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ASPECTS OF FLORAL MORPHOLOGY AND DEVELOPMENT IN THE SEAGRASS SYRINGODIUM FILIFORME (CYMODOCEACEAE)

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Inflorescences in *Syringodium filiforme* are initially racemose and subsequently extensively cymose, with terminal units referred to as "flowers." The species is dioecious. Each unit is normally enclosed by a pair of bracts which may subtend renewal shoots. The male flower consists of four pairs of microsporangia which arise by equal subdivision of two lobes of the floral apex. Each pair of microsporangia is associated with a late-developing protuberance, which collectively fuse to form a "perianth ridge," soon obscured by the enlarging microsporangia. The female flower is naked and consists of two carpels which arise separately on the floral apex. The carpel is initially peltate but matures as a closed structure with a single pendulous ovule and two styles. The homology of these structures with the parts of a normal flower is discussed and compared with several related genera for which similar information is available.

Introduction

Detailed studies of floral development in seagrasses are lacking because of the difficulty of obtaining material. Nevertheless, this information is useful in providing comparative data for systematic purposes and is helpful in understanding biological processes associated with underwater pollination (e.g., PETTITT and JERMY 1975; DUCKER and KNOX 1976; YAMASHITA 1976).

We undertook this study largely to supply the necessary background information for this biological approach and also to circumscribe more clearly the family Cymodoceaceae (*sensu* TAYLOR 1909), since the same kind of information has been made available for the Zannichelliaceae (*sensu* DUMORTIER) (POSLUSZNY and TOMLINSON 1977). Since these aquatic monocotyledons are represented at an elementary level of organization, presumably by reduction, it is appropriate to continue to establish precise morphological information by which their discreteness and affinities can be assessed.

TAXONOMY OF THE CYMODOCEACEAE.—The five genera of seagrasses—*Amphibolis* (two species), *Cymodocea* (five species), *Halodule* (perhaps seven species), *Syringodium* (two species), and *Thalassodendron* (two species)—form a natural entity in terms of habit, floral morphology, pollen structure, and aspects of anatomy; they have long been recognized as a distinct group, either as Cymodoceeae (ASCHERSON and GRAEBNER 1907) or Cymodoceoideae (DEN HARTOG 1970) within a larger Potamogetonaceae, or as a separate family Cymodoceaceae (TAYLOR 1909), supported by several subsequent authors (AIRY-SHAW 1966; TAKHTAJAN 1966; TOMLINSON and POSLUSZNY 1976). Accumulating morphological information, of which this study forms a part, continues to support the categorization at higher rank and a dissociation from the fresh-water group Zannichelliaceae, in contrast to the opinion of J. E. DANDY (in HUTCHINSON 1959), who includes both groups of genera in a more widely conceived Zannichelliaceae.

Information on floral morphology in Cymodoceaceae, summarized by DEN HARTOG (1970), has been augmented by the studies of ISAACS (1969) and KAY (1971) on *Thalassodendron* and *Cymodocea* and DUCKER and KNOX (1976) on *Amphibolis*. Plants are apparently dioecious; the reproductive structures are associated with reduced leaves (bracts); the female "flower" consists of a pair of carpels each with a pair of filamentous styles; and the male "flower" has a single axis, sometimes appendaged distally and bearing four pairs of pollen sacs.

We extend these studies to *Syringodium* and provide detailed information about floral development and some aspects of anatomy, adding information which helps to establish the fundamental construction of the cymodoceaceous flower.

Material and methods

Inflorescences of *Syringodium filiforme* Kütz., fixed in FAA, were collected during several recent summers at Matheson Hammock Wading Beach, Dade County, Miami, Florida. The most generally useful specimens in terms of developmental stages were collected in February 1976. In addition, material from the Enconana River, Gulf of Mexico, supplied by H. F. BITTAKER has proved useful for comparison with the Miami population.

Dissections of early floral stages were prepared, stained, and photographed by the techniques of SATTLER (1968). Direct morphological study was complemented by study of serial sections of paraffin-embedded material, stained in either safranin and fast green or safranin and Delafield's hematoxylin, according to standard techniques.

Gross morphology

Syringodium filiforme ("manatee grass") is a common constituent of shallow-water marine com-

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munities in appropriate stable substrates in the Caribbean. Plants show shoot dimorphism since they extend by means of a horizontal monopodial rhizome, bearing scale leaves separated by quite long internodes (fig. 1). The scale leaves each subtend erect shoots with foliage leaves and usually quite short internodes; the erect shoots are normally ultimately determinate by flowering (DEN HARTOG 1970; TOMLINSON 1974). Proliferative branching of the rhizome is facultative, since it usually is stimulated by damage to rhizomes. The species is dioecious, and apparent clones of one sex are often quite extensive, suggesting that proliferative branching maintains and extends individual genets. In South Florida, flowering apparently begins as early as January, so that ripe fruits may be collected as early as June. However, the flowering season is clearly extended, although there are no detailed phenological data. The extended flowering season and elaborately cymose construction of the inflorescence make it relatively easy to assemble material showing a wide range of developmental stages.

INFLORESCENCE MORPHOLOGY.—Branching of the inflorescence is essentially cymose, at least in later stages. The inflorescence is superficially paniculate (fig. 2) and branched in one plane. The size of the inflorescence depends on the age and vigor of the plant; larger ones may include 30–50 flowers of different ages (fig. 2). For the first two or three nodes the inflorescence branches racemosely (fig. 5), with a single bract subtending a branch that bears a basal prophyll (fig. 3), both axes extending. Soon branches become cymose, with pairs of bracts enclosing a single flower. The internode between the bracts of one pair is suppressed; that between bracts of successive pairs is usually quite extended (fig. 9). The lowest bracts on an inflorescence consist of a basal sheath and a distinct blade (fig. 4) that is often several centimeters long. Distally bracts at increasingly higher levels have progressively reduced blades; the blade in the ultimate bracts is usually vestigial. Three possible kinds of arrangement occur in association with each bract pair, with the axis above the bracts terminating in a flower in each kind (figs. 6–8).

In the most complex condition both bracts subtend a prophyllate branch, both branches growing out as renewal shoots so that the inflorescence is elaborated (figs. 7, 14). In the most common condition only the lowest bract subtends a branch; the upper bract is empty (fig. 6) and a linear sympodium results. Least commonly, the lateral buds abort (fig. 8). All axes are terminated by the third kind in which neither bract subtends a lateral branch so that the system cannot extend further (figs. 10, 11).

