# ON THE MORPHOLOGY AND ANATOMY OF TURTLE GRASS, *THALASSIA TESTUDINUM* (HYDROCHARITACEAE).

## I. VEGETATIVE MORPHOLOGY

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## ABSTRACT

In an introductory account of the vegetative morphology of *Thalassia testudinum* König, a very constant organ symmetry is described. A horizontal long-shoot bearing only scale-leaves produces lateral buds alternately on opposite sides at regular intervals separated by 9 to 13 internodes. No buds are associated with intervening scales. Buds are opposite, not axillant to the subtending leaf and because of this unusual position and their precocious development it can be disputed that they are lateral. Buds become erect short-shoots bearing, initially, scale-leaves but soon, foliage-leaves. Long- and short-shoots have the same fundamental symmetry. Each is autonomous so that the one can only become the other by branching. Because of the absence of residual meristems, growth of *Thalassia* is largely dependent on activity of shoot apical meristems, even root production being limited to apical regions. In the absence of rhizome apices, isolated fragments do not regenerate.

## INTRODUCTION

Recent research on the ecology of marine angiosperms in Florida waters suffers from lack of basic information about the plants under study. Reasons for the original research interest are not difficult to discern since the marine angiosperms are abundant, widely distributed, and provide an important environment for many other marine organisms. The economic importance of these plants as primary producers, and as essential links in the chain of marine life in tidal and shallow water in tropical and sub-tropical seas, has been repeatedly emphasized and need not be reiterated. A very full account of and bibliography on the ecology of Florida sea-grasses is given by Phillips (1960) to which may be added subsequent papers by Odum *et al.* (1960), Thomas *et al.* (1961), Strawn (1961), Voss & Voss (1960), and Moore (1963).

Reasons for the absence of fundamental botanical information are less easy to understand, but reflect the decline of interest in descriptive plant anatomy and morphology as a worthwhile discipline. *Thalassia testudinum* König (Hydrocharitaceae), the turtle grass of shallow seas around Florida, and widely distributed in the Caribbean, provides a good example of a common organism, the study of which is still incomplete. Earlier accounts

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by Constantin (1886), Magnus (1871), and especially Sauvageau (1890 a, b) were detailed but not exhaustive because these workers never saw the organism in its natural environment and had only limited material for study. Familiarity with turtle grass in its native habitat has revealed an organism of great symmetry and with several peculiar morphological features. There seems to be neither a detailed account of these features nor of the general growth habit of *Thalassia* in publications otherwise dealing with its taxonomy and morphology (*e.g.*, Ascherson & Gürke, 1889).

Since an understanding of the growth habit, construction, and development of *Thalassia* is a prime need in ecological work, it was felt that an augmentation of existing knowledge would serve a useful purpose. The present account deals with the morphology, method of branching, and essential symmetry of vegetative shoots and reflects on the way this is related to a marine environment. Future articles will deal with reproductive morphology and anatomy, and the anatomy and development of leaf, stem and root, whereupon it will be shown that histological peculiarities of *Thalassia* are also related to its mode of life. This investigation may be regarded as nothing more than preliminary. It is hoped that it will stimulate the careful and detailed study which is still needed.

