the Indian-Pacific Ocean than between the West Indies and the rest of the Atlantic. Let us, for instance, examine the marine phanerogamic plants, to the geographical distribution of which ASCHERSON ("Die geographische Verbreitung der Seegräser") has devoted careful study.

Of the genus *Thalassia* belonging to the family of the *Hydrocharitaceæ* there are only two most closely allied species, viz., *Th. Hemprichii* with uniform distribution from the Red Sea, the Northern Indian Ocean (but not the east coast of Africa, nor the Cape!) to the eastern islands of the Pacific, and *Th. testudinum*, confined to the West Indies alone.

A quite analogous distribution is true of the two closely allied *Cymodocea* species, *C. isoetifolia* and *C. manatorum*, which together form the group *Phycoschœnus*, ASCHERS., which is sharply distinct from the other *Cymodocea*-species. The distribution of *C. isoetifolia* almost perfectly coincides with that of *Th. Hemprichii*, that is to say, the Red Sea, the North Indian Ocean, to the eastern islands of the

Pacific, and the distribution of *C. manatorum* coincides with that of *Th. testudinum*, *i.e.* is exclusively confined to the West Indies.

Similar is the distribution of the two *Halodule* species, viz., *H. uninervis* (FORSK.) ASCHERS., in the Indian Pacific Ocean and *H. Wrightii* ASCHERS., in the West Indies. The latter seems to occur also on the west coast of Africa, but not in the south at the Cape. These species are so similar to each other that OSTENFELD ("Flora of Koh Chang," Part V., Hydrocharitaceæ, Lemnaceæ, &c., page 262), who has devoted a comparative study to them, says : "On the whole it is not possible to distinguish the two species when sterile, except using their quite different geographical distribution as criterion."

Also within the genus *Halophila* analogous distribution can be traced. The majority of the *Halophila* species are at home in the Red Sea, Indian Ocean (they do not reach the Cape, however), and the Pacific, and, besides, there occur very closely allied forms in the West Indies, but not from other parts of the Atlantic coasts of South America, nor from the west coast of Africa. OSTENFELD has lately described from the Gulf of Siam (Koh Kahdat) a *H. decipiens* which is so strikingly like the West Indian *H. Baillonis* that he says (*loc. cit.*, p. 261) : "If the geographical distribution was not so quite different I should prefer to regard it as a variety of *H. Baillonis*, but it is not probable to suppose such a connection, as the sea phanerogams generally have very natural and limited areas and *H. Baillonis* is confined to the shores of the West Indian Archipelago."

Ergo : numerous marine species with wide distribution in the Indian and Pacific Oceans, and which are lacking on the east coast of Africa and at the Cape, find their parallel within the West Indies in often closely allied species which are exclusively confined to the West Indies. The marine flora of the West Indies, at least the marine phanerogams and *Caulerpa*, thus show much greater resemblance and affinities to the Pacific and Indian Oceans than to the rest of the Atlantic. That this is the case also with regard to other groups of algae is certain, and I hope to return to this point again.

That the same is the case also within certain groups of the fauna, where relationship is traceable between West Indian and Pacific species, has been pointed out by several investigators (WALLACE).

One is therefore forced to the opinion that the marine flora and fauna of the West Indies, in part at least, is an off-shoot of the Pacific. In the earlier epochs of the Tertiary Age, and at least up to the beginning of the Miocene period, North and South America, as just mentioned, were separated from each other so that the Carribean Sea was only a bay of the Pacific, or a kind of straits between the Pacific and the Atlantic, and not before the transition of the Tertiary Age into the Quaternary Age did the volcanic formations arise which make up the present Isthmus of Panama and which ever since have separated the Atlantic from the Pacific. But since the Carribean Sea was at relatively so late a period no more than a bay of the great unbroken ocean which is formed by the Indian Ocean and the Pacific, what is then more natural than that this part of the Atlantic should still often show resemblances to the Pacific more than to the rest of the Atlantic. And that such a primitive and old group of plants as *Caulerpa* already then had species that still survive, is highly probable ; since other tertiary organisms are, as far as their species go, very closely allied to or the same as still existing species. And that also such a primitive group as the sea phanegorams in the West Indies and in the Pacific and Indian Oceans should be represented by species that are very closely allied, if not quite identical, follows then as a matter of course. That the species are not quite identical, perhaps only shows that they, after being isolated, have undergone somewhat different evolution, which however has not led them very far apart. This is best shown by this, that among the species in common there are no less than two genera (*Thalassia*, *Halodule*) and one very characteristic sub-genus (*Phycoschœnus* of *Cymodocea*), all of which consist of only two species, of which one is exclusively confined to the West Indies, the other to the Indian-Pacific Ocean.

By assuming that the similarities between the algal floræ of the West Indies and Pacific and Indian Oceans depend on a former direct connection across the present American belt of land, a number of peculiarities in the distribution of some algæ can be explained which cannot be explained by the

hypothesis of a connection by way of the Cape. Thus there are several *Caulerpa* species which the West Indies and the Pacific-Indian Ocean have in common that do not occur farther west than Ceylon and the peninsula of India. Such are *C. verticillata*, *taxifolia*, and *cupressoides*, and to these could also be added one species which is only known from the West Indies and the Pacific, but not from the Indian Ocean, viz., *C. fastigiata*. These species have, therefore, a distribution which in the West does not reach the east coast of Africa, but have, on the other hand, a more eastern centre of distribution in the Pacific. To suppose that these species too, could possibly have come by way of the Cape to reach the West Indies, or *vice versa*, seems unreasonable, for in that case they could scarcely have failed to leave traces in Africa, whereas their distribution is very naturally explained by the supposition of a connection between the Atlantic and Pacific across Central America.

I therefore consider it much more probable that the explanation of the resemblances pointed out by MURRAY between the algæ of the West Indies and those of the Indian Pacific Oceans, must be looked for rather in the historical development of the connection of land between North and South America, which shows that the whole Carribean Sea was once only a bay of the Pacific, than in the assumption that it depends on a connection *viâ* the Cape in a time when the external conditions for tropical algae were more favourable there than to-day.

For a definitive proof of the above a more detailed comparative investigation of the whole algal vegetation must, of course, be undertaken, and I hope to be able to return to this matter before long.

For the present I will content myself with pointing out that the geographical distribution of *Caulerpa* as well as that of the marine phanerogams, clearly indicates that the relation of the marine flora of the West Indies to that of the Pacific-Indian Ocean must not be determined without taking into consideration the geological history of the connecting link of land between the two Americas.

VI.—LIST OF THE SPECIES.

1.—**CAULERPA VERTICILLATA**, J. G. AGARDH.

J. G. AGARDH, Till Algernes Systematik, I., p. 6.

A. WEBER v. BOSSE, Monographie des Caulerpes, p. 267.

SYN. *Stephanocoelium verticillatum*, KÜTZ.

MURRAY, Catalogue of Ceylon Algæ in the Herbarium of the British Museum, p. 38.

EXSICC.: WITTROCK et NORDSTEDT, Algæ exsiccatae, No. 347!

FERGUSON, Ceylon Algæ, No. 233 and 425!

This plant occurs at Galle in a small but clearly defined district where it constitutes almost the whole of the vegetation. It grows at Galle exclusively around the mouth of the stream or canal that enters the sea at Victoria Park to the north of the town proper. The low rocks, which are here quite covered by sand and mud formed by the stream are entirely coated with *C. verticillata* together with a little *Ceramiaceæ*, and these form the bulk of the vegetation. However, *C. verticillata* did not grow higher than up to the low-water mark, so that it was never exposed at low-water.

Structure of the shoots.—As Professor REINKE in his work on Caulerpa (page 7), in describing this species, confesses that he has been unable to confirm the statement to be found in the literature of the subject, viz., that it has a horizontal rhizome, we may here briefly describe the structure of its shoots and its manner of growth (fig. 1).

It always grows in thick tufts, surrounded by sand, out of which the green tufts stick up so high that they are fully exposed and wave to and fro in the swell. If we examine such a vertical assimilating branch, we shall find that it is rather richly ramified below the sand, and consists of up

growing axes which all grow out of a more or less pronounced horizontal stem (fig. 1 *a*). Horizontal axes occasionally start higher up the vertical branch (fig. 1 *b*). Both the horizontal and the vertical axes bear roots, round which grains of sand are very firmly fastened, so that they do not come away even if violently shaken in water. With careful manipulation we can observe down in the sand remains of "assimilators" (in REINKE's terminology), that have evidently been sanded over. As, moreover, the older horizontal axes often grow quite deep, this characteristic reminds us to some extent of many dune grasses, which when covered with sand form their regenerating shoots from axes higher up the stem, by which means the plant continues to keep on the surface of the sand. The danger of over-sanding may be very great sometimes for *C. verticillata* in its home at Galle, since after heavy showers masses of sand and earth are carried out to sea from the stream, so that the water becomes quite muddy. The subterranean system seems to resemble the rhizomes of the higher plants in that it functions as a store for reserve-material, for its basal branches and axes are quite filled up with starch. The grains of starch, which are comparatively few in the assimilating branches, increase in the lower axes and in the horizontal rhizomes, and are so numerous there that the rhizomes are stained quite dark blue by iodine. They probably function as stores during the plant's resting-time, for in *C. verticillata* there are clear indications of periodicity.

Fig. 1.—*C. verticillata*, J. G. AG. (1 × 1).

Periodicity.—From notes taken by me it seems that *C. verticillata* at Galle reaches its highest development during the months from November to March, when it occurs in masses at the mouth of the river. On visiting the identical spot in August of the same year (1903) it was scantier, but *Ceramia* and other Florideae were more abundant. The specimens of this plant collected by Prof. KJELLMAN (WITTROCK & NORDSTEDT, Algæ exsicc. No. 347) at Galle during the expedition of the "Vega" also date from December.

Geographical Distribution.—CEYLON: Galle! Colombo (FERGUSON No. 233, 22-1-1871); THE EAST INDIES: (Tuticorin, FERGUSON No. 425) to the Friendly Islands (HARVEY); THE WEST INDIES, in several places.

2.—**CAULERPA SCALPELLIFORMIS** (R. BROWN) WEBER v. BOSSE.

WEBER v. BOSSE, Monographie des Caulerpes, p. 286.
MURRAY, Catalogue, p. 38
f. intermedia, WEBER v. BOSSE.
f. denticulata (DECAISNE) WEBER v. BOSSE.
EXSICC.: FERGUSON, Ceylon Algæ No. 411!

Only observed once locally in shallow water on the projecting spit of land on the west side of Paumben Pass (3-4-03) together with quantities of *Codium* and *Chrysymenia*. I have not seen it anywhere else in Ceylon.

It is, in general, an extremely large *Caulerpa* with leaves attaining as much as 36 cm. in length, but with an average of about 20 cm. The lobes vary considerably in shape, being now quite narrow

and scarcely dentated and curving upwards, now short and broad, clearly dentated, but not curved. Such different forms of lobes occur both on different leaves from the same rhizome and also on *the same leaf*. Of forms that have already been described the main mass of my material resembles most closely the *v. intermedia*, WEBER v. BOSSE, especially the specimens from the Mauritius (according to specimens in AGARDH's Herbarium in Lund, No. 16,431) sketched by WEBER v. BOSSE ("Monographie des Caulerpes," Pl. XXIII, Fig. 7). In Ceylon there are, therefore, transition-forms between *f. intermedia* and *f. denticulata*, but on the other hand I have never seen *f. typica*, WEBER v. BOSSE (*C. scalpelliformis*, J. G. AGARDH), a characteristic type that seems to be confined exclusively to Australia.

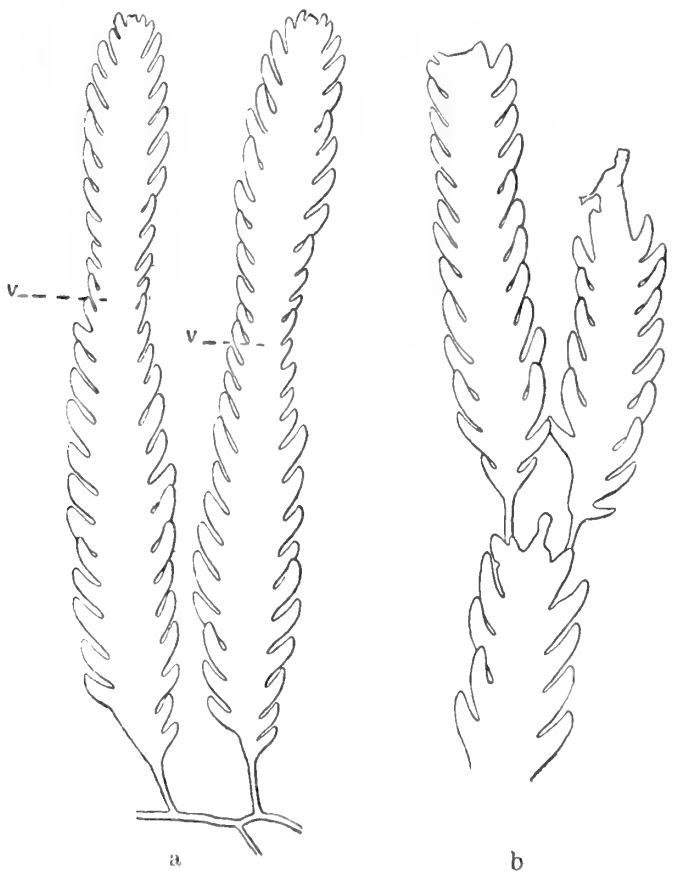

Fig. 2.—*C. scalpelliformis* (R. BR.) W. V. B. (1 × 1).

Structure of the shoots.—Especially characteristic of this species is the rich formation of regenerating shoots, precisely as J. G. AGARDH (Till Algernes Systematik I., p. 13) has asserted of it. These arise either from the points of the lobes, or from the median part of the lamina. Fig. 2 *b* shows an example of this kind of regeneration. But the leaves could increase in another way too without there being any sharp difference in the shape of a petiole. It seems to be such kind of regeneration to which J. G. AGARDH refers when in the description of his *C. scalpelliformis* (*loc. cit.* p. 13) he says: "Frondes saepe quasi innovatione prolongatae, lobis in una parte innovationis brevioribus, dein iterum longioribus," and a very fine example of this can be seen in a *C. scalpelliformis* (Herb. J. G. AGARDH, No. 16,425) collected by HARVEY in Australia. Another case can be seen in fig. 2 *a*. The terminal point of growth of the leaf (once situated at *v*) has after a short period of inactivity, resumed its activity, whereby the leaf has grown longer. This shows itself most clearly in the fact that the leaf has increased in breadth, so that the newly formed basal part has become broader than the upper part of the older portion of the leaf. (An example of the same kind is afforded by HARVEY's Plate XVII. in "Phyc. Australia" I.)

A proliferation has consequently taken place without the previous formation of a petiole. The leaves of Caulerpa show, therefore, examples of a continued and repeated apical-growth which is unknown in leaves of higher plants, but on the other hand is known in leaves of ferns and lower plants. This goes to prove the predominant shoot-nature of the assimilators, even if they have a shape analogous with leaves. This apical growth, although rhythmical, seems to be rather undefined. From this it is easily explained why the leaves in this species can attain such a great length, greater than in any other *Caulerpa ;* and it is such long growing forms that make up the *f. intermedia.*

If we examine such a leaf more exactly, we shall always find that it shows regularly alternating narrower and thicker parts, due to its development having gone on rhythmically, while the growing point has not worked uniformly, but periods of relative rest have followed periods of more active increase :

consequently a kind of pronounced periodicity in development. The same seems to me to be clear from WEBER v. BOSSE's drawings, (*loc. cit.*, Pl. XXIII., fig. 2, 5, 7).

Fg. 3. *C. scalpelliformis* (R. BR.) W. v. B. (1 × 1).

This unlimited increase in length appears to be more characteristic of *f. intermedia* than of *f. denticulata* (WEBER v. BOSSE, *loc. cit.* Pl. XXIII.), which, even if not always, has yet frequently shorter leaves which are not so strongly proliferate.