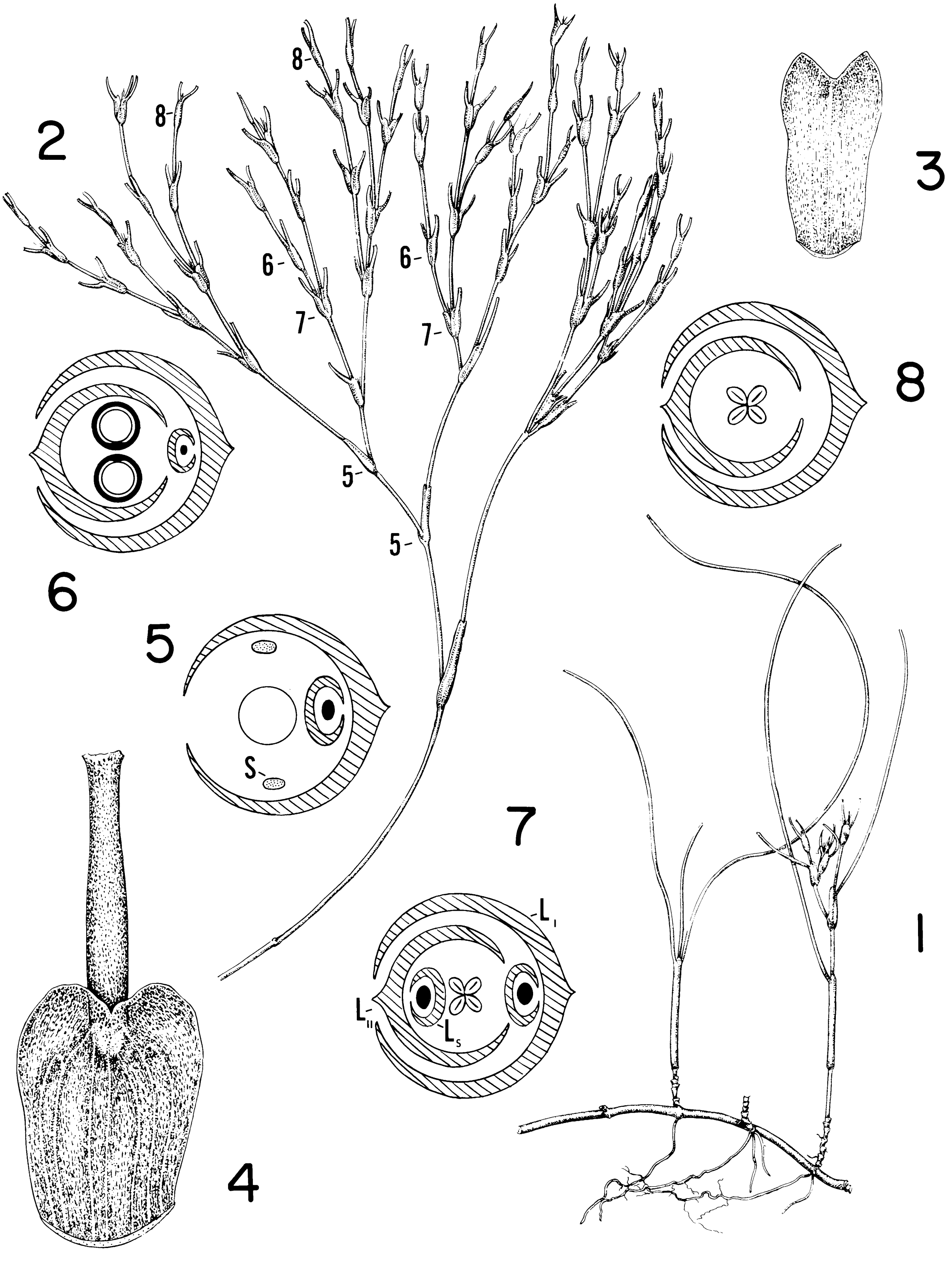
Bracts (fig. 4) are well-developed structures. The basal sheath includes a conspicuous median and four to six lateral veins which unite at the top of the sheath and form the pair of lateral veins of the blade. Prophylls (fig. 3) are always scarious, bladeless, and with a median and one or two obscure lateral veins; they neither develop a blade nor subtend a lateral bud. The prophyll remains within the enclosing bract, enveloping the base of its parent lateral axis. Squamules (intravaginal scales) are common at all nodes, including the prophyllar nodes, and usually form a lateral pair. In early stages squamules may be proportionately large in relation to the primordia of other organs (e.g., fig. 24).

FLORAL MORPHOLOGY.—For descriptive purposes we have applied the term "flower" to each biologically discrete unit enclosed by a bract pair within the branch complex we have called the "inflorescence." The descriptive convention is not intended to convey any interpretative information, which is discussed later. The female unit can be recognized by the extended stigmata (fig. 10); in the male unit the anther remains enclosed until anthesis (fig. 14).

The female flower consists of a pair of carpels on the common axis but without any additional perianth or ridge, as is clear in the unit with bracts removed (fig. 12). Each carpel includes a single bitegmic ovule pendulous from the apex of the locule (fig. 13). The carpel continues as a short style which further extends into two rather stout stigmata. At maturity the stigmata protrude between the enveloping bracts, but there is no extension of the floral axis (figs. 10, 11). The pair of carpels originate in a plane at right angles to the plane of distichy of the subtending bract (figs. 6, 34), but subsequently they are often displaced into an oblique position. Both carpels can develop into fruits, but there is frequent abortion of one or both of them.

The male flower terminates a unit of the sympodium and consists of four pairs of microsporangia inserted directly on the axis and enclosed by the bract pair (fig. 16). A shallow ridge, obscured by the basal extension of the microsporangia, encircles the axis at the level of insertion of the microsporangia

FIGS. 1–8.—*Syringodium filiforme*, habit and inflorescence construction. Fig. 1, Older part of rhizome with erect leafy shoots, one with a terminal inflorescence; × 3/8. Fig. 2, Mature female inflorescence from a vigorous plant; × 1/2 (numbers indicate examples of the types of branching in figs. 5–8). Fig. 3, Prophyll from branch base laid flat to show venation; × 4. Fig. 4, Bract with short blade, basal sheath laid flat to show venation; × 5. Figs. 5–8, Diagrams of different possible kinds of units within a single inflorescence (regardless of whether male or female); L = bract, L_s = prophyll, S = squamule, outline = main axis or flower parts, solid black = branch axis; fig. 5, lower node with monopodial branching from the axil of a single bract; fig. 6, node with pseudomonopodial branching below a terminal female flower; one renewal shoot in the axil of the lowest bract; fig. 7, lower node with sympodial branching (two renewal shoots) below a terminal male flower; fig. 8, terminal unit without renewal shoots, below a male flower; no axillary branching.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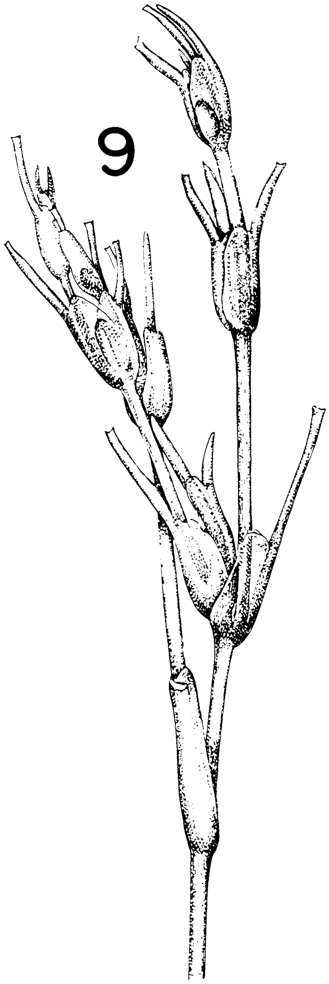
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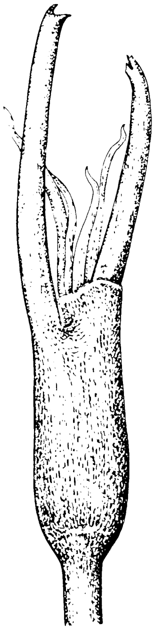
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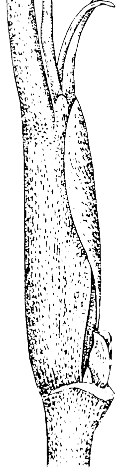
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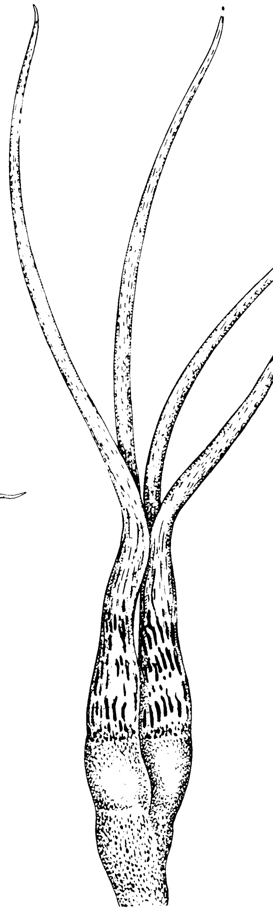
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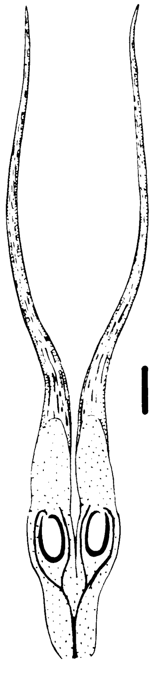
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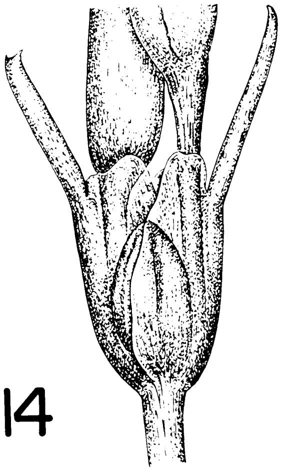
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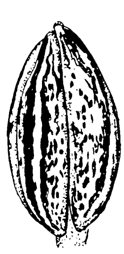
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(fig. 30). The surface of the anther is provided with numerous large tannin cells, except for the narrow longitudinal line of dehiscence.