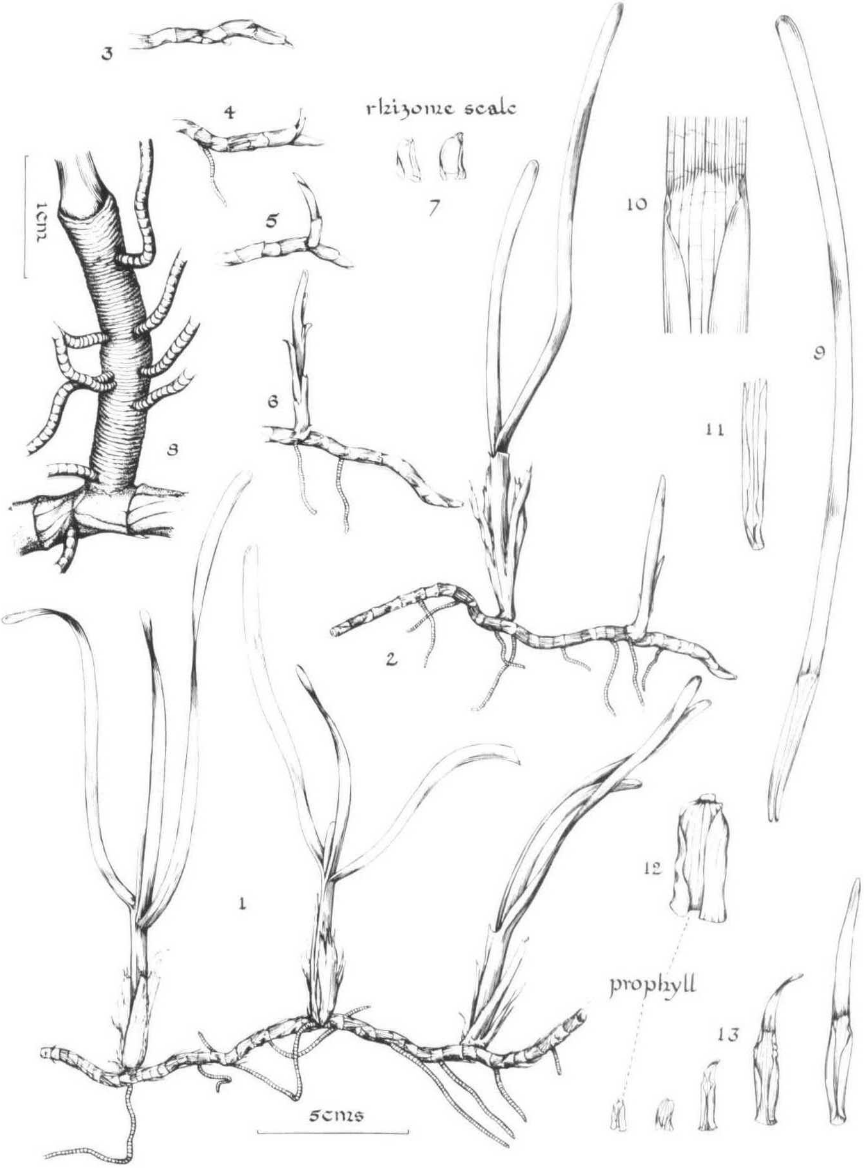
## MATERIAL AND METHODS

The distribution of *Thalassia* and some of the factors influencing this have been discussed by Moore (1963). The present account does not deal with morphological variation between plants from differing environments although this is likely to be considerable as is indicated by Phillips (1960). The details recorded below, nevertheless seem applicable to *Thalassia* generally.

Morphological observations were made largely on plants from a single area, growing in thick deposits of *Rhizophora* peat off the wading beach, Matheson Hammock Park, Biscayne Bay, Miami, Florida. Here the rhizomes are entangled and form dense mats without the open texture of plants in looser substrata. Observations and illustrations were made from fresh material supplemented by material fixed in 5 per cent formalin-seawater. A more detailed account of anatomical methods will be given in subsequent reports.

## VEGETATIVE MORPHOLOGY

Axes consist of horizontally creeping "long-shoots" (rhizomes) buried a short distance in the substratum and giving off erect lateral "short-shoots" (Figs. 1,2). Rhizomes bear only colorless scale leaves separated by distinct internodes (Figs. 1-6, 16-18). Short-shoots largely produce foliage leaves separated by very short internodes (Figs. 8,15). Typically,



FIGURES 1-13. *Thalassia testudinum* (× ½, except Figs. 8, 10, 12, × 2).— 1, General habit.—2, Apex of long-shoot including young short-shoot.— 3-6, Stages in development of short-shoot.—7, Scale leaves from long-shoot.— 8, details of short-shoot, all but youngest foliage leaves removed.—9, Foliage leaf.—10, Same, details of transition from sheath to blade.—

little more than the blades of foliage leaves projects above the substratum. Flowers occur only on short-shoots. The short-shoots are interpreted as lateral branches of the monopodial long-shoot although other interpretations are possible as will be described later.

*Long-shoot (Rhizome).*—Scale leaves on the rhizome are arranged distichously, the plane of distichy more or less horizontal so that as seen from above scale leaves project alternately left and right. Scale leaves (Fig. 7) are colorless, non-assimilating organs serving temporarily as rigid protective structures, those most recently matured enclosing the rhizome apex as it pushes through the substratum (Fig. 16). Older scales, their protective function accomplished, decay rapidly, but their shrivelled remains, and particularly the fibrous remains of their vascular bundles, are persistent (Figs. 1,2,8,15). Each scale at its insertion encircles the rhizome incompletely, this insertion always being marked by a distinct scar in old rhizomes from which all remains of the scales otherwise have decayed. Scale leaves are triangular, scarcely tubular at the base when mature (Fig. 7). Opposite margins of each developing scale as it encloses the apex overwraps considerably (Figs. 19,20) but they diverge as the enclosed bulk of tissue expands. Adjacent scales usually overlap somewhat even on adult parts (Fig. 16). The few rhizome apices which have been examined in serial section suggest that overwrapping of scale leaves is consistently neither homotropous nor anatropous (see p. 757).

Morphologically scale leaves are equivalent to the reduced base of a foliage leaf, as comparative study demonstrates below.