Although in general the internal construction of the Caulerpas is not dealt with in this paper, I cannot refrain from touching on the arrangement of the protoplasm strings and of the chloroplasts, so characteristic of this species, as shown in fig. 3. The same has already been pointed out by JANSE ("Die Beweg. d. Protopl. v. C. prol." p. 190) in connection with the description of the same phenomenon in *Caulerpa prolifera.* Numerous main veins run through the centre of the leaf, and from them fan-shaped veinlets run into the lobes, but curve back again toward the main veins, and hence arises the characteristic structure which is shown in fig. 3. It is specially chacteristic of *C. scalpelliformis.*

Geographical distribution.—INDIA: Paumben! (*f. intermedia* and *f. denticulata*), Tuticorin (FERGUSON, No. 411); the Pearl banks in the Gulf of Mannar (Dr. HERDMAN in E. S. BARTON's, "List of Marine Algæ collected at Ceylon in 1902.") From the RED SEA to the INDIAN OCEAN (Mauritius—Australia—Tasmania); ATLANTIC (Angola on the West coast of Africa according to several specimens in J. G. AGARDH's Herbarium in Lund! Brazil, according to MURRAY's "Catalogue of Ceylon Algæ," p. 38).

3.—**CAULERPA CRASSIFOLIA** (AGARDH) J. G. AGARDH.

J. G. AGARDH, Till Algernes Systematik I., p. 13.
M. A. HOWE, Phycological Studies II., p. 574.
SYN. *Caulerpa pinnata*, WEBER v. BOSSE, Monographie des Caulerpes, p. 289.
Caulerpa Harveyana KUTZING, Tab. Phyc. VII.: 5, III.
Caulerpa mexicana SOND. in MURRAY, Catalogue p. 38.
EXSICC: FERGUSON, Ceylon Algæ Nos. 154, 337, 412!

By examining the original type specimen of the younger LINNAEUS' *Fucus pinnatus* in the herbarium of the Linnaean Society in London, HOWE has shown that this plant belongs to the group Sedoideae and consequently has nothing to do with the *C. taxifolia* (VAHL) *v. crassifolia* AGARDH, which is the type for J. G. AGARDH's *C. crassifolia* created by him as a distinct species in "Till Alg. Syst." 1, p. 13. I have had an opportunity of examining the specimens HOWE mentions in his paper (*loc. cit.* p. 575), and which are to be considered as the type specimens for *crassifolia.* They are Nos. 16,445 and 16,446 in J. G. AGARDH's herbarium in Lund, and the specimens of this species that I have collected in Ceylon are quite identical with these, the original specimens from the West Indies. The same is the case with the specimens collected by FERGUSON (Ceylon Algæ, Nos. 337, 154, 412), which are kept in the Peradeniya herbarium under several different names, such as *C. taxifolia* AG. (C. A. 412), *C. mexicana* SOND. (C. A. 154), and *C. crassifolia v. Harveyana* (KG.) GRUNOW (C. A. 337).

There is no doubt left that this plant occurs both in the Indian and the Atlantic Oceans as WEBER v. BOSSE (*loc. cit.* 291) mentions, even if C. AGARDH's note "In mari Indico & rubro," as HOWE has shown, depends on faulty identification of the younger LINNAEUS' *Fucus pinnatus.* It is worthy of remark that in the AGARDH herbarium itself there are, of *C. crassifolia*, only specimens from the Atlantic but none from the Red Sea, nor from the Indian or the Pacific Oceans.

C. crassifolia occurs in Ceylon rarely in the littoral zone. Thus I have only found it at Weligama (9-3-03) inside the little reef at a depth of 1½m., where the water was very thick with sand. On the

other hand, it seems much more common on the Pearl Banks in the Gulf of Mannar. Thence come fine large specimens from North Moderagam Paar (Gulf of Mannar, leg. JAS. HORNELL, 3-4-03) from a depth of about 10m. (sandy bottom with *Halophila*).

C. crassifolia from Ceylon is, in respect to the increase of the leaf, defined (even if sometimes, though rather exceptionally, a repeated point growth may be observed) as is typically the case in *C. scalpelliformis*.

That such a pronounced growth can occur in *C. crassifolia*, however, is shown by specimens of the species collected by LENORMAND in Venezuela (Herbarium in the Royal Riks-Museum of Stockholm as well as by several specimens in the AGARDH herbarium in Lund. *e.g.* Nos. 16,457–16,460) : from the creeping horizontal axis rise several assimilators and these have very clear proliferations ; the growing point is, as it were, continued in a petiole which supports a new leaf, or, again, the formation of a petiole is wanting, and only the size of the lobes is diminished, to increase again later on. By this means different stories are built up of longer and shorter branches above one another. In passing, mention may be made of the fact that LENORMAND'S specimen also very clearly shows that the point of an assimilator can change its character and grow into a rhizome.

It is impossible for me to distinguish any different forms of *C. crassifolia* in Ceylon. A few specimens have, it is true, somewhat more vertically erected lobes, but they do not seem to have the character even of local forms.

Geographical distribution.—CEYLON : Weligama, at a depth of about 1½m. ! The Pearl Banks in the Gulf of Mannar (at a depth of about 10m.), collected by JAS. HORNELL ! FERGUSON, Ceylon Algæ No. 337! ; Tuticorin, collected by FERGUSON (Ceylon Algæ No. 412)!

RED SEA, INDIAN OCEAN, PACIFIC, ATLANTIC (from the West-Indies to the Canaries).

4.—**CAULERPA TAXIFOLIA** (VAHL) WEBER v. BOSSE.

WEBER v. BOSSE, Monographie des Caulerpes, p. 292.
MURRAY, Catalogue, p. 38.
EXSICC. : FERGUSON, Ceylon Algæ, No. 80 !

f. typica. Pinnules pronouncedly sickle-shaped, curved upwards, 4-5 times as long as the breadth of the main axis.

SYN. *Caulerpa falcata*, KUTZING, Tab. Phyc. VII., 5, v.

f. tristichophylla. Like to the foregoing form, but some of the assimilators have the pinnules at the base clearly arranged in three rows (fig. 5).

f. asplenioides (GREVILLE), WEBER v. BOSSE, *loc. cit.* p. 292 (fig. 4).

f. interrupta. Like the foregoing, but smaller and between the pinnules almost naked parts of the main axis. This variety is formed by repeated rhythmical point-growth of the assimilator (fig. 6).

C. taxifolia occurs on the shores of Ceylon in several forms, which, however, are not sharply distinct, but in places occur mixed together. Most common in the littoral zone is the form described as *f. typica*, illustrated by Kützing under the name of *C. falcata* ("Tab. phyc." VII., 5, v).

But I have also observed *f. asplenoides* GREV. growing together with the main form, especially at Matara in pools filled at low-water. The form *asplenioides* is, in its more pronounced forms (fig. 4), fairly characteristic, with its short, straight, not sickle-shaped pinnules, but transitions into the *f. typica*, are rather common. *F. asplenioides* seems to occur especially in deep water, and this is also the form

that occurs on the pearl-banks on the shells of the pearl-oyster (*Margaritifera vulgaris*), where it has been collected by HORNELL (Nov., 1902).

Besides these there occur also some other forms, which, however, are rare, and which do not play any characteristic part in the vegetation. One, which I have called *f. tristichophylla* (fig. 5), I have also observed together with specimens of the *f. typica* at Paumben (3-4-03).

Fig. 4.—*C. taxifolia* (VAHL) W. V. B. *f. asplenioides* (GREV.) W. V. B. (1 × 1).

Fig 5.—*C. taxifolia* (VAHL) W.V.B. *f. tristichophylla*, *n.f.* (1 × 1).

From a horizontal axis with a predominant number of assimilators of the main type, shoots forth a branch here and there with a few pinnules in three rows (fig. 5). It is, therefore, closely allied to *C. falcifolia*, and constitutes one of the links between *C. taxifolia* and *C. falcifolia*, as predicted by WEBER v. BOSSE. As *f. tristichophylla* has only a few assimilators with pinnules in three rows and, moreover, only at the base, and as in all other respects it corresponds with *C. taxifolia*, I have come to the opinion that it must be classed under this species, the more as I agree with REINKE in considering that to point out a link of this kind between two otherwise well distinct forms does not necessarily prove that these extreme forms belong to the same species. I am therefore of opinion that in spite of this form one is quite justified in maintaining both *C. taxifolia* and *falcifolia* as different species. Probably they have a common origin. In reality one can observe also in, for instance, HARVEY'S specimen (Friendly Islands Algæ No. 70, Herb. J. G. AGARDH No. 16,522), a few branches with pinnules in only two rows, *i.e.* typical *taxifolia* branches, but for the rest all the others are provided with pinnules in three rows. *C. taxifolia* stands in exactly the same relation to *C. falcifolia* as *C. sertularioides* to *C. selago*. *C. taxifolia f. tristichophylla* is consequently analogous with *C. plumaris f. Farlowii*. WEBER v. BOSSE ("Monographie" p. 295).

Fig. 6. *C. taxifolia* (VAHL) W. V. B. *f. interrupta*, *n. f.* (1 × 1).

As for the *f. interrupta* (fig. 6) it is a little deep-sea form from the pearl banks in the Gulf of Mannar growing together with *f. asplenioides* on the shells of the pearl-oyster. It is a reduced *f. asplenioides* with small, weak branches and small assimilators, with the pinnules in groups on the main axis and branchless parts in between. It is clear that it has originated in a manner analogous with *C. scalpelliformis f. intermedia* : that is to say, that the point-growth of the assimilators has gone on rhythmically and hence similar formations have arisen, which can be best compared with proliferations. The form seems to be more occasional, but is, however, of theoretic interest as being a form analogous with similar forms of other species, as for example *C. plumaris f. umbellata*, WEBER v. BOSSE (*loc. cit.*, p. 295).

Geographical distribution.—CEYLON : local and occasional as at Matara ! (*f. typica* ! and *f. asplenioides!*) in rock-pools ; Weligama! (at a depth of about 2 m. inside the reef together with *Halimeda gracilis*) ; Colombo (*f. typica*, FERGUSON Ceylon Algæ, No. 80 !) ; Pearl Banks in the Gulf of Mannar ! (*f. asplenioides*

and *f. interrupta* at a depth of about 10 m.), also at Paumben! (South-India) at a depth of about 6 m. (*f. typica*). INDIAN OCEAN. PACIFIC (*f. asplenioides* at Sandwich-Islands). ATLANTIC (the West Indies).

Note that the closely allied *C. falcifolia* has its distribution in the Pacific and on the coasts of Australia.

5.—**CAULERPA SERTULARIOIDES** (GMELIN) HOWE.

HOWE, Phycological Studies II., p. 576.

SYN. *Caulerpa plumaris* (FORSKAL) WEBER v. BOSSE. Monographie des Caulerpes, p. 294.
Caulerpa plumaris, AG. MURRAY, Catalogue p. 38.

EXSICC.: HARVEY, Ceylon Algæ No. 61!; FERGUSON, Ceylon Algæ Nos. 3, 40!; WITTROCK *et* NORDSTEDT, Algæ exsiccatae No. 344!

f. brevipes (J. G. AGARDH).
WEBER v. BOSSE, loc. cit. p. 294.

f. longiseta (J. G. AGARDH).
WEBER v. BOSSE, loc. cit. 295.

f. umbellata (WEBER v. BOSSE)
WEBER v. BOSSE, loc. cit. 295.

Caulerpa sertularioides f. brevipes (fig. 7) is a common littoral form at the surface of the water and seems to prefer spots somewhat exposed, where it grows in company with other green algæ, often in thick tufts (fig. 8). So it occurs on the western, more exposed side of the Galle reef, especially on the flat coral rocks below the Star bastion. On the surface it is often very short and the vertical axes often do not attain more than 1 cm. in height.

Fig. 7. — *C. sertularioides* (GM.) HOWE *f. brevipes*, (J. G. AG.). (1 × 1).

Fig 8.—*C. sertularioides* (GM.) HOWE *f. brevipes* (J. G. AG.). (1 × 1).

The leaves in *C. sertularioides* are often characterized by the same rhythm as I have already described before in several other Caulerpas, *e.g.*, *C. scalpelliformis*, *crassifolia*, and *taxifolia*. The growing point after a period of rest begins a new activity, whereby the first formed pinnules are very short and afterwards increase in size. As now the activity of the growing-point lasts only a very short time and consequently only a small increase in the leaf takes place each time, we thus get the characteristic *f. umbellata* (fig. 9), which is characterized at a hasty glance by its external likeness to *C. verticillata*, in that the branches are arranged in tufts around the main axis. Of course a sharp difference is constituted by the fact that *f. umbellata* has the pinnules predominantly in two directions, in contrast to *C. verticillata*. That *f. umbellata*, however, can also have them in several directions follows from WEBER v. BOSSE's note (*loc. cit.* p. 295).

Fig. 9. *C. sertularioides* (GM.) HOWE *f. umbellata* (W. v. B.). (1 × 1).

The two forms *f. brevipes* and *f. umbellata* are thus rather closely allied to one another; they grow promiscuously, and from the same *rhizome* there arise also both the one and the other form.

Also *f. longiseta* (fig. 10) characterized by its long, narrow pinnules in close rows, is not uncommon on the shores of Ceylon. But it occurs scarcely ever, if at all, in the upper part of the littoral zone, but usually in somewhat deeper water. It commonly grows, not together with *f. brevipes*, but, as far as I

have observed it, in deeper water, *e.g.*, at Trincomalee at a depth of from 10 to 15 m. It often grows together with *C. taxifolia* as at Weligama, where these two species occurred at a depth of about 1·5-2 m It also occurs at the same place inside cavities in coral stones at a depth of about 3 m.

Fig. 10.—*C. sertularioides* (GM.) HOWE *f. longiseta* J. G. AG. (1 × 1).

Geographical distribution.—CEYLON; in many places; in the upper part of the littoral zone (*f. brevipes* and *f. umbellata*) and also in deeper water (*f. longiseta*) : Tangalla (*f. brevipes*) ! Weligama (*f. longiseta*) ! Galle (*f. brevipes*, *f. umbellata* and f. *longiseta* [KJELLMAN in WITTR. et NORDST. Alg. exsicc. No. 344]) ! Colombo (FERGUSON, Ceylon Algæ Nos. 3, 40! in *Herb.* J. G. AGARDH No. 16,474 (*f. umbellata* and Nos. 16472, 16473, *f. longiseta*); Jaffna (*f. brevipes* and *f. umbellata*) ! Trincomalee (*f. longiseta*) !

RED SEA, INDIAN OCEAN, PACIFIC (to the Friendly Islands), ATLANTIC (from the West Indies to Cape Verde).

6.—**CAULERPA FREYCINETII,** C. AGARDH.

f. lata, WEBER v. BOSSE, Monographie des Caulerpes, p. 313.

I have observed this *Caulerpa* only once, namely, on the south beach of the island of Mandaitivu outside Jaffna in the north of Ceylon, at a depth of about half a metre at low water. It is a pronounced sand form, which has a strongly and well-developed rhizome creeping in the sand with short coarse assimilators. These are spirally bent with branches entangled, forming as it were small matted balls that stick up out of the sand. *C. Freycinetii* is very rich in forms and has an extensive distribution. *f. lata* occurs in the Red Sea, in the Gulf of Siam, and the Indian Archipelago as far as the Marian Islands and the Friendly Islands. REINKE mentions that *C. Freycinetii* occurs in East India, but does not specify any definite locality. In any case it has not been noted before from Ceylon* where, however, it seems to be a rare and accidental constituent, at least in the littoral flora.

Geographical distribution.—CEYLON : Jaffna (the island Mandaitivu) ! RED SEA, INDIAN OCEAN PACIFIC, ATLANTIC (the West-Indies).

7.—**CAULERPA CUPRESSOIDES** (VAHL) WEBER v. BOSSE.

var. typica, WEBER v. BOSSE, Monographie des Caulerpes, p. 327.