The male flower is initially enclosed by its pair of bracts, but at the time of dehiscence the floral axes elongate about 10-fold. This pushes the bracts aside (although the flower does not usually extend beyond them) sufficiently for the pollen sacs to be released (fig. 15). As in all Cymodoceaceae, the pollen is filamentous.

Development

In both sexes the floral apex originates as a lateral axis in the axil of a bract of the previous flower complex; most often this is the lowest bract (figs. 17–24, 31–37). The lateral axis initiates prophyll and bracts before there is any evidence of floral differentiation in the apex itself.

MALE FLOWER.—The developmental sequence is observed by freeing the complex of outer enveloping bracts (figs. 17–30), a random selection revealing units at differing ages. As an indication of the relative stages of development of successive units, the lateral apex (fig. 28) is at an earlier stage than the floral primordium (fig. 17).

The first indication of floral differentiation is expansion of the shoot apex and development of two lobes at right angles to the plane of distichy of the bracts (fig. 17). At this stage the flower is partially enveloped by its prophyll (L_s), and the two bracts are well developed (fig. 18,*L* and *L* arrow). Subsequently the two lobes themselves become bilobed (fig. 19), so that the floral apex is now represented by four equal lobes which are the primordia of the microsporangial pairs (fig. 20). At this stage the complex is partially enveloped by the prophyll (fig. 20,L_s), and the lowest bract has to be removed to reveal its subtended bud (*V*) and the anther (*A*). The subtended lateral meristem (*V*) has the possibility of forming a continuing renewal shoot. The second bract occupies a position on the same side of the axis as the prophyll. The situation is made somewhat complex by the series of squamules within each leaf axil which are revealed when the subtending leaf is removed (e.g., fig. 21,*S*).

At the time the floral apex takes on its definitive four-lobed shape, a subtending appendage is initiated below each lobe (fig. 19,*B*). Through extensions of the distal portions of these appendages, a shallow ridge of tissue is developed encircling the base of the floral axis (figs. 22, 23). For a limited period the ridge is relatively conspicuous (fig. 23), but with the final expansion of anther lobes it is essentially obscured. This expansion of the anther lobes, both basally and apically, continues so that the floral apex becomes overtopped and obscured while the lengthening floral axis is also enveloped (figs. 22–28). During this period of enlargement the renewal shoot (*V*) in the axil of the lowest bract becomes differentiated, and the prophyll (L_s) and bracts (*L*) of the next unit of the sympodium are produced (figs. 20, 24, 27, 28).

Further growth involves the enlargement of all parts except squamules up to the stage when the anther is fully mature but still enclosed within the leafy bracts. The girdling ridge (*B*) does not take part in this enlargement (fig. 30).

FEMALE FLOWER.—In early stages the floral apex of the future female flower closely resembles the male, with the same arrangement of a prophyll (L_s) and two bracts together with associated squamules (figs. 31, 32). As in the male flower, early differentiation is indicated by the broadening of the floral apex (*G*), which becomes bilobed in a plane at right angles to the plane of distichy of the bracts. Each lobe is a carpel initial. Carpel development is indicated by the elaboration of each lobe as a peltate structure (figs. 32, 33). The single ovule of each carpel is developed on the inner (adaxial) side (i.e., fig. 34,*O*). This early stage of the open carpel is rapidly superseded by intercalary growth so that the carpel becomes flask shaped, enclosing the ovule which is carried to the apex of the locule (fig. 13). Stigmata are initiated at the apex of each carpel (figs. 35–37); they elongate markedly later, with intercalary growth producing the style.

Relative stages of development of the next lateral branch of the sympodium (*V*) in relation to the parental unit show that the axes of two successive orders maintain the same developmental proportions (figs. 33–37). At the time the stigmata (*Si*) on one unit are initiated, the primordia of the carpels of the next higher order are evident (fig. 36,*G*) and another developmental cycle can be reconstructed (cf. fig. 31).

Where two renewal shoots develop, one from the axil of each bract, the upper unit is always later in development than the lower unit so that there is an acropetal sequence of development maintained within one complex.

FIGS. 9–16.—*Syringodium filiforme.* Details of inflorescence complexes and flowers. Figs. 9–13, female; figs. 14–16, male. Fig. 9, Portion of a female inflorescence showing several kinds of branch arrangement, mostly corresponding to types in figs. 5–8; × 3/2. Fig. 10, Terminal unit, bract pair enveloping a terminal female flower; × 4. Fig. 11, Same as fig. 10 with lower (outer) bract removed to show aborted axillary renewal shoot; × 4. Fig. 12, Female flower, the bicarpellate structure enclosed by the bract pairs; × 6. Fig. 13, Longitudinal section of bicarpellate flower with central vascular system; × 4. Fig. 14, Male flower with two renewal shoots, one from each axil of the bract pair; × 3 (cf. fig. 7). Fig. 15, Male flower at anthesis, the upper bract pushed aside by extension of the floral axis; × 3. Fig. 16, Male flower with bracts removed to show superficial tannin cells; × 4 (cf. fig. 30).

Floral vasculature

The vascular system of the floral axes corresponds to that in the vegetative axes of the rhizome and leafy erect shoots, both in its general histology and in the distribution of traces to appendages (SAUVAGEAU 1891; MONOYER 1927; TOMLINSON, unpublished observation). There is a central axial strand, which includes a central xylem lacuna surrounded by two to four phloem strands together with four to six cortical strands (figs. 38, 39). Median traces of leaves, bracts, prophylls, and branch axes diverge from the central strand (e.g., figs. 40, 41, arrows), whereas lateral traces of leaves and bracts are derived from the cortical system. There is a direct connection between the cortical vascular system of a parent axis and its branch axis.

In the male flower (fig. 42) the central strand continues to the floral apex, where it expands, developing an extensive tracheary mass, but ends blindly. The cortical system ends blindly at the level of the inconspicuous ridge of tissue near the insertion of the microsporangia. This ridge, however, is not vasculated.

In the female flower (figs. 43–46) the cortical system ends blindly at the base of the common carpellary axis. The central strand at this level enlarges and divides equally to produce one trace to each carpel (fig. 44); at a higher level each carpel trace divides (fig. 45) to give a dorsal trace (which becomes the ovular trace, extending and bending into the funiculus) and a ventral trace (which extends as far as the base of the style, which it does not enter, ending blindly at about the level of insertion of the ovule on the opposite side) (fig. 13). Consequently, in a slightly oblique section (fig. 46), both traces are visible in the left-hand carpel, but only the ventral trace is visible in the right-hand carpel cut at a higher level.