Rhizomes are not bilaterally symmetrical about the plane of insertion of scale leaves. This is most obvious in the position of roots which arise adventitiously on the lower surface of the rhizome only (Figs. 1-6). Root production is intimately associated with shoot development since they originate in acropetal order close to the rhizome apex. This is most obvious in microtome sections of the rhizome apex because the uniseriate arrangement of the root primordia may be distorted during their subsequent development. Less obvious asymmetry is that which brings each scale leaf slightly above the horizontal, as is most clearly indicated by the position of their median vascular bundles forming a shallow V in Figures 19 & 20. This is important in directing the lateral short-shoots vertically.

*Origin of Short-shoots.*—Branching of the rhizome is interpreted as monopodial. Lateral short-shoots arise from buds developed alternately on opposite sides of the long-shoots at wide but regular intervals, separated

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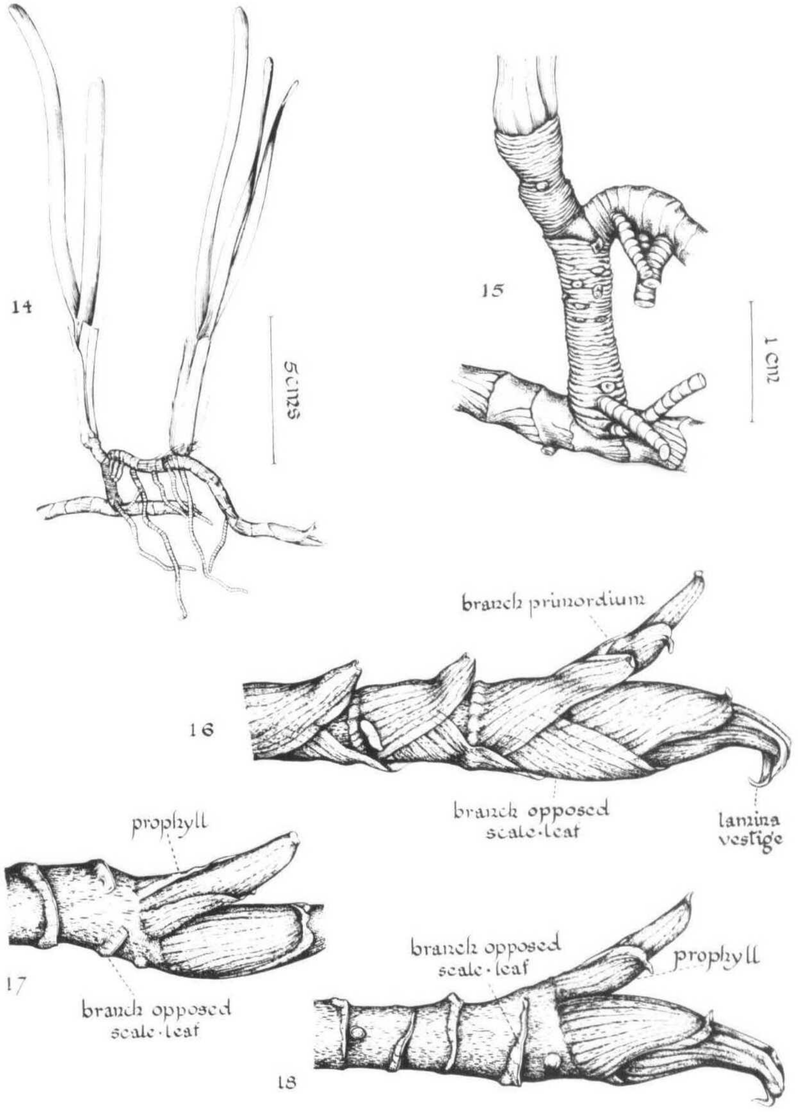
11, Leaf sheath with blade broken off naturally.—12, Prophyll (× 2), vestigial blade is pronounced.—13, Transitional series, beginning with prophyll, of successive leaves along a short-shoot showing gradual development of blade.