I have found this *Caulerpa* only once in the district investigated, namely in the upper littoral zone at Paumben Pass, where it grew together with *C. longistipitata*, *Chrysymenia sp.* and others. The plant is thus very rare within the Ceylon marine-flora district, in any case in the littoral region at least. WEBER v. BOSSE (*loc. cit.* p. 330) points out that the characteristic for this form (= *var. typica* WEBER v. BOSSE) is the great regularity with which the sub-navicular pinnules are arranged in three rows along the main axis, while at the same time an occasional branch with the pinnules only in two rows is not rare. This *C. cupressoides* from Paumben Pass corresponds exactly with this description and with WEBER v. BOSSE drawings (*lo . cit.* Pl. XXVII, 7 b, 2a, 3, and XXVIII., 1). In general the main branches are three-sided, but of the side branches of the last order an occasional one is two-sided. Moreover it corresponds exactly with the specimens collected by BORGESEN from the West Indies.

Geographical distribution.—SOUTH INDIA : Paumben Pass ! ; INDIAN OCEAN, PACIFIC, ATLANTIC (the West-Indies).

* It is however reported from the Laccadive Islands, Minikoi (GARDINER).

8.—**CAULERPA LESSONII,** Bory.

Bory, Voyage de la "Coquille," Crypt. p. 193. 1828. Atlas, Pl. 22, Fig. 3.

Kutzing, Tab. Phyc. vol. 7, tab. 6.

Syn. *Caulerpa fissidentoides*, Greville, Remarks on some Algæ bel. to the Genus Caulerpa. Ann. and Magazine of Nat. Hist., vol. XII, sec. ser. (1853), p. 3, Pl. II.

Caulerpa Lessonii, J. G. Agardh, Till Alg. Syst. I., p. 24 (1872).

Caulerpa pennata, J. G. Agardh, loc. cit. p. 26 (1872). Type-specimen in Herb. J. G. in Lund. No. 16.624 (Harvey, Friendly Isl. Alg. No. 68; note ! some specimens largely intermixed with *C. sertularioides* [Gmelin] Howe !).

Caulerpa Lessonii Weber v. Bosse, Monographie des Caulerpes, p. 339 (1898).

Caulerpa plumulifera, Weber v. Bosse, loc. cit.

Syn. ? *Caulerpa amicorum*, Harvey. Friendly Island Alg. Nos. 62, 63 (Herbarium J. G. Agardh in Lund. Nos. 16,630, 16.631).

Exsicc. Ferguson. Ceylon Algæ No. 413 (Tuticorin, South India)!

f. typica. The vertical axes more or less branched. The assimilators about 5 mm. in breadth with predominantly two-sided (but sometimes at the base also three-sided) pinnules, often larger than the main axis, which goes up to 2 mm. in breadth (fig. 11).

f. tuticorinensis. The vertical axes repeatedly furcated with the basal parts cylindrical for a good way up and without pinnules. The assimilators of three kinds: the majority not above 2 mm. in breadth, flat, with two-sided pinnules of about the length of half the main axis, others flat, as before, of a breadth of up to 5 mm. with two-sided pinnules somewhat bent upward, rather longer than the main axis, which is 2 mm. in breadth (that is, of the same kind as the *f. typica*), and finally too, though rare, assimilators with cylindrical main axis and only three-sided pinnules (fig. 12).

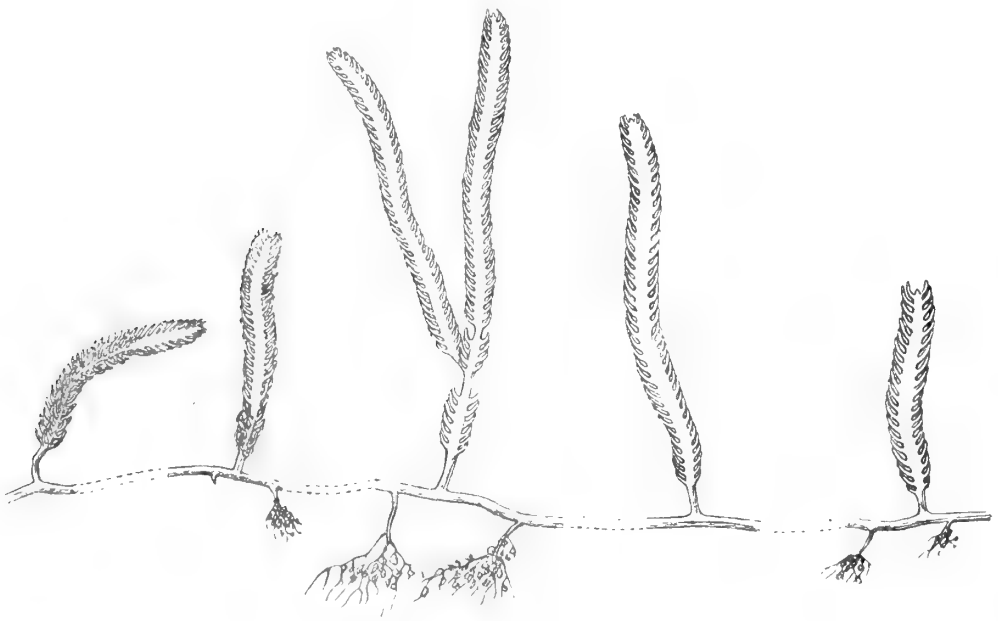

Fig. 11.—*C. Lessonii* Bory *f. typica*. (1 × 1).

The plant designated by me as the main form (fig. 11), was collected in the district by J. Hornell, east of the East Cheval Paar in the Gulf of Mannar, at a depth of about 10 m. It is a sand *Caulerpa* with the same mode of growth as *C. Freycinetii* with a very coarse horizontal stem, which often grows very deep in the sand.

The horizontal stem has very big root-branches which spread themselves in tufts of very fine branchlets, on which particles of sand are affixed very firmly. The basal parts of the assimilators are cylindrical and often without branchlets or pinnules for shorter or longer spaces.

The form *tuticorinensis* (fig. 12) has not been observed by me otherwise than in preserved specimens, and I can say nothing about its mode of growth.

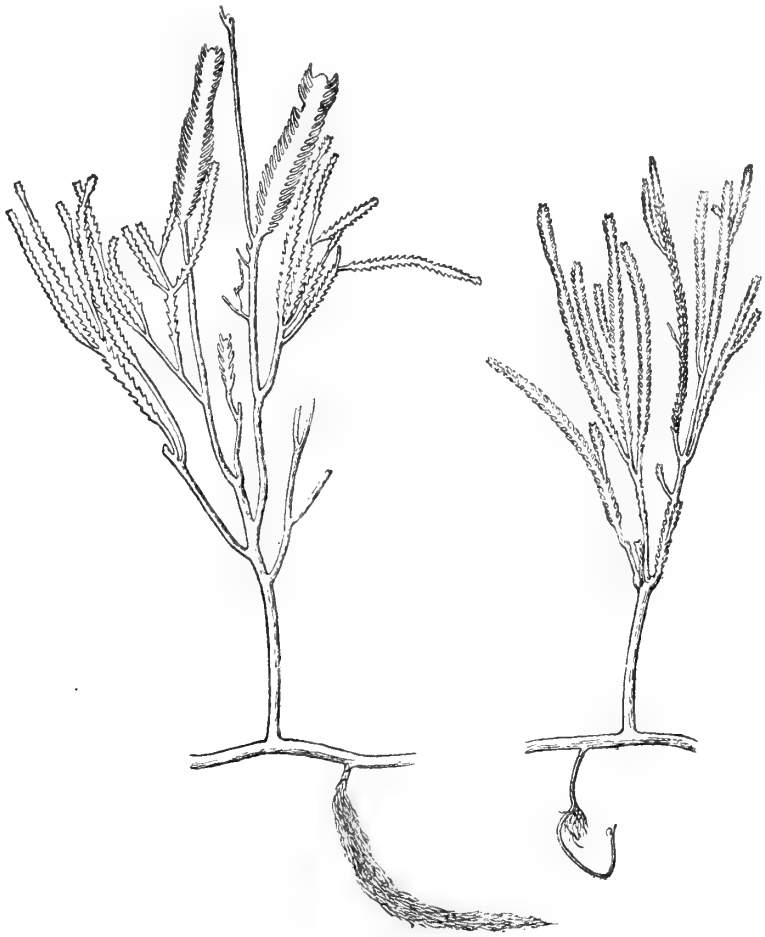

Fig. 12. —*C. Lessonii*, BORY, *f tuticorinensis n. f.* (1 × 1).

Remarks on the species.—Few Caulerpas, one may say, are so variable as those belonging to the group Thuyoideae. Hence, too, the nomenclature of these species is very confused and hard to disentangle. With respect to the species in question it seems to me that the following remark should be made to make clear my opinion about *C. Lessonii* and its synonymy.

The alga that BORY ("Voyage de la Coquille") described under the name of *Caulerpa Lessonii* is characterized by its flat main axis, distinguished by relatively great breadth, with usually two-sided branchlets. Even if, as WEBER v. BOSSE mentions (*loc. cit.* p. 339) BORY's fig. (or, at least, the copy in Kutzing, "Tab. Phyc." V. T., Tab. 6) has been drawn somewhat too broad, in any case Bory's *Lessonii* must have been characterized by relatively great breadth in comparison with related forms. These latter are to be looked for, on the one side, especially among the *C. cupressoides* series and particularly among var. *lycopodium*, WEBER v. BOSSE, and var. *disticha*, WEBER v. BOSSE; and on the other, also among the *C. Freycinetii* series var *pectinata*. But the main axis in these forms never, in general, approximately reaches the breadth which has been figured in *C. Lessonii*, BORY. Clearly, then, this character must be laid stress on when diagnosing *C. Lessonii*. The fact is that the main axis in this

species reaches as much as 2 mm. in breadth (exclusive of pinnules, of course) and is evidently flat, with two-sided pinnules.

That the plant I have reproduced here from Ceylon (fig. 11), collected by HORNELL on the pearl-banks in the Gulf of Mannar, is identical with GREVILLE'S *fissidentoides* (see GREVILLE, Pl. II., *loc. cit.*) seems to me to be beyond any shadow of doubt. GREVILLE'S figure has the main axis in certain parts almost 2 mm. in breadth, and in my figure (drawn natural size from formalin material) the main axis in many places is fully 2 mm. Also the circumstance that *C. fissidentoides*, GREV., has been collected on "the shores of the Peninsula of India" supports to some extent the assumption that these plants are quite identical. But, on the other hand, this species is, according to WEBER v. BOSSE—who had an opportunity of examining the type specimens—synonymous with *C. Lessonii*. Curiously enough J. G. AGARDH does not mention—as far as I have been able to find—anything about GREVILLE'S *C. fissidentoides*.

If, now, it is quite evident that the alga from the pearl banks is identical with GREVILLE'S *C. fissidentoides* and therefore also with BORY'S *C. Lessonii*, on the other hand the matter is by no means equally evident as far as another alga hereunto belonging is concerned, which has been collected by FERGUSON at Tuticorin in S. India and numbered 413 in his "Ceylon Algæ." It has been determined by GRUNOW as *C. Lessonii*—on the label in the Peradeniya Herbarium one reads "C. pectinata, Kutz"—and it is presumably the very same alga as MURRAY calls *C. fissidentoides* in his "Catalogue of Ceylon Algæ," p. 37. WEBER v. BOSSE, on the other hand, will not accept this determination (cf. "Monographie," pp. 339, 340) but is of the opinion that FERGUSON'S Ceylon Algæ No. 413 is to be referred rather to *C. plumulifera*, ZANARDINI (= *C. pennata*, J. G. AGARDH), at the same time as the author questions whether *C. plumulifera* is not possibly to be coupled with *C. Lessonii*, a matter which can only be settled when fresh specimens have been examined. In the Algal Herbarium in Peradeniya, which was kindly placed at my disposal, there are several specimens of this FERGUSON'S Ceylon Alga 413, but also another one too (FERGUSON, C. A. 161) labelled "*C. fissidentoides*," though of the last-named there is only one very poor specimen, only a few indeterminable fragments.

Where do these forms belong? The first named (C. A. 413) fairly corresponds in the main with WEBER v. BOSSE'S description and figure of *Caulerpa plumulifera*, ZANARDINI (*loc. cit.* p. 340, Pl. XXXI., fig. 3). It is, then, distinguished by assimilators with fairly long cylindrical petioles and with many branches (fig. 12). For the rest, the greater part of the branches also look as in WEBER v. BOSSE'S figure (*loc. cit.* Pl. XXI. fig. 3), which seems to justify this form being referred to *C. plumulifera*. But on a closer examination of the Peradeniya specimens it is soon clear that some are characterized by branches of a quite different kind, viz., partly broad, coarse ones, which by their size and breadth are sharply distinct from the others (the transitions to which are also very abrupt), and partly weak cylindrical ones with three-sided pinnules.

Fig. 12 shows specimens of FERGUSON'S C.A. 413. It is remarkable how the great broad branches absolutely correspond with the character which has been pointed out as characteristic for *Lessonii*, *i.e.* the relative breadth of the axis (up to and above 2 m.m.)and the length of the pinnules. A comparison between these branches and *C. Lessonii* in fig. 11 shows, therefore, a perfect correspondence. But from this it is also the more explicable how GRUNOW has been able to call this Alga *C. Lessonii*, and how MURRAY has included *C. fissidentoides* in his Catalogue of Ceylon Algae. On the other hand, these broad branches are not found in all specimens —*e.g.* not in FERGUSON'S specimens in AGARDH'S Herbarium (Nos. 16614, 16615) —and probably were not in the material that WEBER v. BOSSE had an opportunity of examining—they are not figured in her monograph Pl. XXXI., fig. 3—and from this it is quite natural that she should not have combined this species with *Lessonii*, but rather with *C. plumulifera*, ZANARDINI. But the appearance of the broad branches in the Peradeniya specimens shows, on the other hand, that one is justified in combining it with *Lessonii*, granting it to be a special form, characterized—as so many other *Caulerpa* forms—by some branches showing an appearance that corresponds with one species, other branches with another. As far as the third kind of branches is concerned, they have an appearance that

can be seen from fig. 12. They are narrow, weak, and covered in all their length with small three-sided branchlets or pinnules. By their weakness, and by the fact that they are covered in all their length with three-sided pinnules, these branches differ from those with three three-sided pinnules only at the base in the plant from the pearl-banks. The peculiar transition form which FERGUSON collected at Tuticorin, and which is of great interest owing to the construction of its shoots, I call *f. tuticorinensis*. The nature of this kind of shoots, etc., I have already discussed before in the general part of this work, and I will only emphasize in this place that I am not of opinion that the classification of this form *under Lessonii* as the main species must necessarily be so explained that *f. tuticorinensis* is subordinate to *Lessonii f. typica*. I have only wished in this manner to point out their close genetic relationship.

I think, therefore, that I have shown that BORY's *C. Lessonii*, described and figured as early as 1828, must be retained as at least relatively a well-characterized form. The name *fissidentoides* (GREV.) from the year 1853 must therefore be placed in the list of synonyms. And in my opinion we should also refer *C. pennata* (J. G. AGARDH) from 1872 to the same list. The type-specimens (Herb. J. G. AGARDH No. 16,624) which served AGARDH as the material for his description, are evidently smaller forms of the same species I have figured in fig. 11. Such weaker branches are also to be found among the material of *C. Lessonii* collected by HORNELL. But then AGARDH's *C. pennata* is of the very same coarse structure as *C. Lessonii* and with rather broad main axes. AGARDH, also, in the diagnosis speaks about "rachis atiuscula," just as he says about the plant that is it "robustior." To avoid confusion one must remember that AGARDH's specimens are, as he himself expressly pointed out (Till. Alg. Syst. I., p. 26) mixed with *C. sertularioides* (= *C. plumaris* (FORSK.). It follows as a matter of course that *C. plumulifera*, according to WEBER v. BOSSE's definition, must also be ranged among the synonyms. If ZANARDINI's specimens should also be included is an open question, as I have not had an opportunity of examining ZANARDINI's type-specimens.