Discussion

A universal feature of the Cymodoceaceae is the terminal position of the reproductive unit. *Syringodium* offers immediate contrast to other Cymodoceaceae because of its expanded, sympodially constructed inflorescence (OSTENFELD 1916), whereas other genera seem superficially distinct in having flowers either on lateral shoots of the erect leaf system (*Amphibolis*, *Thalassodendron*) or immediately terminal on the leafy erect shoots themselves (*Cymodocea*, *Halodule*). In the latter two genera, shoot dimorphism is neither consistent nor regular (TOMLINSON 1974). KAY (1971) emphasized that *C. serrulata* has a terminal flower (his description is restricted to the female flower) but that sympodial branching can occur by the development of a renewal shoot from the axil of a subfloral foliage leaf. His description corresponds to the account by DEN HARTOG (1970) of the genus *Cymodocea* as a whole,

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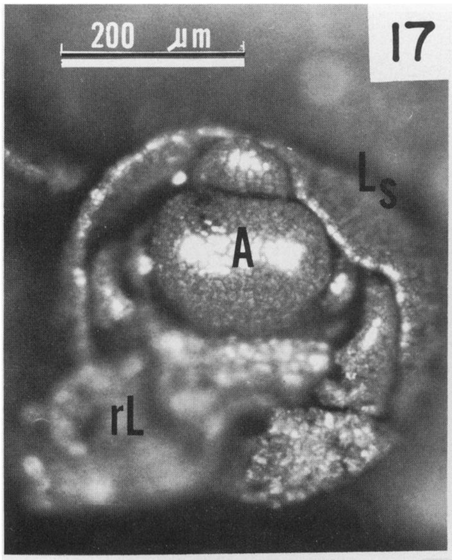
FIGS. 17–24.—*Syringodium filiforme*, early stages in the development of the male flower; all × 120. Fig. 17, Young male primordium enclosed in a sheathing prophyll (L_s), from above; the first bract removed (*rL*), the apex of the second bract just protruding on the same side as the prophyll (L_s); the primordium (*A*) showing by lateral expansion the first indications of microsporangial development. Fig. 18, Lateral (adaxial) view of a similar stage to that of fig. 1 with prophyll removed, both bracts (*L*) present; *A* = floral apex. Fig. 19, Oblique view of male flower showing the two lobes that will each develop into two pairs of microsporangia; the perianth ridge (*B*) is just evident below the lobed apex (*A*). Figs. 20–24, Lateral view of progressively older male flowers; fig. 20, the initial lobes seen in fig. 18 have divided to form the primordia of the four pairs of microsporangia (*A*); L_s is the prophyll partly enclosing the shoot and opposite the apex of the renewal shoot (*V*) developing in the axil of the first bract; figs. 21–23, stages in the development of the perianth ridge (*B*); squamules (*S*) are evident in the axils of bracts which have been removed, some in dorsal position (e.g., *S* in fig. 23); fig. 24, male flower primordia of two orders; L_3 is a possible third bract on the abaxial side; *V* is the apex of the renewal shoot in the axil of bract which has been removed but whose squamules (*S*) remain; *L′* is the second leaf produced by *V*.

FIGS. 25–30.—*Syringodium filiforme*, lateral view of male flowers at later stages in development; all × 120 (cf. fig. 17). In these structures, the perianth ridge (*B*) is more or less obscured by surrounding bracts (*L*), squamules (*S*), and microsporangia, except in figs. 29 and 30 where enveloping organs have been removed; L_s is prophyll of axillary renewal shoot (*V*). Fig. 25, Flower from abaxial (i.e., prophyll-opposed) side; the renewal shoot in the axil of the first bract, which has been removed, has initiated its own prophyll (L_s) and first bract (*L*). Fig. 26, Flower enveloped by sheath of second bract; renewal shoot in axil of first bract, which has been removed, overtopped by its own first bract. Fig. 27, Flower with first bract removed to show precociously enlarged squamules (*S*) and renewal shoot at about same age as in fig. 17. Fig. 28, Flower with bisporangiate condition of each anther sac clearly established; renewal shoot (*V*) with all appendages initiated. Fig. 29, Male flower with all appendages removed to show perianth ridge (*B*) contiguous with microsporangia. Fig. 30, Perianth ridge (*B*) displaced and obscured by expansion of axis and microsporangia; surface tannin cells clearly differentiated.

FIGS. 31–37.—*Syringodium filiforme*, early stages in the development of the bicarpellate gynoecium of the female flower; all ×120 (cf. fig. 17). Fig. 31, Young renewal shoot, future female flower indicated by laterally expanded apex (*G*); prophyll (L_s) and second bract (on same side of axis as prophyll) still attached; first bract removed (*rL*). Fig. 32, Female flower obliquely from above, differential upgrowth of carpel primordia (arrows) initiating their peltate form. Fig. 33, Later stage, with apex of renewal shoot (*V*) in axil of first bract. Fig. 34, Ovule primordia (*O*) initiated on the inner margin of each peltate carpel; renewal shoot with its prophyll. Fig. 35, Late stage of carpel development, enclosure of the ovule complete; stigma lobes (*Si*) evident; renewal shoot (*V*) with all its appendages initiated; squamules (*S*) disproportionately large in relation to other primordia. Figs. 36–37, Late stages in flower development, the common style of stigmata (*Si*) still unelongated; the primordium of the next flower (*G*) is well developed, in fig. 36 already with a further renewal shoot (*V*) evident.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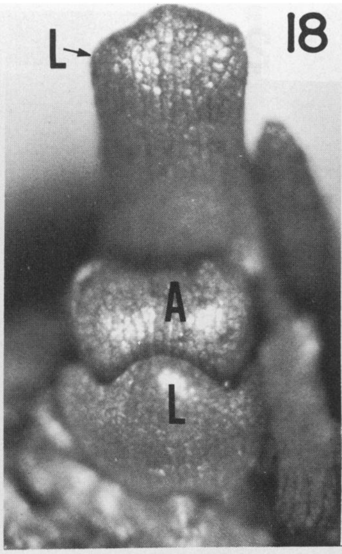
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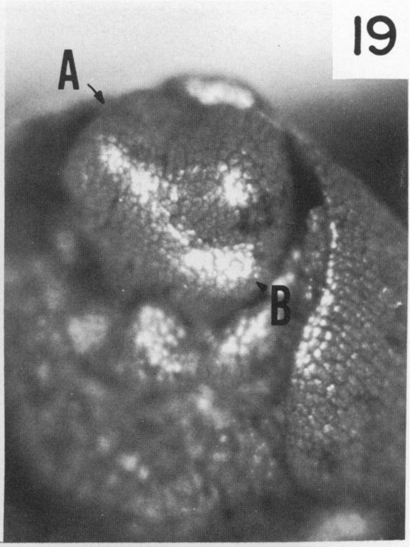
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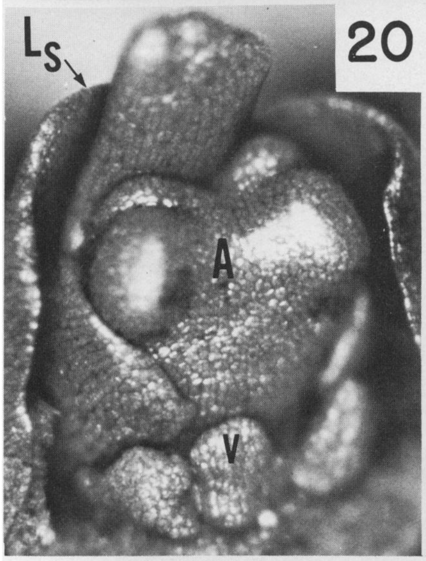
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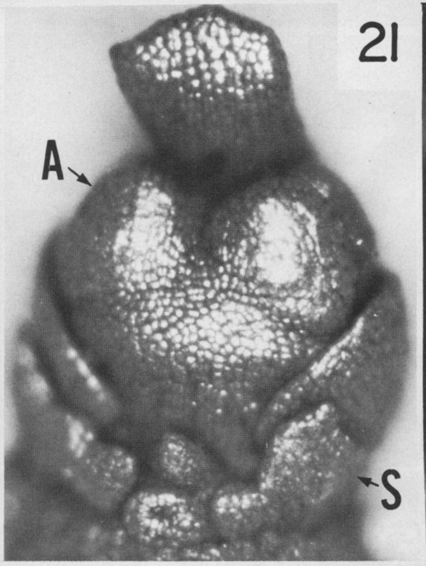
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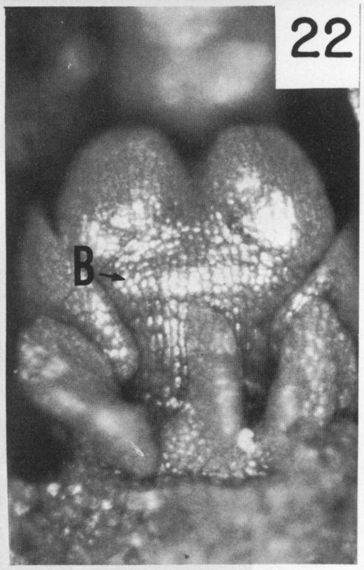
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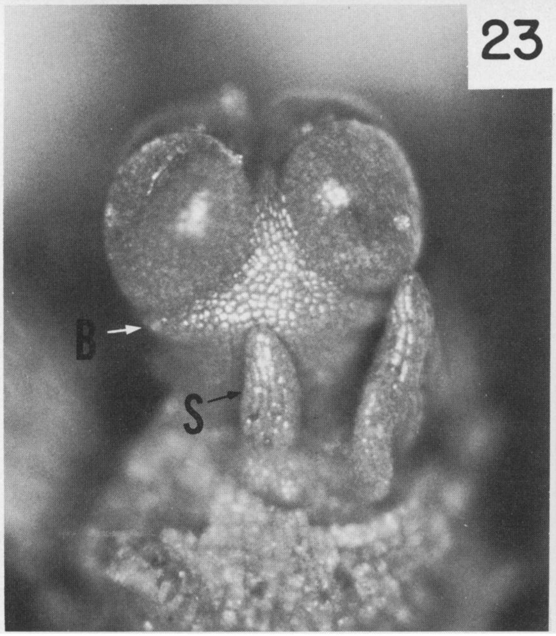
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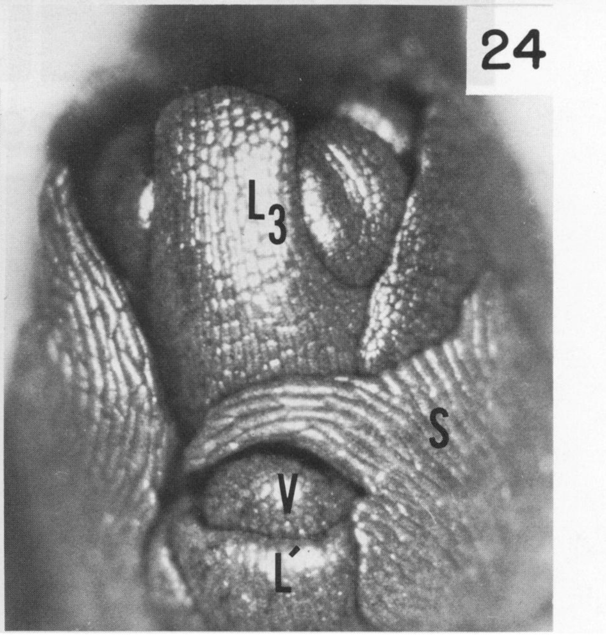
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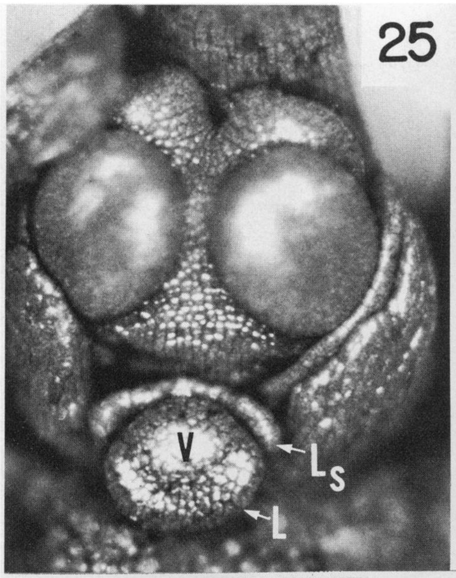