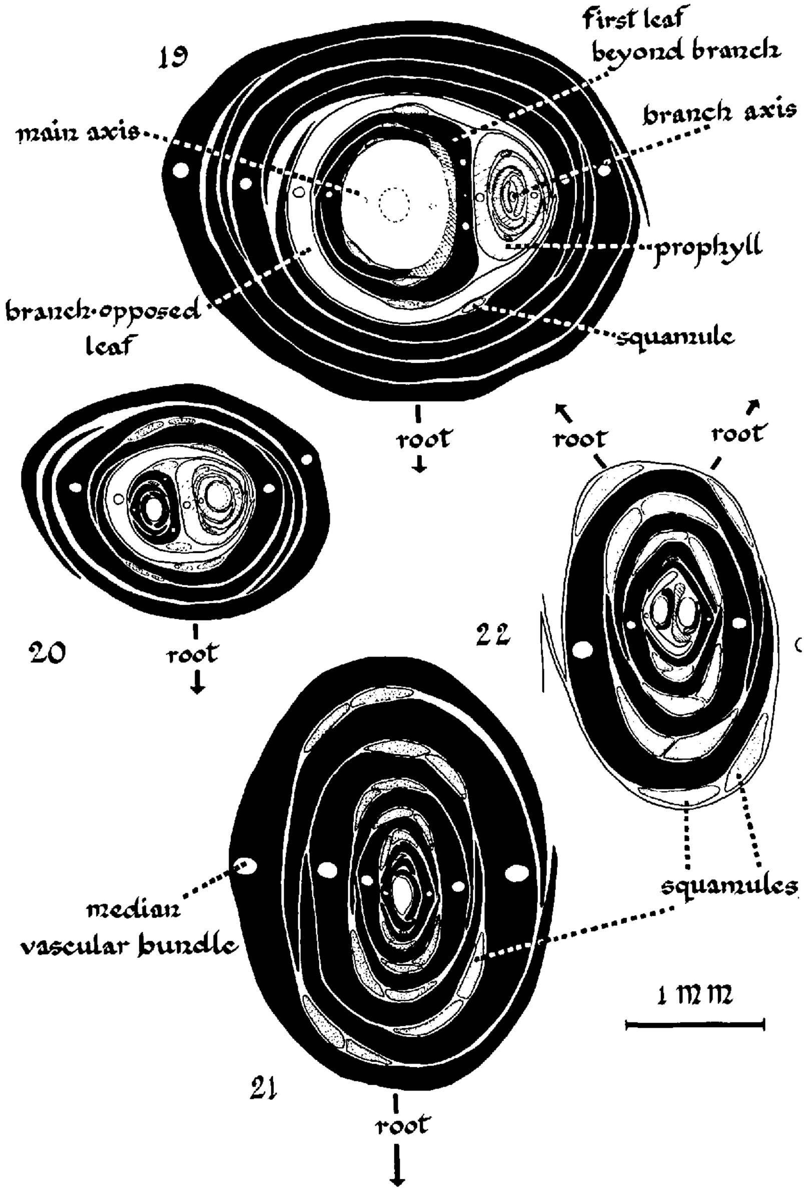
FIGURES 14-18. *Thalassia testudinum* (× 2, except Fig. 14, × ½).—14, General habit showing long-shoot originating as a branch from short-shoot.—15, Details of branched short-shoot of Figure 14, all but youngest foliage leaves removed.—16, Long-shoot apex initiating branch primordium.—17, Same from above with scale leaves removed.—18, Same from side. The relation of the parts in this shoot is somewhat distorted (*cf*., Fig. 19).

by a fairly constant number of internodes. Few scale leaves are associated with branches because no dormant buds are developed in association with intervening nodes.

The position of buds is unusual since they are leaf-opposed (Figs. 17-20), so that the short-shoot at maturity is situated on the ventral side of its associated scale leaf some way above the node. At maturity the short-shoot is inserted halfway between two nodes (Fig. 8). Such extra-axillary buds, 180° from the normal axillary position are infrequent in monocotyledons. They do occur in some families, *e.g.*, Musaceae (Skutch, 1932), but seem otherwise not characteristic for the Hydrocharitaceae.

The position of each bud makes it difficult to interpret the type of branching involved, but it seems most satisfactory to regard the bud as lateral despite its extra-axillary position. Chief evidence in support of this interpretation is the position of the first leaf on the hypothetical lateral short-shoot, and the position of leaves on the hypothetical continuing long-shoot. The first leaf on the branch is always in the adaxial (*adossierte* of German authors) position, that is backing towards the main axis, and so occupying the prophyllar position normal in monocotyledonous branching (Figs. 17-20). It is not, however, two-keeled as is usual for the prophyll on monocotyledonous branches. In addition, the distichy of the scale leaves below the level of branching is continued into the hypothetical main axis (Figs. 19,20). If this branching were interpreted as sympodial it would involve a change of leaf sequence on the evicted main axis which is otherwise unknown in sympodially-branched monocotyledons.

However, evidence against the interpretation of this as monopodial branching is the precocious development of the lateral, and the structure of the first leaf on the rhizome above the branch. Development of buds is always precocious so that initially the lateral may be larger and have developed more leaves than the terminal shoot (Fig. 20) a situation which is soon reversed as growth of the main axis becomes dominant once again (Fig. 19). This could suggest that branching is sympodial, the "precocious lateral" actually being the main axis evicted by an increasingly vigorous lateral. This would then explain the extra-axillary position of the apparent lateral, but not the continuing distichy of leaves along the axis of the rhizome at each point of branching. Another peculiar feature requiring some explanation is the reduction of the dorsal vein in the rhizome leaf inserted immediately above the branch. Two large submedian veins are associated with this reduced dorsal vein (Figs. 19,20). In addition this leaf is often somewhat two-keeled so that it resembles a prophyll both in its external morphology as well as anatomy. This might support the interpretation of the rhizome as a sympodium, but it is more reasonable to regard the distinctive features of this leaf as resulting from its compression in a prophyll-like manner, by the precocious lateral branch, rather than being a true prophyll inserted on a lateral branch.