That *C. Lessonii* is closely related to *C. cupressoides* is beyond a doubt. Especially the broader forms among the *lycopodium* series are very similar to *C. Lessonii*, and I have been very doubtful about *f. amicorum* in particular, as it offers great resemblance to *Lessonii*. It seems to me not improbable that perhaps several of these forms classed by WEBER v. BOSSE among the comprehensive *C. cupressoides* might with equal reason be transferred to the *Lessonii* group. This may also apply to some *C. Freycinetii v. pectinata* forms. For as WEBER v. BOSSE writes (*loc. cit.* p. 316) about this plant: "Souvent une partie de la fronde, ou des frondes entières, portent de petits ramules opposés, pectinés, *presque aussi grand que ceux du Lessonii.* * Ces échantillons portent dans les livres et la collection de MAZÉ et SCHRAMM les noms erronés de *C. pectinata*, KUTZ. ou de *C. Lessonii*, BORY."

But it is precisely the occurrence of large broad shoot branches with opposite pinnules that seems to refer these forms rather to *Lessonii* than to *Freycinetii*. As for these forms belonging to the Thuyoideae series, it is of more importance that a critical study of them be made in their natural habitat, combined with experimental cultures, and of their geographical distribution, than of perhaps any other Caulerpas, in order to get an insight into the principles governing the variation of these plants, which is necessary as a basis for their taxonomy.

In this connection we may point out that this FERGUSON's C. A. 413, according to notes in the Peradeniya Herbarium, was collected by him at Tuticorin in S. India, and consequently does not really belong to the Ceylon flora. But as all the algæ collected by FERGUSON at Tuticorin have been distributed in the collection "FERGUSON, Ceylon Algae," it is explicable that several forms have been mentioned in literature as being from Ceylon, although, strictly speaking, they have not been found there. For reasons mentioned in my introduction, they are more conveniently dealt with in connection with the Ceylon marine vegetation in general, though not belonging to the flora of Ceylon in a strict politico-geographical sense.

* Italicised by the present author.

Finally, with regard to the plant named *C. fissidentoides* (FERGUSON, Ceylon Algæ No. 161) in the Peradeniya Herbarium its determination is quite impossible, owing to its insignificance and poor condition. It seems to be closely related to such a form as *C. plumulifera* on Pl. XXXI, fig. 2 (but not fig. 3) in WEBER v. BOSSE's Monograph. On the other hand, it also seems to be very like *C. Freycinetii* var. *pectinata* (Pl. XXVI., fig. 3) and especially the specimens of this form from Koh Kahdat (Gulf of Siam) collected by JOHS. SCHMIDT (No. 108) determined by WEBER v. BOSSE and now in the collections of the Botanical Museum at Copenhagen.

Geographical distribution.—CEYLON: Pearl Banks in the Gulf of Mannar (*f. typica*) collected by J. HORNELL! SOUTH INDIA; Tuticorin (*f. tuticorinensis*) collected by FERGUSON (Ceylon Algæ No. 413)! INDIAN OCEAN; PACIFIC OCEAN.

9.—**CAULERPA CLAVIFERA** (TURNER) C. AGARDH.

C. AGARDH, Species Algarum, p. 437.

J. G. AGARDH, Till. Alg. Syst. I., p. 36.

SYN. *C. racemosa v. clavifera*. WEBER v. BOSSE, Monographie des Caulerpes, p. 361.

EXSICC. WITTROCK ET NORDSTEDT, Algæ exsiccatae No.345. FERGUSON, Ceylon Algæ No.17.

f. macrophysa (KÜTZING), WEBER *v.* BOSSE, *loc. cit.*

f. remota. The vertical axes and also the stalks of the branchlets more or less elongated; the branchlets separated by rather long intervals (fig. 14). This form grows in deeper water.

Caulerpa clavifera is the most common *Caulerpa* in Ceylon. It occurs in somewhat different localities both on rocks and amongst corals, but especially amongst the latter, on both sheltered and more exposed places. Amongst corals, on spots with rich supplies of changing water it seems to reach its highest development, and it seems to be one of the very few algæ which can grow together with living corals and Actinians. It grows in rather large tufts (fig. 13) with the horizontal branches creeping amongst the Actinians, and with only the always short vertical axes with their large sparsely scattered spherical branchlets sticking up above them. When it grows directly on stones the roots are rather more numerously arranged as adhesive organs and it becomes a form with a relatively fewer number of coarser branches. Also the vertical axis can attain somewhat different development in different localities. But what is so characteristic of this form is, that the whole assimilation system, *i.e.*, the spherical branches in general, is horizontally spread out in one level. This can be seen best if we look at fig. 13. From the coarse horizontal axis issue these vertical axes, but they are often exceedingly short, so that the spherical branchlets seem almost to be situated directly on them. If, on the other hand, the vertical axes are longer, they frequently come to lie recumbent with the spherical leaves directed only in one direction. A *Caulerpa clavifera* tuft seen from above consequently shows only a mass of small green spheres without any clear arrangement of axis system (fig. 13). It seems to me as if J. G. AGARDH has best drawn attention to this in his description of this plant ("Till. Alg. Syst." I., p. 36) when he says: "Surculi breviores, magis ramosi et intricati quam in plurimis. Frondes erectiusculæ quoque saepe breviores. Hinc ramificatio multo magis irregularis saepius adparet, surculis repentibus, frondibus erectis radicibusque non prope distinguendis, sed in speciminibus exsiccatis quasi sine ordine invicem mixtis." It follows from this

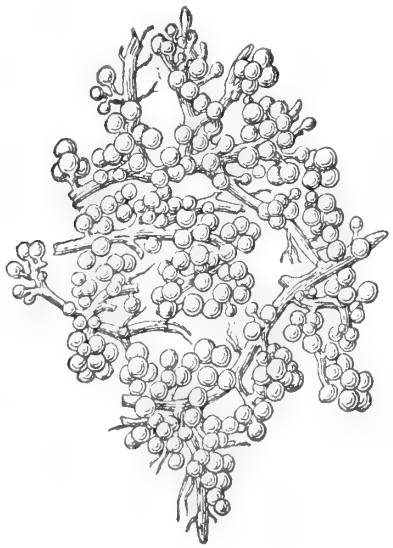

Fig. 13.—*C. clavifera* (TURN.) C. AG. (1 × 1)

manner of growth that this *Caulerpa* in a natural state assumes a very characteristic appearance, which can be gathered from Mrs. PEASE's description of the mode of growth of this plant in Jamaica when she says : (F. S. COLLINS, "The Algæ of Jamaica," p. 237) : "*Caulerpa clavifera* grew like little clusters of green grapes in big raggy masses." TURNER has also succeeded in describing the same characteristic appearance in his "Historia Fucorum" I., p. 126 : "The name of *F. clavifer* has been taken from the appearance of the plant when recent, in which state the branches look as if merely a cluster of small clavate bodies." But the idea of this mode of growth cannot be clearly gathered from even carefully prepared herbarium specimens (cf. for instance WITTR. et NORDST. Alg. Exsicc. No. 345 as 1,204), and this fact has not been sufficiently pointed out in the descriptions.

This *C. clavifera* is a pronounced littoral alga, which is only met with exceptionally in deeper water, and then often under a changed appearance. I have frequently seen it so near high-water mark that at low-water it is only washed by the swell and is thus always fully exposed to almost the whole strength of the tropical sun. And, pressed against the substratum as it is, it might not unappropriately be compared with that type of heath-plants which has been called "espalier plants" (WARMING)—it then receives that strength of light from practically one direction only.

With respect to the size of the spherical branchlets, this varies a little. In general the majority of the forms seem as if they ought to be referred to the *f. macrophysa*, at least acoording to WEBER v. BOSSE's definition of this form in her Monograph (p. 361).

Fig. 14.—*C. clavifera* (TURN.) C. AG. f. *remota n. f.* (1 × 1).

As has been mentioned above, *C. clavifera* forms are, as a rule, never met with in other places than in the uppermost part of the littoral region. Sometimes, however, one can find in deeper water a *Caulerpa* form which apparently is closely related to *clavifera*. Fig. 14 shows such a one, which I found at Galle in a dark deep pool growing on another alga. It differs in that the vertical axis system has been elongated and the branchlets or pinnules have been separated, and especially in that the stalks of the branchlets are often considerably longer than the spherical vesicles, while the main axis itself has been also considerably elongated. The whole plant gets through this, a habit which reminds one of *C. Lamourouxii*, at least its forms which have always cylindrical main axis. The original *f. Lamourouxii*, as it was described by TURNER—and according to him by C. A. and J. G. AGARDH—had only cylindrical axis. But, owing to the occurrence of transition forms to such forms as have flat axis, WEBER v. BOSSE has brought together all these forms under var. *Lamourouxii*, which thereby has received a very extended sense.

Whether such a form as this should be classed under the *Lamourouxii* series, however, seems to me to be very doubtful. There are no transition forms at all from *clavifera* to such ones with flat main axis to be found in Ceylon. This form should, on the contrary, most certainly be derived from *clavifera*, the only closely related form that grows in the district and of which it must be considered as a deeper water or shade form. Naturally it could imaginably be derived from *C. uvifera*, but this *Caulerpa* does not occur at all within the south-west region of Ceylon, but only in the north. Whether it is identical with J. G. AGARDH's *C. racemosa laxa* (Till. Alg. Syst. I p. 35) can only be determined by examining the type-specimens, but there are none in AGARDH's Herbarium. I propose to call this form *f. remota*.

I have not found any periodicity at all in the development of this species; it seems to have the same appearance all the year round.

Geographical distribution.—CEYLON: very common along the coast, but especially on the south-west, more rocky part with coral reefs. Tangalla! Dondra Head! Matara! Weligama! Galle (with *f. remota*)! Ambalangoda! Beruwala! Kosgoda! Jaffna! Kangesanturai! Trincomalee!

RED SEA; INDIAN OCEAN; PACIFIC; ATLANTIC (West-Indies).

10.—**CAULERPA UVIFERA** (TURNER).

SYN. *C. racemosa* β. *uvifera*, J. G. AGARDH. Till. Algernes Syst. I., p. 35.

C. racemosa var. *uvifera*, WEBER v. BOSSE, Monographie des Caulerpes, p. 362.

F. COMPRESSA, WEBER v. BOSSE, loc. cit. p. 363. EXSICC.: HARVEY, Ceylon Algæ No. 63.

f. intermedia, WEBER v. BOSSE, loc. cit. p. 363.

f. planiuscula. Some branchlets flattened out from above, but between these and the spherical ones regular transition forms are to be found (fig. 16, 17).

SYN. *C. racemosa* var. *uvifera f. intermedia* WEBER v. BOSSE. loc. cit. (pro parte) Fig. 24 a, b, Pl. XXXIII.

What constitutes the main difference between the *clavifera* and the *uvifera* series is that in the latter (fig. 15) the vertical axes (= assimilators, REINKE) reach a higher degree of development, while at the same time they are not so close. They are, as a rule, somewhat longer and have more numerous extremely close branchlets, which are situated around the vertical main axis. The assimilation system does not, therefore, lie on the same level, but each assimilator forms a more limited whole. This probably depends to some extent on the mode of growth.

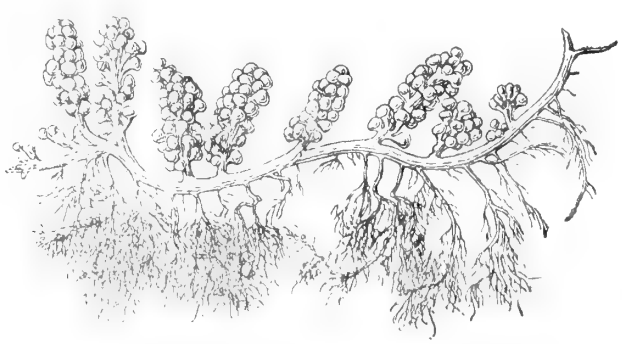

Fig. 15.—*C. uvifera* (TURNER). (1 × 1).

For, in Ceylon, *C. uvifera* is not to be found in the same places as *C. clavifera, i.e.*, in the strictly littoral regions. On the contrary, I have never seen this *C. uvifera* on the coral reefs or rocks in the south-west of Ceylon, where rocks predominate; I have only found it at Jaffna and Kangesanturai in the north of Ceylon from rather deep water and where the shores have quite a different character, with a loose bottom consisting of sand and coral-mud. At Kangesanturai it occurred abundantly, lying free

on the beach, washed ashore probably from somewhat deeper regions. It is also remarkable that in regard to the root-system quite a remarkable difference prevails between *C. racemosa* and *C. uvifera*. The latter has, as can easily be seen by comparing figs. 13, 14, and 15 a much more richly developed root-system.

The root branches are longer and more branched, parting into innumerable fine root-branchlets. These adhere so firmly to sand and shell particles that on uprooting these plants masses of sand and the like will loosen and accompany the roots sooner than these latter break. The *clavifera*, preferably growing on corals and stones, on the other hand, has not by a long way so finely branched a root-system, but is fixed by few and coarser root-branchlets.

The difference that exists between *C. racemosa* and *C. uvifera* in respect to their organization corresponds therefore with different localities. The majority of Ceylon forms of *uvifera* observed by me seem to belong to *f. intermedia* (WEBER v. BOSSE), at least when chief importance is laid on the character which is laid stress on in the diagnosis, viz., that " les ramules " are evidently stalked.

The *f. compressa* WEBER v. BOSSE (HARVEY, Ceylon Algæ 63) I have been unable to find again. On the other hand, in the Peradeniya Herbarium there is a little form from Bentota labelled " *C. sedoides* Ag. " which seems indentical with Harvey's C.A. 63. Probably it is a mere accidental form, which does not play any very important part in the vegetation.

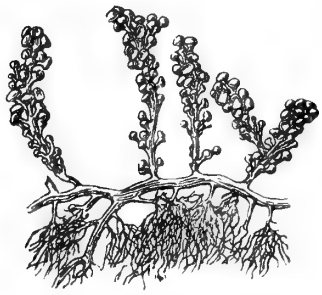

Fig. 16.—*C. uvifera* (TURNER *f. planiuscula n. f.* (1 × 1).

Fig. 17.—*C. uvifera* (TURNER) *f. planiuscula n. f.* Different kinds of branchlets—a, b, c from the base, d, e from the top. (3 × 1).

The *f. planiuscula* is of a great theoretical interest. Fig. 16 shows a picture of it. WEBER v. BOSSE has, in her monograph figured such a form (*loc. cit.* Pl. XXXIII. fig. 24 *a* and *b*.) and also described its origination, though only in the explanatory text accompanying the figure (p. 401, &c), without, however, giving it a special name and only arranging it under *f. intermedia*. She does not mention it in dealing with the different forms of *C. uvifera*. As to the mode of growth and habit, it corresponds with other *uvifera* forms. On a closer examination of the axis, however, we shall find that, especially at the point, flattened out vesicles occur together with transition-stages to the spherical ones (fig. 17). Such branches remind one somewhat of *C. peltata* and *C. Chemnitzia*, but from these the *f. planiuscula* differs partly by the lack of cylindrical branchlets at the base, partly too by the flattened branchlets being more sharply distinguished—the vesicle being more distinctly set of from the stalk and not with the shape characteristic of *Chemnitzia*. The organisation of *f. planiuscula* means, as we can see, a certain increase of the assimilating surface, in analogy with *C. peltata* and *C. Chemnitzia*. But whereas, as for instance in *Chemnitzia*, the flattened branchlets are derived from strictly cylindrical branchlets, in *f. planiuscula* they are formed by transformation of spherical branchlets (cf. fig. 17). These different forms consequently show a fine example of how forms externally similar may be developed in different ways.

Geographical distribution.—CEYLON: *f. intermedia* on the north coast of Ceylon in the deeper parts of the littoral zone; the islands around Jaffna! Kangesanturai! *f. compressa*, Bentota (FERGUSON) and HARVEY (without any more clearly defined locality); *f. planiuscula*, Jaffna!

RED SEA; INDIAN OCEAN; PACIFIC; ATLANTIC (West Indies).

11.—**CAULERPA CORYNEPHORA**, MONTAGNE.

SYN. *C. racemosa* var. *corynephora*, WEBER v. BOSSE, Monographie des Caulerpes, p. 364.

f. complanata (J. G. AGARDH) WEBER v. BOSSE, loc. cit.