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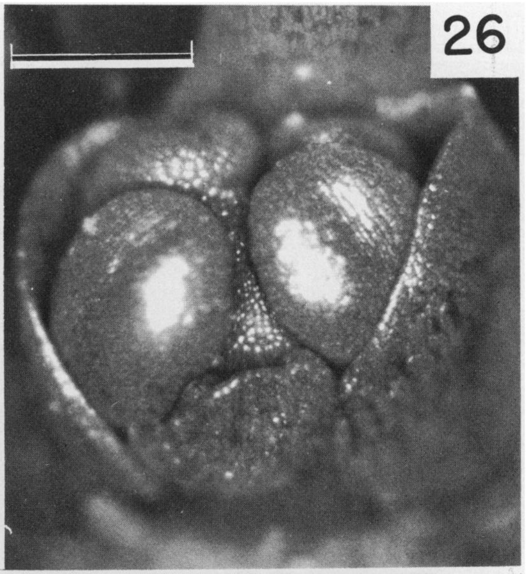

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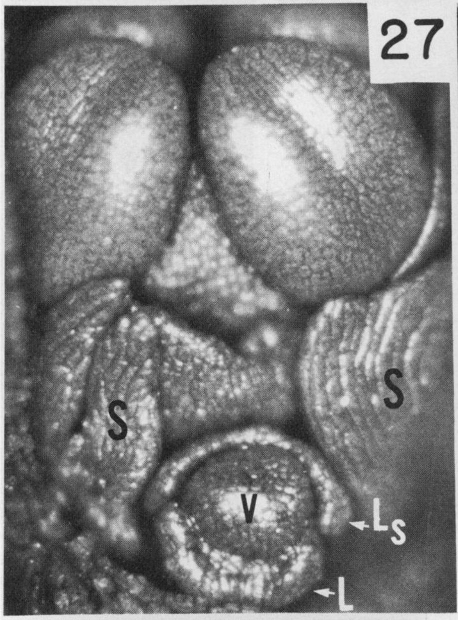

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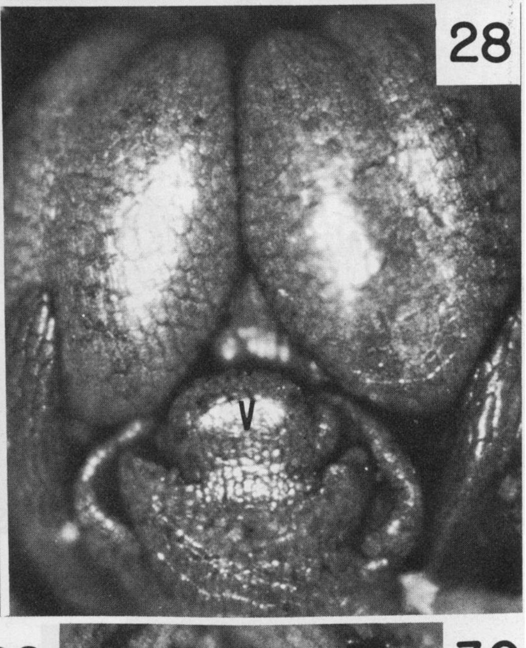

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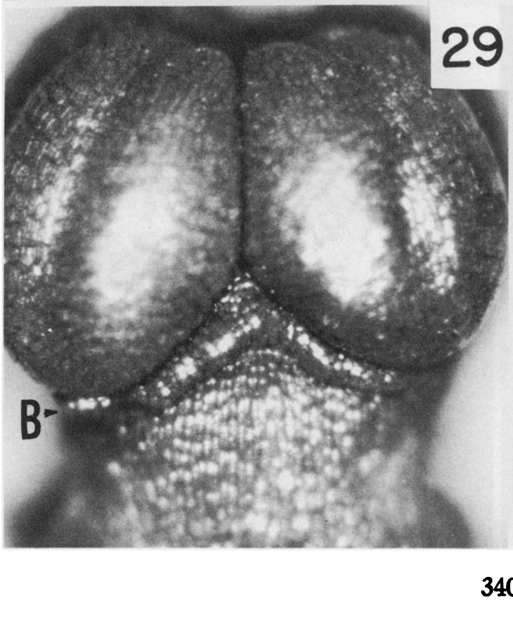