FIGURES 19-22. *Thalassia testudinum* (× 20) transverse sections of long-shoot (Figs. 19 & 20) and short-shoot (Figs. 21 & 22) apices drawn from microtome sections.—19, Long-shoot with late stage in branch development; at level of shoot apex of branch. Innermost leaf on main axis still attached on ventral side.—20, Long-shoot at early stage of branch development; branch more

This subject will be discussed further when the anatomy of the rhizome is described. For the present, short-shoots will continue to be regarded as lateral branches of a long shoot, this being itself a monopodium.

Lateral shoots undergo no inhibition; once initiated each bud grows without interruption into a short-shoot (Figs. 3-6). Size of a short-shoot thus reflects its age, well-developed shoots with long axes being remote from a rhizome apex, little-developed shoots being close to the rhizome apex. There is no other source of short-shoots but the rhizome apex.

Short-shoots originate as horizontal laterals (Fig. 19), but by rapid differential growth they soon turn erect (Figs. 3-6). This displacement may involve some distortion so that symmetry evident in the rhizome apex (Figs. 19,20) is lost in the mature axis (*cf.*, Figs. 16-18). The oldest parts of rhizomes are usually denuded of their short-shoots, the former position of these being indicated by annular scars.

*Frequency of Short-shoots.*—This can be expressed as the number of internodes intervening between successive short-shoots and can be determined simply by counting the number of scale-leaf scars between successive short-shoots, counting the first branch-opposed leaf as "one." Counts of shoots of all ages and sizes have established that the numbers are always odd, and the most frequent numbers are 9, 11, and 13. The odd number is a simple result of buds originating alternately on opposite sides of the rhizome. Thus if a bud is opposed to leaf 0, the next bud is opposed to leaves on the opposite side of the stem, leaf 0 + 1, 0 + 3, 0 + 5,—etc., *i.e.*, 1, 3, 5,—etc. internodes distant. Because odd numbers are consistently observed there is good agreement with the theory that successive short-shoots arise on opposite sides of the rhizome, as, of course, can be verified by direct examination.

The counts also show that usually 8, 10, or 12 leaves not associated with a bud intervene between each pair of branch-opposed leaves. There is a bimodal distribution of frequencies with a second but much smaller maximum of values approximately double the main frequency. This probably results from a tendency to overlook obscure branch scars in making the counts so that a double value results (theoretically an even number), and a tendency for branches to abort. The control of short-shoot production in the rhizome of *Thalassia* is clearly a well ordered process

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vigorous than hypothetical main axis.—21, Short-shoot just below level of shoot apex.—22, Short-shoot with early stage in development of precocious lateral. Position of first root primordium (or primordia) below apex, but not included in section drawn, is indicated by arrows. Scale leaves and foliage leaves of main axis are black; leaves of branch are hatched; branch-opposed-leaf is outlined; median vein of leaf is represented by white circle; squamulae intravaginales are dotted.

which could be discussed in terms of inhibitors emanating from the short-shoot competing with promoters produced by the rhizome apex. However, these physiological considerations are beyond the scope of the present article.

*Short-shoot Morphology.*—Development of a leaf-opposed lateral bud into a short-shoot is continuous, proceeding without a period of dormancy. Each short-shoot differs strikingly from the rhizome on which it originates. It grows erect, produces mostly foliage leaves separated by very short internodes. It branches vegetatively at apparently irregular (not obviously regular) intervals. It bears axillary clusters of flowers at the appropriate season. Despite these differences the essential symmetry of the short-shoot agrees with that of the long-shoot.

The first leaf (prophyll, Fig. 12) on the branch is in the adaxial position between the branch and the parent axis (Figs. 17-20). It is not bicarinate because, as has already been discussed, the branch to which it belongs is precocious in development, pressure being exerted upon the leaf on the main axis, immediately above, which backs onto the branch. Early growth of a lateral bud is somewhat like that of a rhizome in that the first leaves are reduced to scales, but the transition to foliage leaves is very abrupt (Fig. 13). This transition occurs as the lateral branch turns from the horizontal to the erect position and the two processes may be correlated.

There is no change in the plane of distichy at branching since subsequent leaves are arranged distichously in the same plane as the prophyll. The eviction of the short-shoot may distort this relationship somewhat, but it is clear in sections of the rhizome apex (Figs. 19,20).