Fig. 18.—*C. corynephora* MONT. *f. complanata* (J.G. AG.) W. v. B. (1 × 1).

In the Herbarium in Peradeniya there is, under the name of "*Caulerpa clavifera* var. ? DICKIE," a *Caulerpa* collected by FERGUSON at Tuticorin (Ceylon Algæ No. 414) on the Indian Coast. As these algæ are in his collection of Ceylon Algæ and as Tuticorin is situated close to the flora district of Ceylon, a mention of this *Caulerpa* form may not be without interest. Fig. 18 shows the appearance of this *Caulerpa*. It has a strongish horizontal rhizome with a vertical axis clearly flat and the branchlets arranged in two opposite rows. It is evident that it belongs to the *corynephora* series in WEBER v. BOSSE's opinion, and corresponds well with J. G. AGARDH's description of *C. complanata* ("Till. Alg. Syst." I., p. 33), as also with type-specimens in AGARDH's Herbarium in Lund. We may call special attention to the correspondence with AGARDH's description of the branchlets (ramenta) as can be seen from the picture. That is to say, they are partly more regular in breadth, partly also constricted at the base, and consequently more clavate at the point. When branches of the latter kind predominate this form has a resemblance to the *Lamourouxii* series, with which the *corynephora* series has evidently some relationship.

Geographical distribution.—SOUTH INDIA: Tuticorin (FERGUSON, Ceylon Algæ, No. 414)! CELEBES; Tropical Coasts of AUSTRALIA.

12.—**CAULERPA LÆTEVIRENS**, MONTAGNE.

SYN. *Caulerpa racemosa* var. *lætevirens*, WEBER v. BOSSE, Monographie des Caulerpes, p. 366.

f. laxa (GREVILLE). WEBER v. BOSSE, loc. cit. p. 367.

GREVILLE, Remarks on some Algæ bel. to the Gen. Caulerpa, Pl. II., figs. 1, 2. Ann. and Magazine of Nat. Hist., vol. XII, sec. ser. (1853).

Caulerpa laxa, GREV. MURRAY, Catalogue p. 38.

EXSICC. HARVEY, Ceylon Algæ No. 64.

f. depauperata. In all respects very slender and weak, smaller than any other forms; it is most nearly allied to *f. laxa*, of which it is probably to be considered a *dwarf* form (fig. 20).

f. cæpitosa. Branchlets swollen up, rigid, cylindrical, or somewhat clavate, the vertical axis short, not above 15 mm. in height and the whole plant firmly and closely tufted with very rigid branchlets rather closely pressed together (figs. 21, 22).

C. laetevirens is perhaps one of the rarest *Caulerpa* forms in Ceylon. I have only observed it at Galle (*f. laxa*, *caespitosa*, and *depauperata*) and Weligama (*f. laxa*) on the south coast, and only at the first-mentioned place in any great quantity, forming a distinct association. At Galle it grows on the ledges north of Victoria Park; there it constitutes by itself almost the whole vegetation in localities strongly exposed to swells, where the slender assimilators swing to and fro in the waves.

In its organization it also shows adaptations to such a mode of life. The rhizome (fig. 19 *a*) or the creeping horizontal axis is relatively strongly developed, and very long, with numerous closely set

root-branches fixed to the scarred rocks ; on the other hand, the vertical axes are few and with rather large intervals between them. The result is that the plant becomes firmly fixed, because the rhizome and the system of roots are so strongly developed in comparison with the relatively few and short assimilation branches which they have to keep attached. The vertical axes are slender with close pinnules. These, in regard to their form, may vary a little, in that they are sometimes quite cylindrical—which is the most common, sometimes more clavate and somewhat flattened laterally. The former kind of branches is the commoner, and if both kinds occur on the same vertical axis the cylindrical ones are to be found at the base, the clavate ones at the top. This form is precisely GREVILLE's *C. laxa* (HARVEY, Ceylon Algæ No. 64) according to specimens in J. G. AGARDH's Herbarium in Lund (No. 6,744).

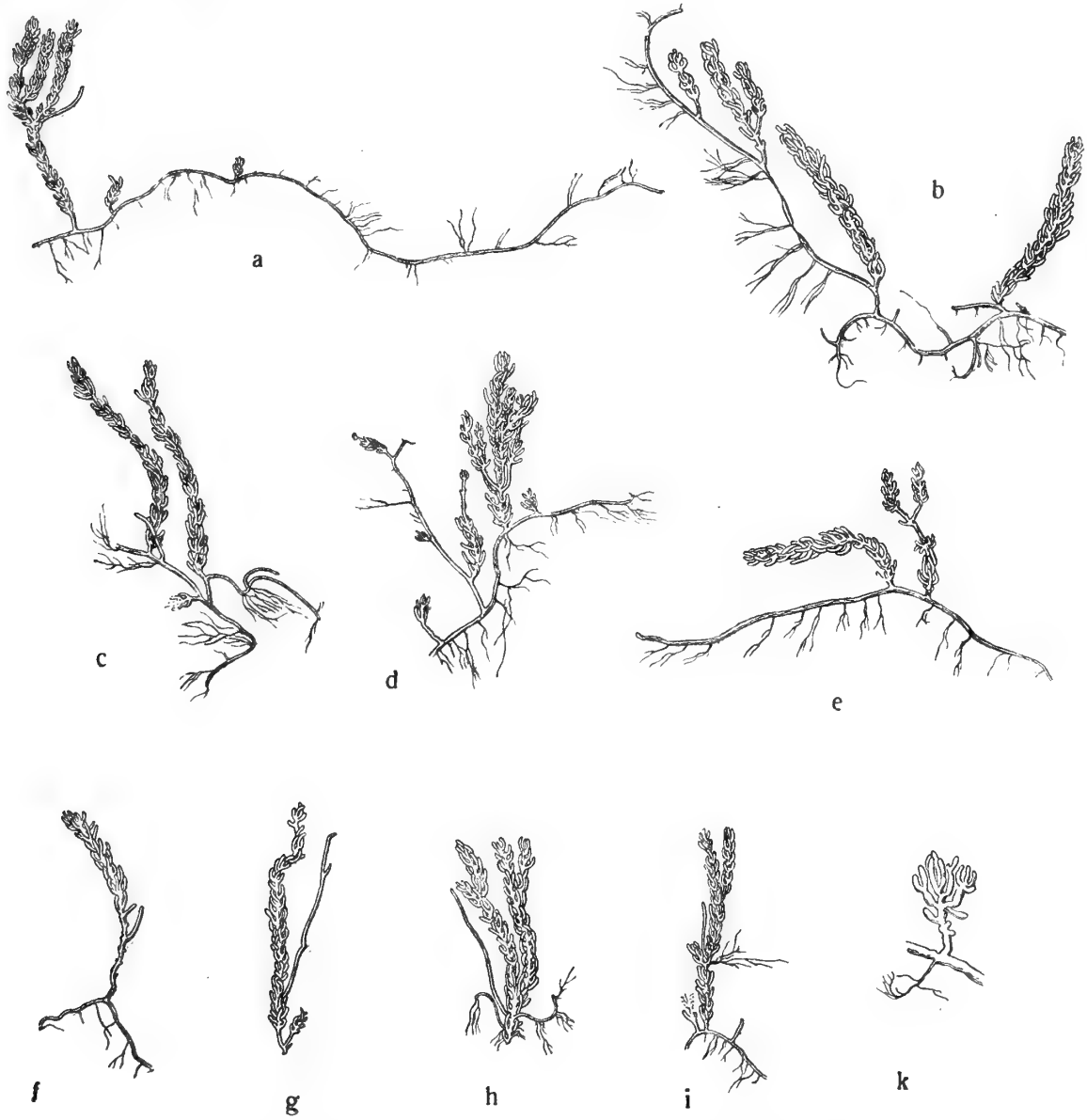

Fig. 19.—*C. lætevirens* (MONT.) *f. laxa* (GREV.); (a—i 1 × 1; k 2 × 1).

As specially characteristic of *forma laxa* and what may also be regarded as a kind of adaptation to its manner of growth in strongly exposed places, is its very strongly developed formation of rhizomes : see fig. 19. In this connection it may be especially pointed out that this form shows great inclination to let the branchlets grow out to horizontal axes which take root and contribute to attach the plant ;

they are consequently a kind of haptera (fig. 19 *a*, *c*, *f*, *g*, *h*, *i*) ; but these branchlets again form vertical axes and behave exactly as the other horizontal axes. The figures show several examples of this : so in fig. 19 *f*. we see a vertical axis where most of the pinnules at the base are gone, and only a few remain, which are just in the stage of growing out. They have not, however, as yet reached any length. Different is the case, on the other hand, with those which are given in fig. 19 *a*, *g*, *h*. In fig. 19 *a*, for instance, may be seen a fully grown branch beginning to branch; in fig. 19 *h*, where, moreover, several branchlets have grown out it has formed roots too; and the same is the case in fig. 19 *i*, &c. In all these cases it has been assimilation branches that have changed character and turned into attaching organs. These changed branchlets might possibly be looked upon as of little value, since they do not develop in the same level as the rest of the rhizome system ; but here we must observe that the rocks are, of course, very uneven, with crevices and cavities, so that the haptera easily grip, even if they are developed higher up. This form with its creeping and climbing rhizomes entangled in each other forms almost mat-like associations, from which here and there rich shoot systems radiate. Of all the Caulerpas I have studied in Ceylon there is none which shows itself in its system of shoots so well adapted for the conditions of life in which it grows as this. That the same seems to be the case with this species in other places, for instance Western Australia, can be gathered from HARVEY's notes ("Phyc. Austr." I., Pl. 30). HARVEY says that the rhizomes form mats of the length of an inch or more with numerous and long roots, an apperance which is also to be seen in his figures of this plant. HARVEY also mentions that it grows "in exposed tide-pools" even if it is not absent in sheltered places.

But the branchlets not only grow out into new rhizomes, but may also directly branch and form new assimilation branches. This is also a rather common case and several examples of it are to be seen in fig. 19 *a*, *d*, *e*, *h*, *i*, *k*. In fig. 19 *d* appears an assimilator where three to four closely set branchlets have grown out in this manner into new assimilators, which are placed as a whorl around the main axis. In fig. 19 *k* is shown, doubly magnified, a young assimilator of which the branchlets have begun to part themselves in several branchlets. In few Caulerpas can the branchlets change so easily both into rhizomes and into new assimilators as in *lætevirens f. laxa*. The branchlets thereby very evidently betray their shoot-nature.

Fig.20.—*C. lætevirens* (MONT.) *f. depauperata n. f.* (1 × 1).

I have never seem any forms so big that they could be classed under *f. typica*, WEBBER v. BOSSE (*loc. cit.* p. 366), nor have I seen any that could be classed under *f. cylindrica* with any certainty ; practically all are identical with *f. laxa*, GREV. But, on the other hand, one can sometimes find forms as exceedingly stunted as those figured in fig. 20 and which I have called *f. depauperata*. Such dwarf forms may also be seen in other Ceylon Caulerpas.

Fig. 21. -*C. lætevirens* (MONT.) *f. cæspitosa n. f.* (1 × 1).

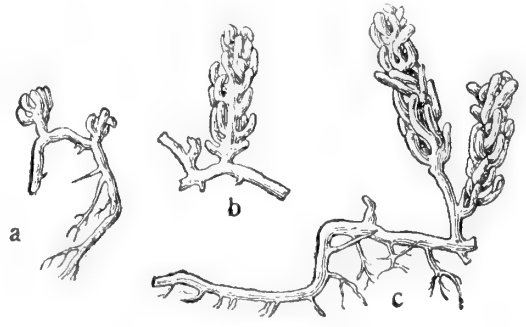

Fig. 22.—*C. lætevirens* (MONT.) *f. cæspitosa n. f.* (2 × 1).

As an ecological form of great interest *f. cæspitosa* (figs. 21, 22) is worth considering. It differs partly by being somewhat smaller and in the form and rigidity of its branches, and partly and

especially in its mode of growth. The vertical axes are very short and closely set. The often flattened branchlets are rather rigid, and turned either up or down, and mostly directed so that as much of the surface as possible is exposed (fig. 22). This is often produced by a torsion of the branch, so that the flat side gets turned upwards. Moreover, the branches sometimes become somewhat enlarged at the point: in any case the result is that a close compact tuft-formation is produced with, at the same time, the exposure of as much of the assimilation-surface as possible. To the rigidity of the tuft-formation contributes, too, the fact that the branchlets are very rigid and not, as in the other forms, easily waved to and fro. This form, so biologically different, was found by me on stones together with several other tuft-forming seaweeds in somewhat deeper water, so that they were not laid bare at low-water and not so strongly exposed to the swell as *f. laxa*.

Finally, it seems to me to be by no means unimportant to point out that the *laxa* forms in Ceylon showed themselves very constant and well defined from other *Caulerpa* forms. In every case transition forms to the *clavifera* and the *uvifera* series were entirely absent.

Geographical ditribution.—CEYLON: Galle (*f. laxa* and *f. depauperata* in exposed places; *f. caespitosa* in somewhat deeper water or not so exposed places)! Weligama! INDIAN OCEAN (Western Australia); ATLANTIC (West Indies).

Fig. 23.—*C. dichotoma n. sp.* (1 × 1).

13.—**CAULERPA DICHOTOMA,** n. sp.

The horizontal axis enlarged, creeping, with the upward flattened vertical axis up to 4 cm. in height with generally opposite, always flattened branchlets with generally furcate dichotomous points (figs. 23, 24).

C. dichotoma comes near to *C. lætevirens* and *C. Lamourouxii*, but differs from both in having the greater part of its branchlets dichotomous.

I found this *Caulerpa* at Weligama at a depth of from 1 to 2 m. on sandy bottom.

What justifies its creation as a special elementary species is its characteristic quality of the branchlets being dichotomous (fig. 23). A typically developed axis with such branchlets is to be seen in fig.

24 *a*. In general, the branchlets at the base seem to be undivided (fig. 24), and the dichotomous branchlets only begin higher up. On the other hand, assimilators from the same horizontal axis occur, with both prevalently simple and prevalently dichotomous branchlets

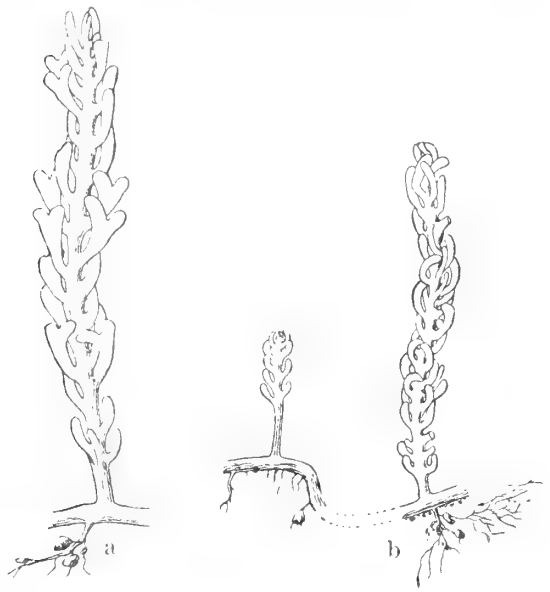

Fig. 24.—*C. dichotoma n. sp.* (2 × 1).

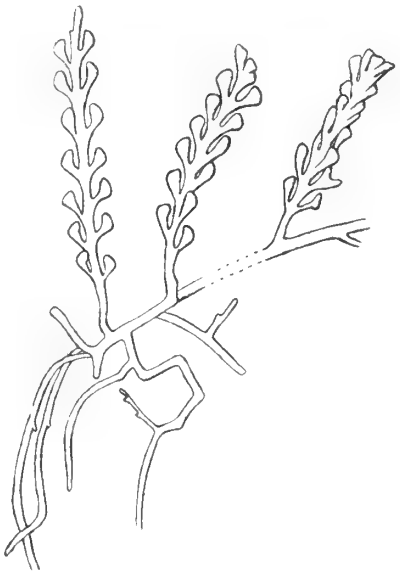

Fig. 25.—*C. Lamourouxii* (TURN.) from Yemen coll. by MONTAGNE. Specimen in the Herb. in the R. Riksmuseum in Stockholm. (1 × 1).