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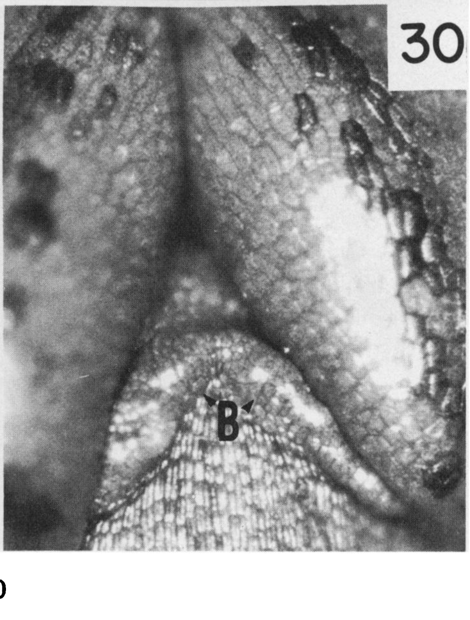

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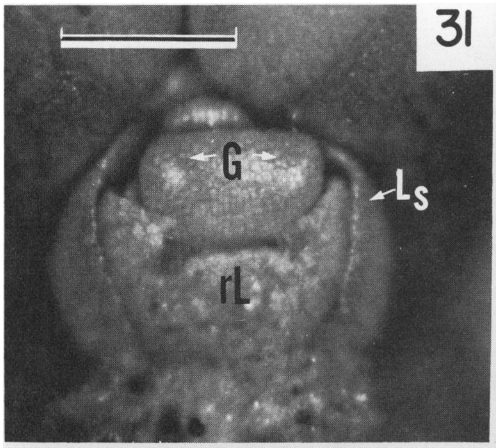
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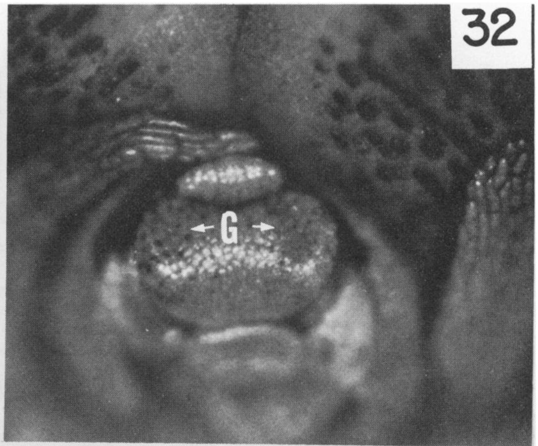
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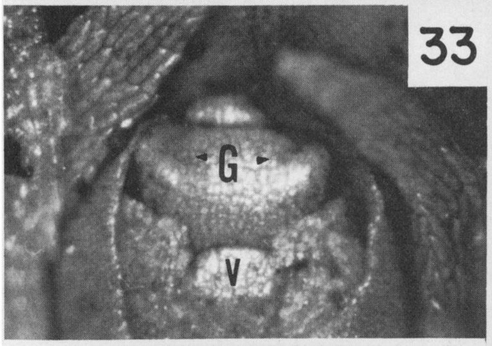
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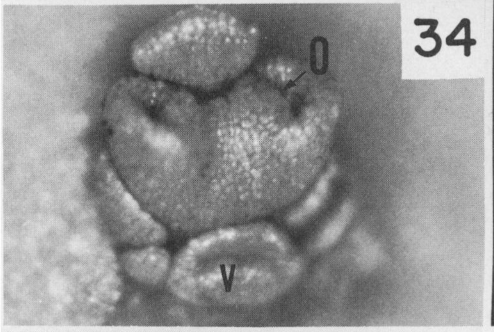
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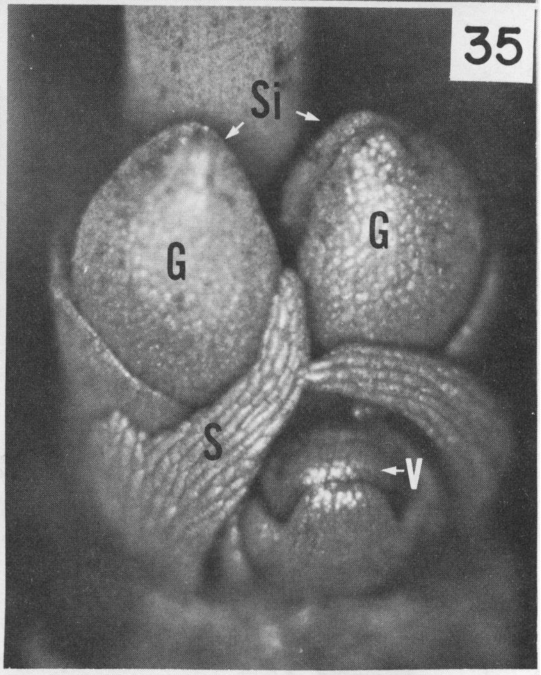
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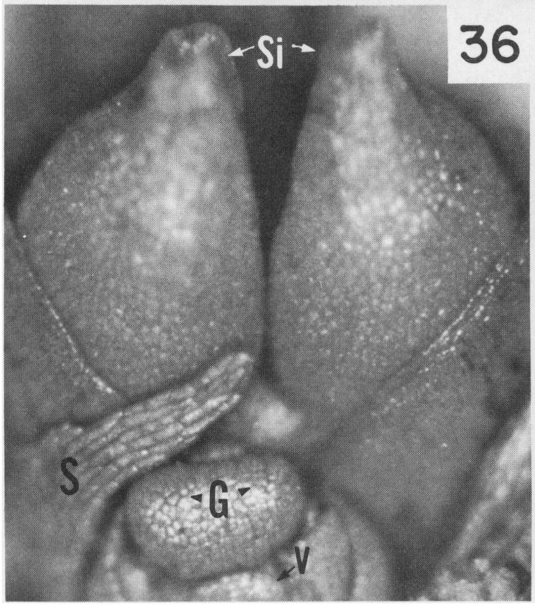
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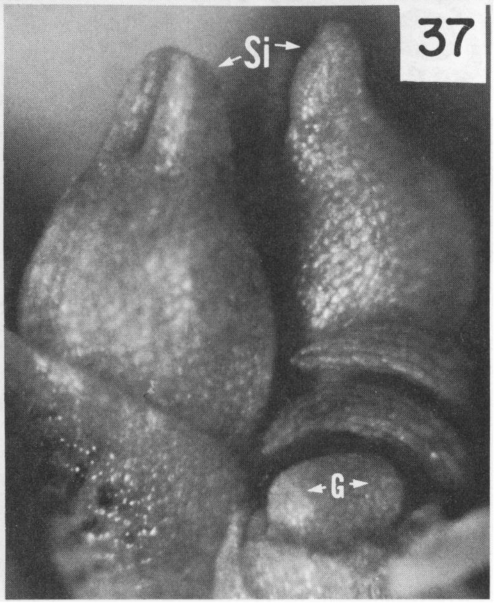
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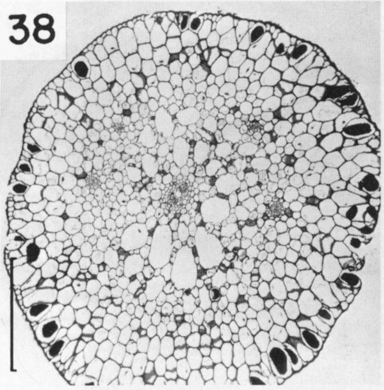

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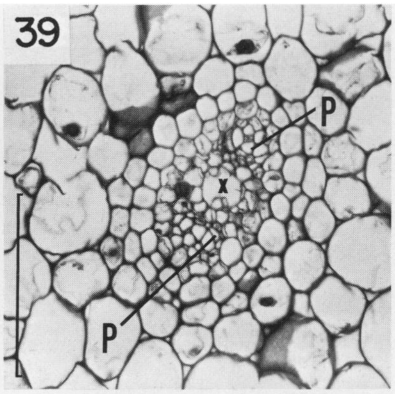