The prophyll and subsequent scale leaves at the base of the short-shoot resemble scale leaves on the rhizome except that they are often somewhat longer. The rapid transition from scale leaves at the base of a young short-shoot to normal foliage leaves distally, results in a brief series of intermediate forms (Fig. 13). These demonstrate that the scale leaf on both rhizome and short-shoot is morphologically equivalent to the shortened base of a foliage leaf with the blade reduced. Often a vestige of this blade is evident on rhizome scales (*e.g.*, Fig. 16). If sufficient shoots are examined a complete series of transitional forms between scale leaves and foliage leaves can be recognized.

Once established, growth of the short-shoot continues unchanged with the production of foliage leaves. Although the leaf blade is readily lost, its sheath, especially the fibrous part of its vascular bundles, is long-persistent and clothes the distal part of the short-shoot as a shaggy, somewhat fibrous but quite soft mass (Fig. 1). Old short-shoots may reach a length of 10 cm before they are lost.

The short-shoot further differs from the rhizome in that it is flattened dorsiventrally, so that the leaf sheaths have a somewhat rectangular outline in transverse section (*cf.*, Figs. 19,21). In addition the overlapping of the leaf-sheaths seems to be consistently homotropous in the terminology Eichler (1884) applied to the Marantaceae, that is the leaves within a shoot all overlap the same way (*e.g.*, Fig. 21). However, I have sectioned insufficient short-shoots to be certain of this point.[3]

Despite these important differences, short-shoots resemble long-shoots in two fundamental ways, roots originate unilaterally, and vegetative branches are leaf-opposed. Roots on short-shoots originate close to the apex, but are normally restricted to one (Fig. 21) or sometimes two (Figs. 8,23) vertical series on one side of the stem. This uniseriate arrangement may be distorted by twisting of the short-shoot axis. The root-bearing side of the shoot is morphologically the lower and directed away from the rhizome, alternate short-shoots directing their root growth to opposite sides of the rhizome. Thus short-shoots are not only right- or left-sided with respect to their insertion on the rhizome, but also right- or left-handed with regard to the side on which roots are born. It is possible that they are also correspondingly right- and left-handed with regard to the overlapping of their leaf bases although this has still to be verified.[4] This would complete the mirror-image symmetry of opposed branches. It will be further noted in Figures 21 & 22 that distichy of the leaves, as represented by their median veins is not symmetrical, but shallowly V-shaped towards the root bearing side, as in the rhizome.

Vegetative branching in short-shoots is rare and without the regularity of rhizome branching. It occurs only in old short-shoots (Figs. 14 & 15). Branches always become new long-shoots and are leaf-opposed. In these two features, therefore, short-shoots resemble long-shoots in producing the reciprocal type of shoot in the same position. Because vegetative branches are unpredictable in short-shoots stages in their development are difficult to locate. Figure 22 is a fortunate example which shows a very early stage in branching. The presumed lateral branch bears exactly the same relation to the presumed main axis as do branches in the rhizome apex and it is also equally precocious (*cf.*, Fig. 20) having already produced two leaf primordia whereas the main axis has produced, as yet, only one. This section is also strongly suggestive of a dichotomy which could be an alternative interpretation of this method of branching. This subject will be discussed when the anatomy of the short-shoot is described subsequently.

*Fate of Short-shoots.*—Short-shoots undergo one of a number of possible transformations as they age. Most commonly, as they become longer, their

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[3] Further examination has recently shown that this overwrapping is not consistently homotropous (Fig. 22). Long- and short-shoots therefore do not differ in this respect.

[4] See Footnote 3.

attachment to the rhizome weakens and they break off to leave an inconspicuous scar. Short-shoots rarely break naturally elsewhere than at their insertion which is thus revealed as a region of mechanical weakness. Otherwise this fate is avoided by the branching of a short-shoot to produce one or more rhizomes (Figs. 14 & 15). In certain instances old short-shoots have been collected which appear to have become transformed directly into long-shoots. Most likely this represents not an exception to the rule that axes are autonomous, but an abortion of the main axis of the short-shoot and its replacement by a lateral, which is necessarily a long-shoot. This needs further investigation.

*Foliage Leaf.*—Each foliage leaf has an open, colorless basal sheath, flattened in the transverse plane. Opposite margins overwrap in the bud but become separated at maturity (Figs. 9-11). The leaf insertion encircles the short-shoot axis almost completely at the node and eventually, like the rhizome scale, is recognized only by a distinct but slightly incomplete annular nodal scar. The transition from sheath to blade is quite abrupt and distinct and is without a ligule (Fig. 10). The wings of the sheath disappear and the boundary between colorless, more or less transparent, sheath and green lamina is seen as a somewhat uneven horizontal line. Mature leaves break readily in this transition region (Fig. 11), for simple anatomical reasons to be described in a subsequent report. The strap-shaped, flaccid blade, with rounded apex varies considerably in length and width (Phillips, 1960). The leaf margin bears minute teeth at intervals of 0.5 to 1.0 cm, the teeth being numerous and most obvious at the leaf apex.