This *Caulerpa* is without any doubt nearly related to both *C. lætevirens* and such types as *corynephora* or *Zeyheri*. The correspondence with *C. lætevirens*, especially the *f. laxa*, shows itself in the simple pinnules, especially at the base, which also in *f. laxa* are somewhat flattened together from the sides. Moreover, the vertical axes are often cylindrical in *C. dichotoma*, in which case also the pinnules radiate from all sides, and this is especially the case at the base. The plant, too, at a first glance gives the impression of a *C. lætevirens*, though the mode of growth is rather different. On the other hand, the flattened axes with their opposite pinnules indicates a close resemblance to *corynephora*. But a new fact is added to this, viz., the tendency of the pinnules to branch dichotomously, and it is this character that justifies the creation of this plant as a special elementary species. A certain resemblance seems to be present to the little weak *f. Zeyheri*, too, which has also the pinnules opposite and laterally flattened; but it is always very slender, and at the same time it has always simple pinnules of somewhat different shape, so that a confusion with *C. dichotoma* is not likely to occur. However, *C. dichotoma* is very similar, or at least analogous in its development to both *lætevirens* and *Lamourouxii* (in WEBER v. BOSSE's definition). In the Herbarium in the R. Riksmuseum in Stockholm there is a *Caulerpa* labelled *C. clavifera* AG. (Yemen) from MONTAGNE's Herbarium. On the same shelf are mounted two distinct forms, not only typical *clavifera*, but also some specimens of another with flat axes and opposite sparse pinnules with the appearance of *C. Lamourouxii* (Pl. XXXII. 1 WEBER v. BOSSE, *loc. cit.*). On one of these (fig. 25) there are a few axes in which some branches show a trace of this very dichotomy which occurs typically in *C. dichotoma*. And on a closer examination of other Caulerpas I also found in the Herbarium in the Copenhagen Museum a Caulerpa on the label of which was only noted that it had been collected in "India orientalis." with similar dichotomous branchlets. It is a rather low, flat *Caulerpa* with sparse single branchlets. One of these is dichotomous. But in none of these latter specimens were the dichotomous branchlets so plentiful as in *dichotoma*. Probably *C. dichotoma* is a form which is closely allied to *lætevirens* and *Lamourouxii*, which two latter are themselves closely allied. But this does not prevent *dichotoma* being distinguished as a special elementary species, and REINKE is undoubtedly right in pointing out that the

discovery of some transition forms between two *Caulerpa* types need not necessarily result in the union of these species.

C. dichotoma has a different mode of growth to *C. lætevirens f. laxa*, for the former does not occur on rocks in very exposed localities, and the latter does. *C. dichotoma* is only to be found on sandy bottoms in somewhat deeper parts of the littoral zone.

Geographical distribution.—CEYLON : Weligama (at a depth of about 1 to 2 m.) !

14.—**CAULERPA CHEMNITZIA** (ESPER) LAMOUROUX.

J. G. AGARDH, Till. Algernes Systematik, I., p. 36.

SYN. *C. racemosa* var. *Chemnitzia*. WEBER v. BOSSE, Monographie des Caulerpes, p. 370.

Few Caulerpas, as far as their definition goes, may be said to be more difficult to diagnose than *C. Chemnitzia*.

It is really indisputable that the opinion—in the main—of the position of this form, as expressed by WEBER v. BOSSE, is right : it is to be considered as a transition form between *C. racemosa* (WEBER v. BOSSE *sens. lat.*) and *C. peltata*. Its distinguishing character is that, as a rule, it has branchlets of different kinds, viz., partly cylindrical ones at the base of the vertical axis, and partly, higher up, such as slowly increase in breadth and are nearly trumpet-shaped. Figs. 26 and 27 show pictures of some which I consider to belong to typical *C. Chemnitzia*.

Fig. 26.—*C. Chemnitzia* (ESP.) LAM. (1 × 1).

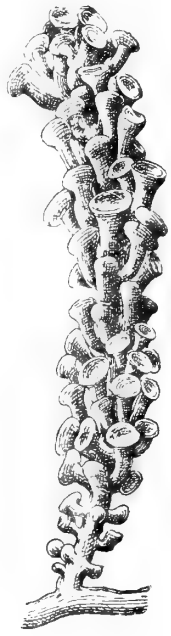

Fig. 27.—*C. Chemnitzia* (ESP.) LAM. (3 × 1).

Fig. 28.—*C. Chemnitzia* (ESP.) LAM. f. *ad peltatam* (1 × 1).

A closer examination of this species shows, however, that it has not always these types of branchlets but that it varies very considerably, and these variations may point in different directions. One type of variation is to be seen in fig. 28 and fig 29 : the cylindrical basal axes are rather few, but on the other hand the trumpet-shaped axes begin very early, and they constitute the majority of the branchlets, ultimately to change—and it is this that is most noteworthy—into typical *peltata* branches with large discs and a sharp limit between disc and stalk (fig. 28.) Herein we can see a good example of the fact that *C. Chemnitzia* can go over to *C. peltata* and that the supposed relationship between *C. Chemnitzia* and *C. peltata*, as supposed by former authors, *e.g.*, DECAISNE, ZANARDINI, is fully justified.

But, on the other hand, there are also forms which point in quite a different direction. In Ceylon too, there are *C. Chemnitzia* forms which have their upper branchlets developed more in a spherical than a disciform way. Fig. 30 shows such a form growing together with other *C. Chemnitzia* forms. Such are more rare on the Ceylon coast, but occur more frequently on other coasts. Thus ASKENASY ("Forschungreise, S. M. S. Gazelle." IV., Algen) mentions such a form from New Guinea, and BORGESEN has collected a similar one in the West Indies at St. John (WITTR., NORDST. ET LAGERH. Alg. exsicc. No. 1,586) which is very characteristic in that the upper part of the vertical axis to nearly half the length of the axis is provided with spherically swollen branchlets. It is also a typical form of this kind that REINKE gives in fig. 57 of his work on Caulerpa. Such forms seem to be more common in the West Indies and it is apparently such a form that J. G. AGARDH has grouped as *β. occidentalis* in his Caulerpa Monograph,

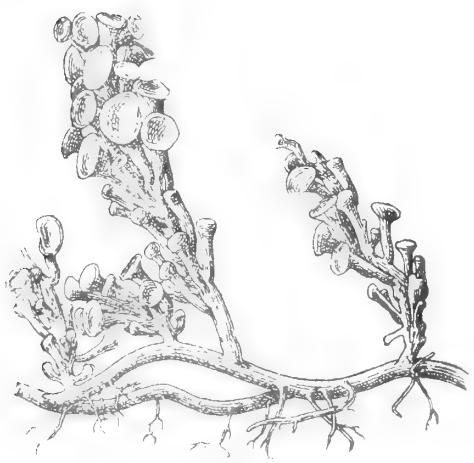

Fig. 29.—*C. Chemnitzia* (ESP.) LAM. f. *ad peltatam*. (3 × 1).

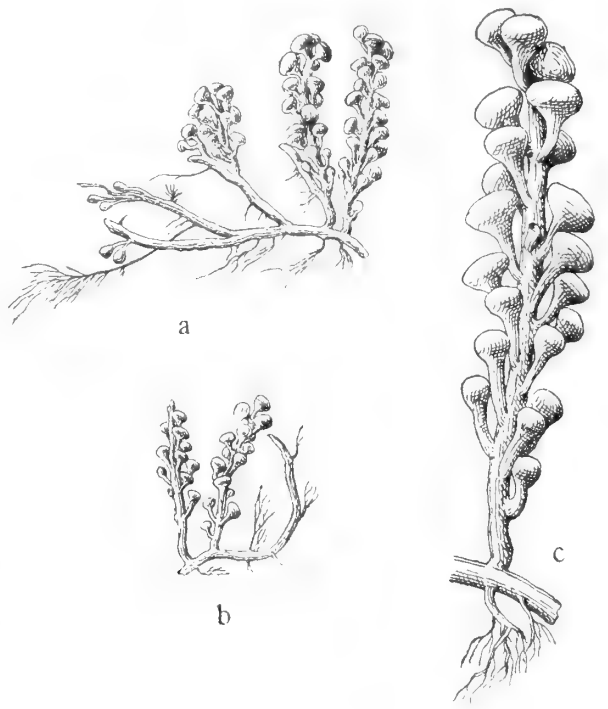

Fig. 30.—*C. Chemnitzia* (ESP.) LAM. f. *ad uviferam*. (a, b 1 × 1; c 3 × 1).

p. 37. And it is naturally the existence of such forms as has induced WEBER v. BOSSE in her monograph to class *C. Chemnitzia* as a variety of *C. racemosa* (*sens. lat.*) thereby following up an idea suggested first by ASKENASY *loc. cit.* p. 16) even if she lays stress on its transitionary position between "*racemosa*" (*sens. strict.* = *uvifera*) and *peltata*.

But if now *Chemnitzia*, as I have already shown, can develop to the same extent in the *peltata* direction as in the *uvifera* direction, it seems evident to me that it could with equal justification be classed under *peltata* as under *racemosa-uvifera* (*sec.* WEBER v. BOSSE). And judging from the variations of this species in Ceylon, one would be inclined to prefer the latter. But in my opinion both would be equally unhappy. For it is clear that *C. Chemnitzia* should be considered as a more original form than either *uvifera* or *peltata*. In reality it can develop into either. That in both variations the *basal* branchlets, *i.e.*, the first formed and earliest developed, are cylindrical seems to prove that this is an original character. If all the branchlets continue to be of this kind we get *C. lætevirens*, while if some begin to show trumpet-shaped swellings, but with flattened points, we have the typical *Chemnitzia*, which—according as the variation assumes the disciform or the spherical shape—gives rise to *peltata* or *uvifera*, respectively. But it follows from this also that *C. Chemnitzia* is to be placed under neither the one nor the other, but

should be classed as independent, as a special elementary species, and that the others should consequently be subordinated to it as varying in different directions.

Also such a form as *C. imbricata* might be directly attached to *C. Chemnitzia*, *i.e.*, by means of the little *f. mixta* with the cylindrical basal pinnules. But since this lacks the slowly tapering trumpet-shaped branchlets, this is a reason that opposes such a suggestion.

Geographical distribution.—CEYLON : only the North parts : Jaffna! Kangesanturai (from somewhat deeper water) ! SOUTH INDIA : Paumben Pass ! RED SEA ; INDIAN OCEAN : ATLANTIC (West Indies) ?

15.—**CAULERPA PELTATA**, LAMOUROUX.

J. G. AGARDH, Till. Algernes Systematik, I., p. 37.

SYN. *C. peltata* v. *typica* (pro parte) WEBER v. BOSSE, Monographie des Caulerpes, p. 375.

This species has a characteristic mode of branching and growth (fig. 31). From the rather coarse horizontal axes spring long vertical axes with plenty of peltate branchlets. As the illustrations of this

Fig. 31.—*C. peltata* (LAM.). (1 × 1).

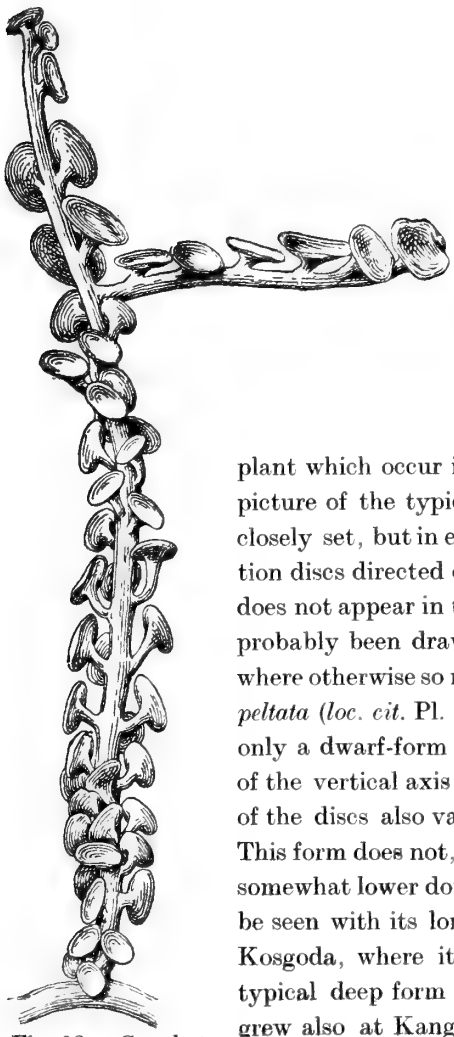

Fig. 32.—*C. peltata* (LAM.) f. *ad nummularium*. (3 × 1).

plant which occur in literature are rather unsatisfactory, I have in fig. 31 given a picture of the typical *peltata* form. The disc-shaped branchlets are more or less closely set, but in every case they radiate in all directions with the peltate assimilation discs directed obliquely upwards. It is precisely this direction of theirs which does not appear in the figures of this form which occur in literature, and which have probably been drawn from dried material. So in WEBER v. BOSSE'S monograph, where otherwise so many Caulerpas have been excellently reproduced, the figure of *C. peltata* (*loc. cit.* Pl. XXXI. 9) is scarcely happy, and in REINKE'S work on Caulerpa only a dwarf-form with discs pointing in one direction is drawn. The length of the vertical axis naturally varies very much from 1 up to 10 cm. The diameter of the discs also varies, but the average diameter may be said to be about 3 mm. This form does not, as a rule, occur in the uppermost part of the littoral region, but somewhat lower down. It is consequently never exposed at low water, but can then be seen with its long axes swaying to and fro in the swell. This was the case at Kosgoda, where it grew on stones in densely shaded pools together with such a typical deep form as *Dictyurus purpurascens*. In very similar circumstances it grew also at Kangesanturai on the island of Jaffna. At the last-named place I observed a rather remarkable form ; fig. 32 is a picture of it. It is a largely branched, elongated form of which the majority of the branchlets are typical *peltata* branchlets Some of the assimilators, however, are clothed only at the base and a little way up with such branchlets : at the top, on the other hand, branchlets of a different kind are developed, especially on the side axes : the joints become longer between the different branchlets, at the same time as their discs

increase in size. Moreover the side axes have a pronounced tendency to develop their disciform branchlets on one side only, *i.e.*, on the upper side ; which apparently depends on their position in relation to the horizontal level. For, horizontal axes form their assimilation system only on the upper side, vertical ones all round, which is natural from the point of view of their exposure to the light of most advantage to them ; this is especially the case if these horizontal axes take root. A transition to *C. nummularia* is thus effected, since, as I will show later on, it is just this form that is characterized by its assimilation discs being one-sidedly developed on the horizontal procumbent main axis.

Also in another respect this form is remarkable in that, as fig. 33 shows, some of the disciform assimilation branchlets are somewhat swollen and thus would very closely remind one of *clavifera* branches, if a rather evident border did not give evidence of the branchlets having originally been flat (fig. 34). WEBER v. BOSSE mentions about *C. macrodisca* (AGARDH), that its great branchlets are " distinctement bombés dans l'eau pour devenir bientôt plates quand ils en ont été retirés." While then in the case of *C. macrodisca* it seems to be the rule, in *peltata* it is rather the exception, the majority of the branchlets having quite flat assimilation discs. It is to be noted that *C. nummularia*, too, seems to have the same tendency. So HARVEY's Friendly Island No. 76 (Herb. J. G. AGARDH, 16814), very evidently shows a mixture of *nummularia* and *clavifera* branches. This form HARVEY has called *C. clavifera v. platydisca*.

Fig. 33.—*C. peltata* (LAM.) f. *ad clavifera* (1 × 1).

Fig. 34. —*C. peltata* (LAM.) f. *ad clavifera*, swollen branchlets from the upper part of an axis. (3 × 1).

Geographical distribution. —CEYLON : in the somewhat deeper parts of the littoral zone : Galle ! Kosgoda ! Kangesanturai ! Jaffna ! distribution for the rest uncertain, because of the incompleteness of the notes previously made about it.

I have seen unmistakable specimens of this form from the RED SEA and from the JAVA SEA (Batavia).