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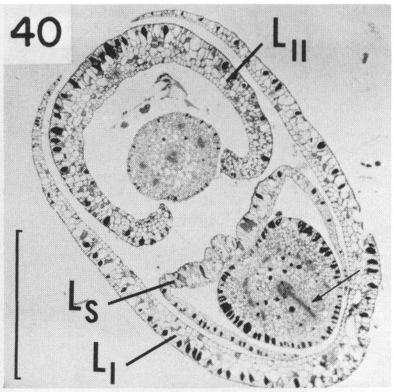

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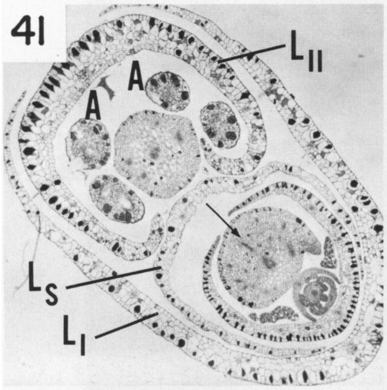

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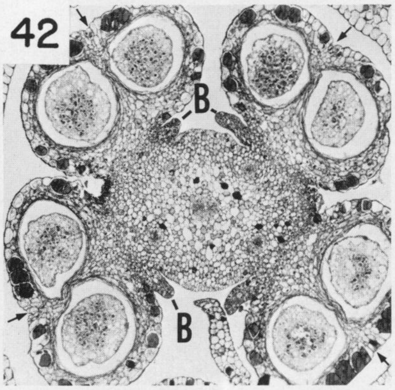

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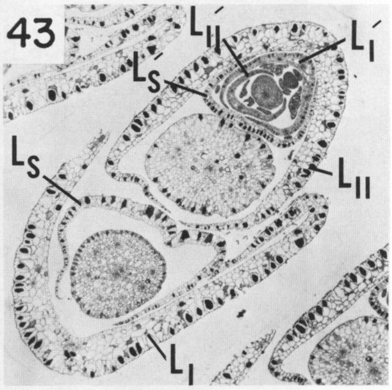

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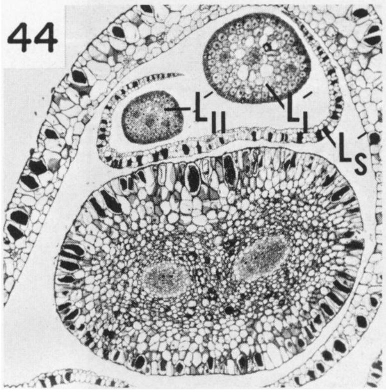

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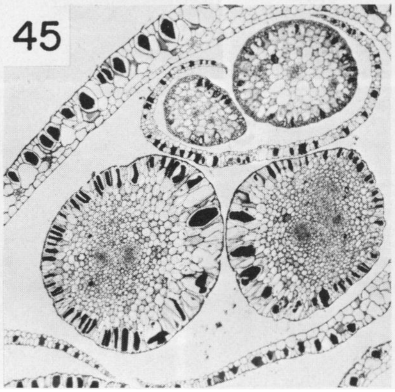

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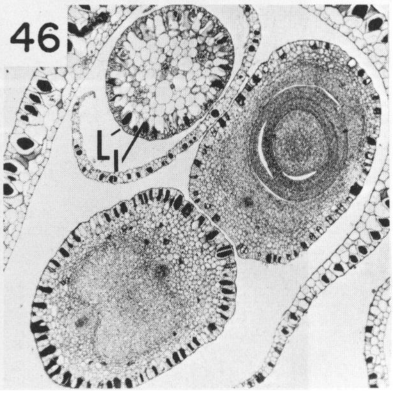

following the detailed descriptions of such authors as BORNET (1864) and OSTENFELD (1916). KAY (1971) also recorded, in *T. ciliatum* from Kenya, male flowering branches with a second male flower in the axil of the third (penultimate) bract of the flowering unit in about 10% of examples studied. There is thus an incipient tendency in other genera for the branching condition strongly expressed in *Syringodium.*

Most authors have adopted a neutral terminology in describing the reproductive parts in the Cymodoceaceae and referred to "flowers" in a biological sense for the individual units associated with specialized bracts (e.g., OSTENFELD 1916; ISAACS 1969; DEN HARTOG 1970; KAY 1971). In an interpretative sense the male flower by description or implication has been considered to consist of two dorsally connate anthers (DEN HARTOG 1970), which seems appropriate in *Halodule* because they are clearly inserted at different levels and because in all genera they consist of four bisporangiate pollen sacs (i.e., with eight separate microsporangia, not four as suggested in the illustration of *Syringodium* by MARKGRAF [1936], his Tafel VIII, 6d). In all genera except *Syringodium* the anthers are also apically appendaged; in *Amphibolis* these appendages become quite elaborate. *Syringodium* therefore shows least evidence of a pair of discrete anthers at maturity, although the initial bilobed floral apex could be interpreted as demonstrating their existence. This evidence, however, is quite tenuous. Vasculature again does not support the interpretation of a dual structure since the stalk has a single vascular supply, somewhat elaborated distally, but scarcely forming two discrete strands.

DEN HARTOG (1970) pointed out that, if two anthers are involved, the common axis is not a filament but a pedicel, implying that he views the unit as a flower with two stamens. All previous authors emphasized the absence of any specialized floral envelope (MARKGRAF 1936). Our present demonstration of a vestigial "perianth ridge," which is initiated as separate primordia subtending each of the four developing staminal lobes (pairs of microsporangia) and becomes a rim of tissue separate from the microsporangia, can be used as evidence that the structure is a true flower. However, the sequence of initiation (staminal lobes preceding the subtending appendages) is in contrast to the acropetal sequence of development in most flowers. Furthermore, there is no comparable structure in the female flower.

DEN HARTOG (1970) made no detailed commentary about the morphology of the female flower, which resembles the male in major features. The male flower of *Thalassodendron,* however, has one fewer bract than the female flower. His family description of the unit as including two separate "ovaries" (where we have used the term carpels) might suggest that he saw it as two separate flowers, but this may not have been his intention in view of his statement about the male flower.

An alternative explanation is offered by MARKGRAF (1936) (see also ASCHERSON and GRAEBNER 1907), who considered each anther (set of four microsporangia) as a separate male flower so that the unit is seen as a partial inflorescence, its stalk a peduncle and not a pedicel. Similarly, the two carpels of the female unit would be regarded as belonging to two morphologically separate flowers. This interpretation is also implied in the description by DUCKER and KNOX (1976) of the unit in *Amphibolis* as "paired female flowers." The multiple (two to three) styles of all genera except *Halodule* certainly support this view.

In *Syringodium* we have shown that the female unit has no associated perianth, and its extreme simplicity both in development and vascular anatomy provides no clues to its typological organization. *Amphibolis* is somewhat exceptional because of the four unequal lobes which crown the carpels below the styles. These might be interpreted as tepals (which would produce an inferior ovary), but since they develop late (S. C. DUCKER and R. B. KNOX, personal communication), they seem a specialized feature related to the pronounced vivipary and method of anchorage of seedlings in this genus.