*Squamulae Intravaginales.*—These "squamules," which are quite characteristic of Hydrocharitaceae and related families (Arber, 1925), occur on both long- and short-shoots in *Thalassia.* On short-shoots the squamules are largest and relatively conspicuous. Here they occur mostly in pairs, two pairs associated with each leaf insertion in a dorsolateral position (Figs. 21 & 22) so that there are four rows of squamules in pairs along the short-shoot, readily revealed if persistent leaf bases are removed. Squamules on the rhizome are smaller, usually solitary but occupy the same position (Figs. 19 & 20). Squamules have a special relation with flowers. Squamules are short, non-vasculated structures, up to 4 mm high and consist entirely of uniform, densely cytoplasmic cells. They are mucilage secreting organs; amorphous material presumably produced by them sometimes persisting even in microtome sections.

*Roots.*—Production of root primordia is closely associated with growth of long- and short-shoots. They are developed unilaterally on both kinds of axis on the morphologically lower surface in one or two series perpendicular to the plane of insertion of the leaves. Because of the erect position of the short-shoots this surface is turned outwards so that roots always originate on the side away from the rhizome. Production of root primordia also seems dependent on apical growth of both kinds of shoot. Roots are never produced belatedly in a truly adventitious manner. This is because their meristematic site in the developing shoot matures as a loose aerenchyma. There is subsequently no suitable meristem for the belated development of roots in adult axes. Because root production is limited in this way, there is a fairly constant number of roots (three to six) for each unit of the monopodium.

## Discussion

To say that *Thalassia* has a growth-habit well-suited to its peculiar environment is little more than a truism, because its existence in a variety of marine environments and its wide distribution clearly indicate this adaptability. Analysis of its growth habit and comparison with terrestrial monocotyledons is instructive. A creeping, monopodial axis producing ephemeral non-assimilating protective scales is well suited to rapid spread of a plant in a uniform and loose substratum. It is found in some terrestrial monocotyledons, particularly members of the grass and sedge families. Restriction of assimilating and sexual reproductive organs to erect shoots of limited growth, arising laterally on the horizontal system, is also common in terrestrial monocotyledons. *Thalassia* differs from such plants, however, in that the growth of the short-shoot is not limited by flowering. Erect shoots in sedges and grasses usually end a relatively short period of vegetative growth by flowering terminally; in *Thalassia* flowers arise laterally on, and do not interrupt growth of the short-shoot. However, the attachment of short-shoot to rhizome is weak and is eventually broken mechanically. It must be remembered that erect shoots in *Thalassia* are supported by sea-water, unlike sedges and grasses, and this may account for their unlimited growth.

*Thalassia* is well-designed to regulate the depth at which it grows. Adjustment to an eroding substratum comes about by downward instead of horizontal growth of the rhizome apices. This adjustment seems rapid because *Thalassia* rhizomes are often much contorted. Contrariwise *Thalassia* is equally well adapted to silting, either because of upward growth of the rhizome apex or by the production of new rhizomes as laterals on short-shoots, necessarily at a higher level.

The most peculiar feature of *Thalassia,* especially in comparison with some other Hydrocharitaceae (*cf.,* Cutter, 1964), is its inability to produce dormant buds. This may be related to the relative constancy of its marine environment. Growth of the rhizome apex is apparently continuous. It is not known if the rate of growth slows in winter months. Leaf production by short-shoots more evidently fluctuates since superficially they seem much less vigorous in winter (*cf.,* Phillips, 1960).

Continuous growth of the organism is entirely dependent on activity of vigorous rhizome apices. No residual meristems are left behind so that adventitious growth, even of roots, is impossible. This is important. Fragments of rhizome and short-shoot are incapable of regeneration. Thus, despite its seeming vigor and profligacy, *Thalassia* is not well suited to asexual propagation by isolated fragments.

*Thalassia,* like some other members of the Hydrocharitaceae (Cutter, 1964), offers itself as being peculiarly suitable as a subject for morphogenetic studies. It has two seemingly unlike, but fundamentally similar, axes with different directions of growth producing entirely different kinds of leaf. The axes are autonomous. One kind cannot be converted directly into another, but only reciprocally by branching; a branch from a long-shoot is always a short-shoot, and vice versa. Branching of the long-shoot is rhythmic and ordered by some internal regulator in such a way that the branch is initially precocious, more vigorous than the main axis, and so unusually sited that the type of branching is difficult to analyze. Finally, branching of rhizomes is so limited that a large number of leaves (8 to 12) intervenes between each pair of branch-associated leaves. Alternation of leaf without and leaf with a bud seems a peculiar property of Hydrocharitaceae, according to Cutter (1964). In *Thalassia* this is carried to an extreme degree.