16.— **CAULERPA NUMMULARIA** (HARVEY) REINKE.

REINKE, Ueber Calerpa, p. 39.
J. G. AGARDH, Till. Algernes Syst. I., p. 38.
EXSICC. : HARVEY, Friendly Island Algæ, No. 77.
FERGUSON, Ceylon Algæ, No. 101.

Under this name HARVEY distributed a Caulerpa from the Friendly Islands (No. 77) which was more exactly described by J. G. AGARDH (" Till. Alg. Syst." I., p. 38). As characteristic of this form he accentuated its great assimilation discs which are often crenulate at the border, and from these crenules new stalks and discs grow out. But AGARDH also points out that the species is closely allied to *peltata* and that the distinguishing character (*i.e.*, the crenulate discs) is far from being constant, for smooth-edged and crenulate assimilation discs occur together from the same horizontal axis. WEBER v. BOSSE also accentuates this character as the main character for her var. *nummularia*. REINKE, however, who in his treatment of the Caulerpas has a sharper eye for the morphopogical differences between the types, finds the boundary between *peltata* (main form) and *nummularia* to consist in the mode of branching. He says : Bei *nummularia* fehlen die Axen der Assimilatoren gewöhnlich ganz, so dass die kreisrunden, gestielten Blätter direkt dem Rhizom entspringen" (" Ueber Caulerpa," p. 39). With this REINKE seems,

in my opinion, to have really hit upon the true character of this type. For, if we examine HARVEY'S type-specimen (Friendly Isl. Alg. No. 77, at least the examples which are preserved in the Herbarium in the R. Riksmuseum in Stockholm) we shall find that, in reality, there are very few discs which are crenulate, and not in a single case have I been able to verify that a new stalk grows out from the crenule of the disc. Every time I thought I had found such a case the stalk in reality shot out from the stalk of another disc ; but owing to the pressing it had had, this was not evident, and it seemed to emanate from the crenule itself. On the other hand, it is very characteristic that the side-branches which support

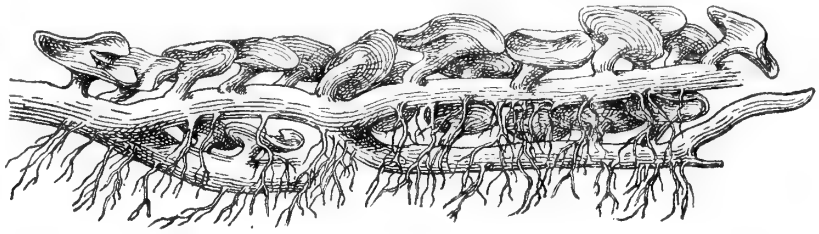

Fig. 35.—*C. nummularia* (HARV.) REINKE. (3 × 1).

the assimilation discs become procumbent and take root ; and the result is naturally a mode of branching as REINKE described it, *i.e.*, the assimilation discs grow directly out from the rhizomes. Fig. 35 shows a picture of *C. nummularia* from the side. From the elongated creeping rhizome emanate numerous side branches and also single branchlets. The former become procumbent and form rows of horizontally placed assimilation discs. The branch formation may be so plentiful and the assimilation discs so numerous and close that such a tuft, seen from above, only shows the shape of a mass of assimilation discs without

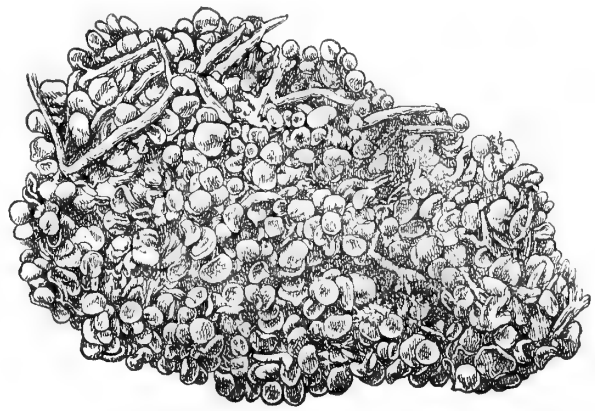

Fig. 36.—*C. nummularia* (HARV.) REINKE. (1 × 1).

apparent order, crowded about each other (fig. 36). This results from *nummularia*, in the same way as *C. clavifera*, being a pronounced light alga, and so belonging to the uppermost parts of the littoral zone just as in *clavifera* its whole assimilation system is horizontally broadened out in one level. Hence the tuft formation is distinctly carpet-like.

Undoubtedly this form is derived, as perhaps an ecological race, from *peltata* (main form), and the transition forms which I have already described show this very evidently ; the horizontal axes in the form from Kangesanturai (fig. 32) have precisely the mode of branching characteristic of *nummularia*. To what extent light directly affects the formation of these forms, I do not venture to decide. But to judge from the difference between the intense light in the upper littoral zone, where *C. clavifera* and *C. nummularia* occur, and which, at low water especially, when they are nearly uncovered, is naturally of great strength compared with the shading that takes place in the deeper localities where *C. uvifera* and *C. peltata* occur, one is tempted to presume that this mode of growth depends to a certain extent on the light. Experiments alone can decide this point satisfactorily.

However it is evident that the most important difference between *C. peltata* and *C. nummularia* lies in the structure of the shoots. An examination of both HARVEY's original types and others shows that *nummularia* always has this mode of growth and the accompanying structure of the shoots. That also an occasional crenulate disc can be met with seldom is true, but this contributes much less to its character than the mode of growth itself. The diameter of the assimilation discs varies, but can be said not to exceed 5 mm.

It must be observed that the big and splendid *C. macrodisca*, which is included by WEBER v. BOSSE as a variety of *peltata*, seems to have quite a different mode of growth. It has not procumbent branches with all the assimilation discs on one level, but it seems to correspond in its mode of growth with *peltata*. It also seems to grow in deeper water, since WEBER v. BOSSE mentions that she had "dredged" it at the mouth of the Maros river, which may point to the fact that it does not belong in every case to the uppermost part of the littoral zone.

Geographical distribution.—CEYLON : in the upper part of the littoral zone on rocks and amongst corals, in many places, at least on the south-west coast, but never occurring in large quantities ; thus, around Galle (in many places on the reef and rocks north-west of Victoria Park, but also amongst the Madrepores below the Utrecht Bastion, and on stones at Watering Point) ! INDIAN OCEAN ; AUSTRALIA; PACIFIC (Friendly Islands).

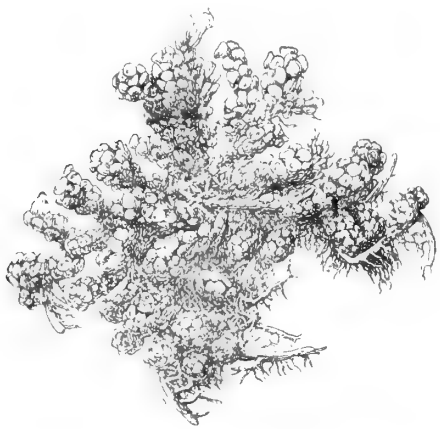

Fig. 37.—*C. imbricata* (KJELLM.). (1 × 1).

Fig. 38.—*C. imbricata* (KJELLM.) (1 × 1).

Fig. 39.—*C. imbricata* (KJELLM.) Flattened branchlets. (3 × 1.)

17.—**CAULERPA IMBRICATA** (KJELLMAN).

KJELLMAN in WITTROCK ET NORDSTEDT, Algæ Exsiccatæ No. 346 (sub nom. *Chauvinia imbricata*).

MURRAY, Catalogue p. 37.

SYN. *Caulerpa peltata* var. *typica f. imbricata* WEBER v. BOSSE, Monographie des Caulerpes; p. 375.

EXSICC. : WITTROCK ET NORDESTDT, Alg. Exsicc. No. 346.

f. minor. In all respects smaller and weaker. The size of the discs is upon an average 1 mm. in diameter (fig. 40).

f. mixta. The basal branchlets cylindrical ; the upper ones are typical imbricata—branchlets with the discs sharply defined from the stalk (fig. 42).

Under the name of *Chauvinia imbricata*, Professor KJELLMAN described and distributed in WITTROCK ET NORDSTEDT, Algæ exsiccatæ, No. 346, a little *Caulerpa* from Galle in Ceylon, collected during the visit of the "Vega" expedition in the month of December, 1879. This *Chauvinia imbricata* was afterwards included by WEBER v. BOSSE as a form under *C. peltata v. typica*. As its character

Kjellman accentuated that the generally shortish vertical axes are thickly clothed or perfectly covered from base to apex with branchlets, which are disciformly flattened at the apex with a diameter of 3-4 mm. (fig. 39). This character is quite sufficient for distinguishing this little *Caulerpa*, which in Ceylon is rather common in the littoral zone. Figs. 37 and 38 show pictures of it. It is generally tufted very thickly and seen from above one sees nothing of such a one but the close vertical axes nearly quite covered with branchlets.

The origin of this form can be imagined in various ways. One is that it is derived from a *parvula* form (see below) in which the branches have been erected and have afterwards radiated, at the same time as the branchlets have become somewhat larger. Some transition forms (*f. minor*) between these two species—which have the mode of branching of *C. imbricata* and the size of the discs of *C. parvula*—also point to the fact that such a development must not be considered as only a hypothesis and without any real foundation. As a matter of fact, these forms also occur in almost the same localities in the upper part of the littoral zone.

But *C. imbricata* can be imagined also to have originated in another way. If we study its organization we might give this as its characterization : *C. imbricata* is a somewhat dwarfed *C. uvifera* in which the branchlets have become somewhat disciformly flattened. In reality forms of this kind do occur which derive directly from *uvifera* by change of spherical branchlets to flattened ones. *C. uvifera f. planiuscula* is such a form. Moreover, there are some transition forms collected by KJELLMAN at Galle and by myself at Jaffna, which point to a relationship with *peltata* main form (fig. 41). If in such a one the vertical branches are shortened and get a more one-sided direction, at the same time as the discs grow smaller and closer, there then arises an *imbricata* form. Hence it seems probable that such a form could be derived from either the one or the other.

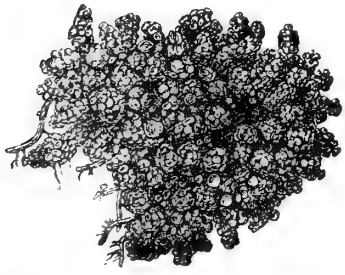

Fig. 40.—*C. imbricata* (KJELLM.) *f. minor* n. f. (1 × 1).

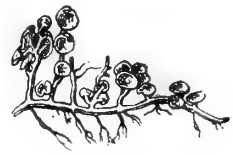

Fig. 41.—*C. imbricata* (KJELLM.) f. *ad peltatam.* (1 × 1).

Fig. 42.—*C. imbricata* (KJELLM) f. *mixta* n. f. (1 × 1).

It is rather remarkable that variations of *C. imbricata* are to be found which are quite analogous with *C. Chemnitzia*. Fig. 42 shows such a form, for which I propose the name *mixta*. The basal branchlets are cylindical, about 3 mm. in length and only 1½ mm. in breadth, and at the apex abruptly cut off, as if truncated, just as in *Chemnitzia*. Somewhat below the middle of the vertical axis commence the typical *imbricata* branchlets—with the discs sharply defined from the stalk—and continue up towards the apex. This form, however, is not *C. Chemnitzia*, for the latter has not only basal branches which are cylindrical, but its upper branches increase only slowly in breadth and are almost trumpet-shaped. (*cf.* fig. 27), and often also the upper branchlets are spherically enlarged as in *racemosa*. WEBER v. BOSSE had also placed *Chemnitzia* under this species, but with the observation that it is an intermediary form between *racemosa* and *peltata*. In the form *mixta* the basal branchlets are cylindrical as in *Chemnitzia*, but the upper branchlets are typical *imbricata* branches. The mode of growth of this form in the upper littoral zone corresponds also in every respect with that of *C. imbricata*.

By reason of *C. imbricata* in Ceylon seeming to be a form or race equally distinguishable from the remaining *peltata* forms, as are *nummularia* and *typica* (WEBER v. BOSSE), I think there is little

justification for placing it only as a form under *peltata* var. *typica*, as WEBER v. BOSSE has done. Var. *nummularia*, *exigua*, &c. should by equal right be included as forms, but WEBER v. BOSSE has given these a systematically higher rank in calling them "varieties," *i.e.*, equal with var. *typica*.

My contention is strengthened by the fact that *C. imbricata* itself shows some variations that could also be classed together. And if we are to place it under any other form it could as well be classed under the small *nummularia* forms, as for instance *f. parvula*, as under any of the others. The plausibility is equally great in either case.

Geographical distribution. CEYLON: in the upper part of the littoral zone amongst rocks and corals, rather common; Matara! Galle (*f. minor*), in many places on the reef (as below the Sailors' Bastion, Star Bastion, Aeolus Bastion, Pigeon Island)! Ambalangoda! Jaffna! SOUTH INDIA: Paumben (*f. minor*, *f. mixta*)!

18.—**CAULERPA PARVULA,** n. sp.

The horizontal axes creeping with their side axes mostly procumbent. The whole plant thus forms mat-like tufts with the assimilation system on one level as in *C. nummularia*. The assimilation discs very small, about 1 mm., never exceeding 2 mm.

Under this name I will distinguish a very weak small form in the *peltata* group which I have observed in several places in the district investigated, and which is figured in figs. 43, 44. The mode of growth approaches that of *C. nummularia* in being richly tufted with the branches procumbent, and all the very small assimilation discs about on the same level, agglomerated together.

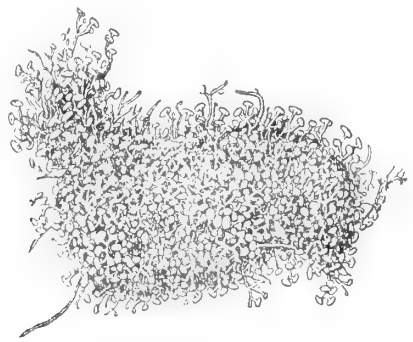

Fig. 43.—*C. parvula* n. sp. (1 × 1).

Fig. 44.—*C. parvula* n. sp. (1 × 1).

To judge from the very small dimensions of this plant—the diameter of the assimilation disc about 1 mm. and never exceeding 2 mm.—one might think it to be closely allied to *f. exigua*, WEBER v. BOSSE (*loc. cit.* p. 377, fig. 11, Pl. XXXI.); but the character distinguishing this latter—viz., its assimilation discs as if perfoliate, and situated as it were in one storey above the other—is entirely lacking. But as the assimilation discs are all in their dimensions rather constant, and the plant in other respects as far as its habitat is concerned, makes an impression quite different from *C. nummularia*, it seems to me to be distinguished as a special form. It forms, one may say, a transition species from the typical *nummularia* to the *imbricata* series. For if the side branches, instead of being procumbent were to grow upwards, and if, together with this, the branching were to become radiate, we should have *C. imbricata*.

At Paumben, in the Island of Rameswaram, I have also collected some transition forms (*C. imbricata*, *f. minor*, fig. 40) between this form and *C. imbricata*.

Geographical distribution.—CEYLON: Rather locally in rock-pools at Beruwala, and at Paumben in the Island of Rameswaram (SOUTH INDIA)!

19.—**CAULERPA LONGISTIPITATA** (Weber v. Bosse).

Syn. *C. lentillifera* (J. G. Agardh) Weber v. Bosse, var. *longistipitata* Weber v. Bosse in Th. Reinbold's Marine Algæ in Flora of Koh Chang by Johs. Schmidt. Part IV., p. 105.

The horizontal axis extended, with rather few vertical axes (= assimilators); these are simple, only exceptionally branched, with the branchlets or pinnules generally opposite in two rows, but sometimes also projecting in all directions. The branchlets at the top provided with a little ball-shaped vesicle of about 1-2 mm. in diameter, bounded by a remarkable constriction. The basal part of the same length or shorter than the vesicle. The diameter of the vertical axis commonly not exceeding twice that of the branchlets.