FIGS. 38–46.—*Syringodium filiforme,* male and female floral units in transverse section (TS), all from serial sections of paraffin-embedded material. Scale in figs. 38, 42, 44–46 = 0.5 mm; in fig. 39 = 100 μm; in figs. 40, 41, 43 = 1 mm. Figs. 38–42, Male inflorescence; figs. 43–46, female inflorescence. Fig. 38, TS axis below floral unit with central and cortical vascular strands. Fig. 39, Detail of central vascular strand with xylem lacuna (*X*) and two phloem strands (*P*); remains of secondary walls of tracheary elements in the xylem lacuna. Fig. 40, TS same floral unit ca. 1.5 mm above 38 to show bract pair L_{I} and L_{II}, the latter empty, the former subtending a branch renewal shoot with prophyll (L_s); the leaf trace of the first bract of the renewal shoot evident (arrow, lower right). Fig. 41, TS same floral unit 320 μm above 40 to show basal lobes of anther sacs (*A*); renewal shoot, lower right, shows the primordia of two further branch orders in the axil of L_{I}, the leaf trace of the second bract of the first branch evident (arrow). Fig. 42, TS floral unit 600 μm above 41 to show four pairs of microsporangia of terminal "flower." At this level parts of the perianth ridge are evident (*B*); the cortical vascular system ends blindly about 30 μm above; region of dehiscence of microsporangial pairs shown by arrows; note numerous epidermal tannin sacs. Fig. 43, TS female unit with pair of bracts L_{I} and L_{II}, each subtending a renewal shoot with prophyll L_s corresponding to fig. 6; the uppermost unit, top right, shows one further order of branching. Fig. 44, TS female "flower" terminating the central axis in fig. 43 at a level 960 μm higher; the central vascular strand bifurcating to supply each separate carpel; cortical vascular system absent; blades of bracts L_{I}' and L_{II}' evident above, enclosed by prophyll L_s'. Fig. 45, TS 450 μm above 44, carpellary trace dividing to give a dorsal and ventral starnd in each carpel. Fig. 46, TS 450 μm above 45, slightly oblique, the level of section passing through the bitegmic ovule of the right-hand carpel.

TABLE 1

COMPARISONS OF FLORAL MORPHOLOGY AND DEVELOPMENT

	CYMODOCEACEAE	ZANNICHELLIACEAE		
	Syringodium filiforme (Dioecious)	*Lepilaena bilocularis* (Monoecious)	*Althenia filiformis* (Monoecious)	*Vleisia aschersoniana* (Monoecious)
Development of fertile branches	First three nodes of inflorescence racemosely branched, soon becomes cymose with pairs of bracts enclosing a single male or female flower	Repeatedly branched sympodia with pairs of subopposite reduced foliage leaves. Sympodia terminate with either male or female flowers	Male and female flowers aggregated in complex lateral sympodia. Male flower usually terminating main axis of each flower complex. Female flower terminal on higher branch orders in each flower cluster	Axial sympodial clusters. Male flower usually terminating first-order branch. Female flower terminating higher-order branches and short branches close to the rhizome
Stamens..........	Possibly two	One	One	One
Male flower......	Four pairs of microsporangia. Apex initially bilobed, then tetralobed, each lobe subtended by a late-forming appendage; becomes "perianth ridge"; encircles axis and obscured at maturity by anther; apex of connective unappendaged	Two to six pairs of microsporangia. Three scalelike bracts at the base of the microsporangia initiate and develop concurrently with the microsporangia they subtend; connective extended into a pointed terminal appendage	Single pair of microsporangia. Three scalelike bracts at the base of the microsporangia initiate and develop concurrently with the microsporangia they subtend	Four pairs of naked microsporangia. Connective terminating in a blunt appendage and with two vestigial outgrowths opposite each other on the central portion, initiated after the microsporangia and obscured at maturity
Female flower....	Two naked carpels, each initiated as peltate primordium. Single ovule formed on adaxial portion of carpel wall. Bilobed stigma	Three carpels, each subtended by a membranous scale which is initiated concurrently with the carpel primordium it subtends. Each carpel initiated as peltate primordium. Single ovule formed on adaxial portion of carpel wall. Feathery-branched stigma	Three carpels, each subtended by a membranous bract which is initiated concurrently with the carpel primordium it subtends. Each carpel initiated as peltate primordium. Single ovule formed on adaxial portion of carpel wall. Peltate stigma	Single carpel basally enveloped by a tubular membrane which is initiated late in carpel development (at ovule inception). Carpel initiated as peltate primordium. Single ovule formed on side wall of carpel. Funnel-shaped stigma
Pollen...........	Filamentous	Spherical	Spherical	Spherical

Parallels might be sought between the Cymodoceaceae and Zannichelliaceae since the latter are most directly comparable to *Syringodium* in their essentially sympodial inflorescence. We have shown, however (POSLUSZNY and TOMLINSON 1977), that the reproductive organs in Zannichelliaceae are more variable and complex than previously suspected and that evidence for typological analysis is very limited. *Syringodium* is compared with certain taxa in Zannichelliaceae for which detailed information is known (table 1). A common feature of these aquatic monocotyledons seems to be the structure of the carpel and its developmental pattern.

Certainly, more morphological information can be added to the present level of understanding, but biologically oriented work will be most profitable. A particular emphasis on developmental morphology and comparative histology, especially in the direction of fruit anatomy, would be welcome, although the chief limitation has always been the availability of material.

Acknowledgments

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LITERATURE CITED

AIRY-SHAW, H. K. 1966. A dictionary of the flowering plants and ferns by J. C. WILLIS. 7th ed., rev. Cambridge University Press, Cambridge.

ASCHERSON, P., and P. GRAEBNER. 1907. Potamogetonaceae. *In* A. ENGLER, ed. Das Pflanzenreich. Vol. **11**, pt. 4, no. 31. Engelmann, Leipzig.

BORNET, E. 1864. Recherches sur le *Phucagrostis* major Cavol. Ann. Sci. Natur. Bot., Sér. 5, **1**:5–51.

DEN HARTOG, C. 1970. The seagrasses of the world. Verhandelingen, Koninklijke Ned. Akad. Wetensh. Natuurkunde **59**(1):1–275.

DUCKER, S. C., and R. B. KNOX. 1976. Submarine pollination in seagrasses. Nature **263**:705–706.

HUTCHINSON, J. 1959. The families of flowering plants. Vol. **2**. Monocotyledons. 2d ed. Clarendon, Oxford.

ISAACS, F. M. 1969. Floral structure and germination in *Cymodocea ciliata*. Phytomorphology **19**:44–51.

KAY, Q. O. N. 1971. Floral structure in the marine angiosperms *Cymodocea serrulata* and *Thalassodendron ciliatum* (*Cymodocea ciliata*). Bot. J. Linnean Soc. **64**:423–429.

MARKGRAF, FR. 1936. Blütenbau und Verwandtschaft bei den einfachsten Helobiae. Ber. Deut. Bot. Ges. **54**:191–229.

MONOYER, A. 1927. Contribution à l'anatomie et à l'ethologie des Monocotyleés aquatiques. Mém. Couronné Acad. Roy. Belg. Cl. Sci. colloque 8° **10**:1–196.

OSTENFELD, C. H. 1916. Contributions to West Australian botany. I. Dansk Bot. Arkiv **2**(6):1–44.

PETTITT, J. M., and A. C. JERMY. 1975. Pollen in hydrophilous angiosperms. Micron **5**:377–405.

POSLUSZNY, U., and P. B. TOMLINSON. 1977. Morphology and development of floral shoots and organs in certain Zannichelliaceae. Bot. J. Linnean Soc. **75**:21–46.

SATTLER, R. 1968. A technique for the study of floral development. Can. J. Bot. **46**:720–722.

SAUVAGEAU, C. 1891. Sur la tige des Cymodocées Aschs. J. Bot. (Paris) **5**:205–11, 235–43.

TAKHTAJAN, A. 1966. Systema et phylogenia Magnoliophytorum. Nauka, Moscow.

TAYLOR, N. 1909. Cymodoceaceae. North Amer. Flora **17**(1):31–32.

TOMLINSON, P. B. 1974. Vegetative morphology and meristem dependence—the foundation of productivity in seagrasses. Aquaculture **4**:107–130.

TOMLINSON, P. B., and U. POSLUSZNY. 1976. Generic limits in the Zannichelliaceae (sensu Dumortier). Taxon **25**:273–279.

YAMASHITA, T. 1976. Uber die Pollenbildung bei *Halodule pinifolia* und *H. uninervis*. Beitr. Biol. Pflanzen **52**:217–226.