This preliminary account will be amplified and probably modified as the results of detailed investigation of the structure and development of each organ is made known.

## ACKNOWLEDGMENTS

We are much indebted to Miss Lesley Jackson and Miss Vroni Oswald for the preparation of microtome sections on which this study is based. The illustrations for Figures 1 to 18 were executed by Miss Priscilla Fawcett.

## SUMARIO

### SOBRE LA MORFOLOGÍA Y ANATOMÍA DE LA HIERBA DE TORTUGAS, *Thalassia testudinum* (HYDROCHARITACEAE). I. MORFOLOGÍA VEGETATIVA

En el recuento de la introducción de la morfología vegetativa de *Thalassia testudinum* König, se describe una simetría orgánica muy constante. Un largo retoño horizontal que tiene sólamente hojas escamosas, produce yemas laterales alternativamente en lados opuestos, a intervalos regulares separados por 9 a 13 internudos. No hay yemas asociadas con escamas interpuestas. Las yemas son opuestas, no axilantes a las hojas abrazadoras y debido a esta posición poco usual y a su precoz desarrollo, pudiera discutirse que son laterales. Las yemas se vuelven cortos retoños erectos que llevan inicialmente hojas escamosas, pero pronto hojas foliáceas. Los retoños largos y los cortos tienen fundamentalmente la misma simetría. Cada uno es autónomo, de modo que el

uno puede volverse el otro, sólamente por ramificación. Debido a la ausencia de meristemos residuales, el crecimiento de *Thalassia* depende grandemente de la actividad de los meristemos de los retoños apicales, aún con la producción de raíces limitada a las regiones apicales. En la ausencia de ápices rizómicos, los fragmentos aislados no regeneran.

## LITERATURE CITED

ARBER, A.
1925. On the 'squamulae intravaginales' of the Alismataceae and Butomaceae. Ann. Bot. (Lond.) *39:* 169-173.
ASCHERSON, P. AND M. GÜRKE
1889. Hydrocharitaceae—*in* Engler and Prantl, Die natürlichen Pflanzenfamilien, *2* (1): 238-258.
CONSTANTIN, J.
1886. Etudes sur les feuilles des plantes aquatiques. Ann. Sci. nat., B. sér., *7* (3): 94-151.
CUTTER, E.
1964. Observations on leaf and bud formation in *Hydrocharis morsus-ranae.* Amer. J. Bot., *51* (3): 318-324.
EICHLER, A. W.
1884. Beiträge zur Morphologie und Systematik der Marantaceen. Abh. K. Preuss. Akad. Wiss., Berlin., *1883:* 1-99.
MAGNUS, P.
1871. Anatomie der Meeresphanerogamen. S. B. Ges. naturf. Freunde, Berlin, p. 85-90.
MOORE, D. R.
1963. Distribution of the sea grass, *Thalassia,* in the United States. Bull. Mar. Sci. Gulf & Carib., *13:* 329-342.
ODUM, H. T., P. R. BURKHOLDER AND J. RIVERA
1960. Measurement of productivity of turtle-grass flats, reefs and the Bahia Fosforescente of Southern Puerto Rico. Publ. Inst. Mar. Sci., Univ. of Texas, *6:* 159-170.
PHILLIPS, R. C.
1960. Observations on the ecology and distribution of the Florida sea grasses. Professional Papers Series, Fla. Bd. Conserv., (2): 1-72.
SAUVAGEAU, C.
1890a. Sur la feuille des Hydrocharidées marines. J. Bot., *4:* 269-275; 289-295.
1890b. Observations sur la structure des feuilles des plantes aquatiques; *Zostera, Cymodocea* et *Posidonia.* J. Bot., *4:* 41, *et seq.*
SKUTCH, A. F.
1932. Anatomy of the axis of the banana. Bot. Gaz., *93:* 233-258.
STRAWN, K.
1961. Factors influencing the zonation of submerged monocotyledons at Cedar Key, Florida. J. Wildl. Manage., *25* (2): 178-189.
THOMAS, L. P., R. M. MOORE AND R. C. WORK
1961. Effects of hurricane Donna on the turtle grass beds of Biscayne Bay, Florida. Bull. Mar. Sci. Gulf & Carib. *11* (2): 191-197.
VOSS, G. L. AND N. A. VOSS
1960. An ecological survey of the marine invertebrates of Bimini, Bahamas, with a consideration of their zoo-geographic relationships. Bull. Mar. Sci. Gulf & Carib. *10* (1): 96-116.