I have observed this *Caulerpa* in the more sheltered places of the littoral zone at the islands at Paumben Pass, especially on stones, with its long creeping rhizomes adhering thereto or entangled in other algæ; sometimes it also occurred drifting and entangled in algæ which had broken loose.

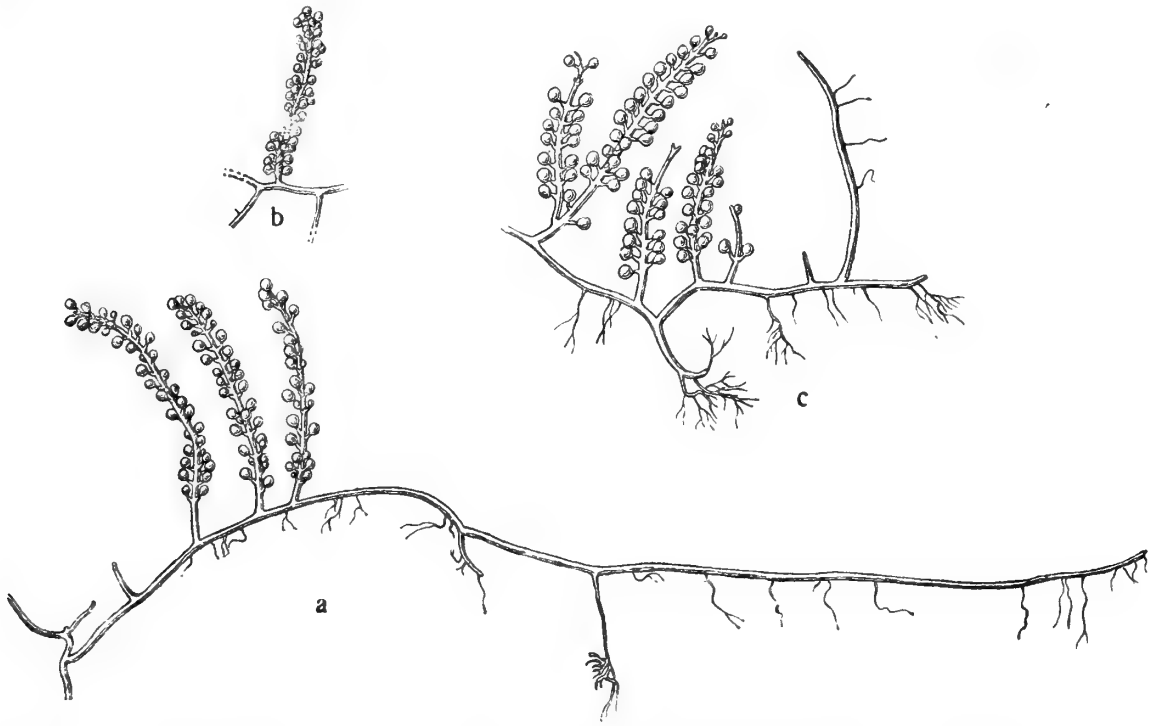

Fig. 45.—*C. longistipitata* (W. v. B.). *b* shows an assimilator with the branchlets in many rows. (1 × 1).

This *Caulerpa*, which I have placed as a species of its own, was first described by Weber v. Bosse as a variety of *C. lentillifera* in Major Th. Reinbold's paper on the algæ from Koh Chang in the Gulf of Siam collected by Dr. Johs. Schmidt. I have had an opportunity of examining these type specimens and I can assert their conformity to the Ceylon specimens. That Weber v. Bosse, with such limited material, was presumably unwilling to create a new species among the Caulerpas is comprehensible when one thinks of the great multiformity of these organisms, and the more so as this author is inclined to form wide-embracing species (so wide-embracing as far as *lentillifera* is concerned, that even a form so different as *C. Kilneri* is included). But my study of this plant from a somewhat richer material from Paumben showed that it is in the main constant, and it seems to me to be rather well characterized and distinct from *C. lentillifera*, with which it is most closely allied.

C. longistipitata differs from *C. lentillifera*, as Weber v. Bosse points out, in the small number of the rows of pinnules (fig. 45). This may vary a little, however, but the predominant number of vertical

axes have the pinnules in opposite order (fig. 46 *b*.), and this gives the plant a rather characteristic habit. Its next important character is the relatively considerable length of the pinnule in comparison with the ball-shaped vesicle, which last is also greater than in *C. lentillifera* in general. In *C. longistipitata* its diameter is rather above than below 1½ mm., and often reaches as much as 2 mm. The length of the pinnules often reaches the same measure, *i. e.*, they are also as long as the vesicles, but in every case always longer than half their diameter. Finally, we must point out that the vertical axes are very weak in comparison with the pinnules, and only about twice as broad, and often not even that, but less. This seems to me to be worthy of accentuating, because it has not been pointed out by WEBER v. BOSSE, who, on the contrary (*loc. cit.* p. 382), is of opinion that this is a very subordinate character depending only on the age of the plant.

An examination of fig. 1 *a*, PL. XXXIV. in WEBER v. BOSSE'S Monograph shows just as the study of the original specimen itself (No. 16,851) in AGARDH'S Herbarium, that *C. lentillifera*, J. G. AGARDH, has relatively thicker vertical axes and smaller vesicles, whereas in *C. longistipitata* the axis in its breadth is most often below or at least never above the diameter of the vesicles (figs. 45, 46). In this respect I have never seen any variation in *C. longistipitata*.

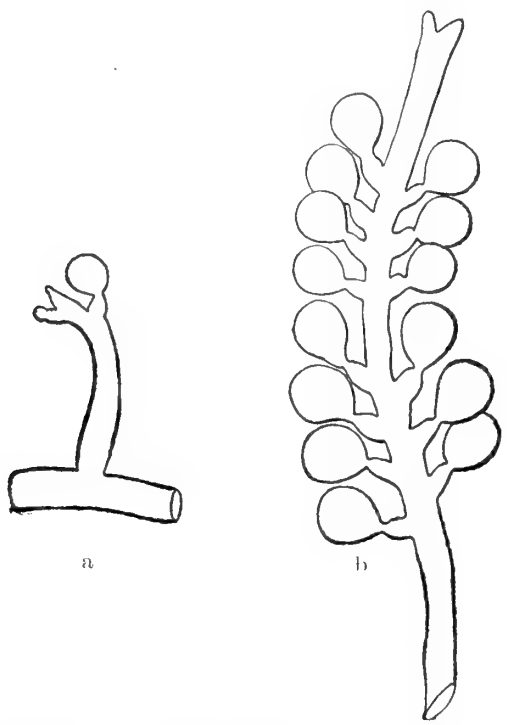

Fig. 46.—*C. longistipitata* (W. V. B.). (*a* 5 × 1, *b* 4 × 1).

For this reason it seems to me to be fully justified if we consider *C. longistipitata* as a distinct elementary species. My opinion here is supported by the fact that in the district where this species occurs, in the islands in the north between India and Ceylon, it showed itself very uniform, nor are any real *lentillifera* forms known from Ceylon. Its geographical distribution also seems to strengthen this view. *C. lentillifera*, J. G. AGARDH, is only known from the Red Sea and the western parts of the Indian Ocean (Madagascar), that is, it has *Western* distribution ; *C. longistipitata*, on the other hand, is known from the Gulf of Mannar and the Gulf of Siam in the north, to New Guinea in the south, consequently it has a more *Eastern* distribution ; *C. Kilneri*, finally, only from the Timor Sea.

Geographical Distribution.—SOUTH INDIA : Paumben Pass ! PACIFIC (Gulf of Siam).

20.—**CAULERPA SEDOIDES** (R. Brown) C. Agardh.

C. Agardh, Spec. Algarum, p. 438.

J. G. Agardh, Till. Algernes. Systematik 1., p. 39.

Weber v. Bosse, Monographie des Caulerpes, p. 387.

f. crassicaulis, J. G. Agardh, loc. cit. p. 40.

f. mixta. In all respects smaller and weaker. The horizontal axis about 1 mm. in diameter. The vesicles (branchlets), ·5 to 2 mm., commonly 1 mm. in diameter, of different kinds, viz., (1) sessile or pedunculate with spherical tops and evident constrictions; (2) sessile with somewhat pear-formed tops ; (3) long, extended, cylindrical.

I have found *C. sedoides f. crassicaulis* in Ceylon in several specimens from Matara, Dondra Head, and Weligama on the south coast (fig. 47). Almost all correspond well with Agardhs's *f. crassicaulis*. Thus the vesicles are, as a rule, always spherical, there are no joints on the main axis, and the closely set branchlets stick out in all directions around the main axis. But, on the other hand, the

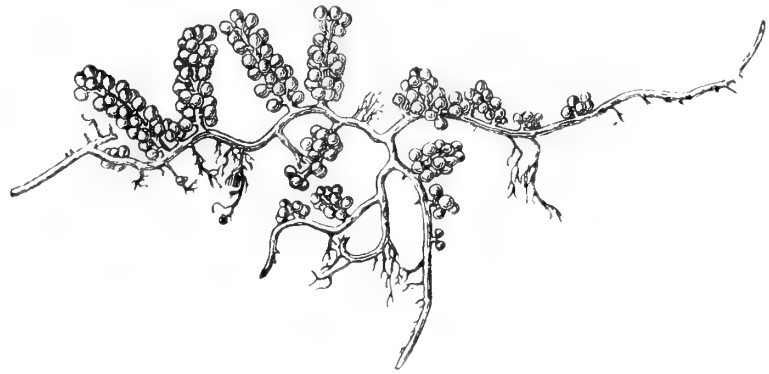

Fig. 47.—*C. sedoides* (R. Br.) C. Ag. *f. crassicaulis* J. G. Ag. (1 × 1).

vesicles are sometimes provided with a very short but distinct stalk (fig. 48), and this seems also to be the case with Agardh's own type-specimens, a character again shown in some high-grown *crassicaulis* forms (in the Herbarium of the R. Riksmuseum in Stockholm) from Torres Strait (Aug. 1846). Also Weber v. Bosse speaks about (*loc. cit.* p. 388) a *Caulerpa* from Upola, in which some branchlets are

Fig. 48.—*C. sedoides* (R. Br.) C. Ag. *f. crassicaulis* J. G. Ag. (2 × 1).

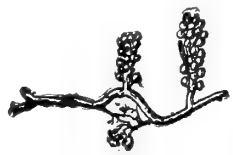

Fig. 49.—*C. sedoides* (R. Br.) C. Ag. *f. mixta n. f.* (1 × 1).

Fig. 50.—*C. sedoides* (R. Br.) C. Ag. *f. mixta n. f.* (2 × 1).

pedunculate, reminding one almost of *C. racemosa v. clavifera*, from which it is however distinct by its constriction. Both in Matara and Weligama the *f. crassicaulis* showed itself very uniform and scarcely variable and gave the impression of being a distinct race.

In the island of Jaffna in the north of Ceylon I found some peculiar specimens of a very exceptional appearance. It is these that I have described as *f. mixta* (figs. 49, 50). In all respects it is more slender and weaker than the preceding form. In addition to small pedunculated vesicles with constrictions below the top, it has pear-shaped branchlets, clearly indicating opposite arrangement just as in *f. geminata*, HARV.; finally, and this is the most characteristic feature, some few branchlets grow out cylindrically to a breadth of 3 mm., and show themselves to be of the same shape as *C. ambigua* OKAMURA (*cf.* OKAMURA, "Algæ from Ogasawara-jima." PI. 1. figs. 4, 6, 7).

Geographical distribution.—CEYLON: Dondra Head! Matara! Weligama (*f. crassicaulis*)! in the last named place at a depth of about 1½ to 2 metres (at low-water) inside the reef together with *C. sertularioides* and *C. taxifolia*; in the other places in the upper littoral zone; Jaffna (*f. mixta*)! INDIAN OCEAN; PACIFIC OCEAN.

C. sedoides in a wide sense is known from Australia, New Zealand, and Tasmania in the south. From Ceylon, the Gulf of Siam (SCHMIDT) in the north, and to the Friendly Islands in the east. The different forms seem to have their different limited districts: thus, *f. tasmanica* and *geminata* have exclusively southern distribution (Australia and Tasmania), whereas *f. crassicaulis* has exclusively northern, true tropic distribution (the tropical coast of Australia, Ceylon to Friendly Is.). This possibly points to the fact that these forms have rather the character of different races or elementary species, an inference that is furthermore strengthened by the fact that, as I have mentioned above, *f. crassicaulis* in Ceylon is constant and uniform. Against this, *f. mixta* seems more local, and, as I have above tried to show, its peculiar branching may probably be explained as a kind of atavistic bud-variation.

21.—**CAULERPA FERGUSONII** (MURRAY).

MURRAY. On some new species of Caulerpa, p. 212, pl. 53, fig. 1.
WEBER v. BOSSE, Monographie des Caulerpes, p. 389 (*sub nom. C. Fergusoni*).
EXSICC.: FERGUSON, Ceylon Algæ, No. 415.

This *Caulerpa*, only known from Ceylon, I have observed once at Paumben Pass, and there very scantily, growing on mud or slime together with *C. longistipitata* and *Enalus acoroides*. To the description of this plant, which we owe to MURRAY, the following may be added:—

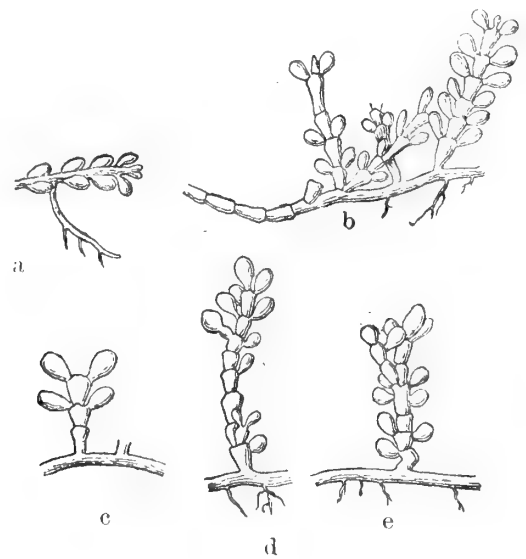

Fig. 51.—*C. Fergusonii*, MURR. (1 × 1).

It does not seem to be uncommon for the branched stem, when situated horizontally, to form coarse roots downwards and jointed side branches upwards. Fig. 51 *a* and fig. 51 *b* show this case,

which is far from being rare among *Caulerpas*, and which seems to occur also in the related *C. cactoides*. (*cf.* MURRAY, *loc. cit.* pl. 52, fig. 8, and WEBER v. BOSSE, *loc. cit.* p. 391). Moreover it seems to happen, though more rarely, that the vertical axes are jointed right up from the base without any branchlets being formed from the joints at the base (fig. 51 *c*). It has been pointed out that the difference between *Fergusonii* and *cactoides* may consist in the former plant being only jointed at the place where the side branchlets are formed, as against *cactoides*, which is jointed the whole way up, though the base seems to lack side branchlets for a part of the way up. This character, though right in the main, does not always hold good, and sometimes one can observe at the base (fig. 51 *c*) some evident joints without any side branchlets at all.

Just as in *C. cactoides*, *C. Fergusonii* can also have regeneration branches, *i.e.*, may repeat the branching of the mother axis. A branchlet in fig. 51 *d* seems to branch ; it looks as if the branchlet itself were jointed. In other cases the branch-formation takes place as follows : between two branchlets the growth of a side axis takes place. Hereby the branches become verticile (fig. 51 *e*), a case which WEBER v. BOSSE has also observed in *C. cactoides*, loc. cit. p. 391. When such a side branch is formed between two branchlets it is, to begin with, quite similar to these, and all three form a whorl of branchlets. By this a formation arises which resembles the verticile branches in the fossil *C. Carruthersii*. It is therefore remarkable that also in living Caulerpas verticile branches may be formed, though it must be considered to be a rare occurrence. From a phylogenetic point of view it is interesting in any case.

From what has been stated above it seems that this form of *C. Fergusonii* is much more closely related to *C. cactoides* than to *C. sedoides*.

Geographical distribution.—CEYLON (FERGUSON). SOUTH INDIA : Paumben Pass, in the littoral zone, in shallow water on mud, together with *Enalus acoroides* !

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