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Floral Morphology and Phylogeny in the Hydrocharitaceae

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FLORAL MORPHOLOGY AND PHYLOGENY IN THE HYDROCHARITACEAE[1]

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Abstract

The vascular anatomy of 13 of the 15 genera of the Hydrocharitaceae has been studied, and certain aspects of floral morphology are considered. The flowers of the family show a broad range of specialized structures combined with primitive characteristics. The origin of paired and single stamens is interpreted as probable modifications of fascicled stamens. Extreme reduction in the androecium is shown for several genera. Tendencies toward reduction and fusion within the gynoecium are pronounced. Most genera are at least slightly syncarpous, but a few are apocarpous. The inferior ovary is appendicular in nature, with some genera exhibiting more complete fusion than others. The carpels are open and show no signs of closure. The multicarpellate genera have the most primitive gynoecia within the family while the tricarpellate genera exhibit the most advanced types in the family. Intermediate forms are *Blyxa* and *Vallisneria*.

Introduction

The Hydrocharitaceae is a small family presently recognized as comprising 15 genera and fewer than 100 species. Most of the genera are tropical or subtropical, and all are aquatics. Three genera are strictly marine. Many genera are monotypic or have but a few species.

All genera except *Ottelia* have at least some species with unisexual flowers which are usually borne on separate plants. The female flowers possess three sepals and three petals except in *Halophila* and *Thalassia* where there are three perianth segments. Many female flowers have staminodia. The ovary is inferior and consists of 3 to 20 carpels, with the number in each taxon being approximately constant. The carpels are free or fused with each other. Most authors have interpreted the gynoecium of the entire family as apocarpous. There are as many styles as there are carpels and these styles are often split into two long stigmatic arms. There are several to numerous anatropous or orthotropous ovules; both types are found in some flowers. The embryology is known for most genera.

The male flowers have one to many stamens, and the number is approximately constant in each genus. Some have staminodia; paired stamens and paired staminodia are frequent. Many have three perianth segments, a few have

four, and others have six. The male flower of *Maidenia* is reported to lack a perianth and the entire flower to be reduced to a single stamen (Rendle, 1916). In those species in which the male flower is very tiny the entire flower breaks loose from the submerged inflorescence and floats upon the surface. The very interesting pollination mechanisms of the various genera have been studied in some detail (Hartog, 1957).

The vegetative anatomy of the family has been studied in detail by Caspary (1858), Rohrbach (1871), Balfour (1879), Cunnington (1912), Solereder (1913), and others. The writer has not attempted to correlate the data obtained in these studies with anatomical characteristics of the flowers. The Hydrocharitaceae is one of the six monocotyledonous families reported by Cheadle (1953) to lack vessels.

Materials and Methods

Fourteen of the 15 genera of the Hydrocharitaceae have been studied. I collected *Ottelia alismoides* in India and the Philippines; *Enhalus acoroides, Halophila* spp. and *Thalassia hemprichii* in Singapore and the Philippines; and *Blyxa* spp. and *Hydrilla verticillata* in Singapore. I also collected *Hydrocharis morsus-ranae* and *Stratiotes aloides* in Germany; *Nechamandra alternifolia* in India; *Vallisneria* spp. in the Philippines, Minnesota, and Nebraska; and *Elodea canadensis* in Minnesota and Nebraska. These collections were made in 1961, 1962 and 1964. *Elodea densa* and *Limnobium spongia* were grown in the greenhouse from commercial stock. *Boottia cordata* was collected in Burma by A. L. Bogle and shipped to the author. *Lagarosiphon* has been studied from herbarium material. *Maidenia rubra*, a little-known monotype from Australia, has not been investigated here.

All specimens were preserved in formalin-acetic-alcohol. Clearings, microtome sections, and hand sections were employed. The materials cleared readily in weak sodium hydroxide solution at 60 C. When clear they were rinsed briefly in distilled water, placed in 85-90

per cent lactic acid and brought to 100C for about ten minutes. They were then ready for study without staining. Those specimens with considerable tannin were bleached quickly in boiling water to which a few drops of sodium hypochlorite were added. They were then transferred to lactic acid. No softening occurred with this method.

Flowers of all genera studied, except *Lagarosiphon* and *Stratiotes*, were embedded in paraffin and sectioned. Larger flowers were sectioned at 20, 30 and 50 microns and smaller flowers at 12 and 15 microns. The sections were stained with safranin and fast green; crystal violet and erythrosin were very unsatisfactory for staining the weakly differentiated tissues. Clarite was used for mounting.

Slightly oblique sections were more useful than perfectly transverse ones. For some genera complete developmental series were obtained. Because the ontogeny of the flowers is beyond the scope of the present paper, data are presented only from sections and cleared material of flowers at or near anthesis.

Observations

OTTELIA ALISMOIDES (L.) PERS.— In *O. alismoides* the sessile bisexual flowers are borne singly within the inflorescence. The three green sepals are alternate with the three large white petals. There are usually six stamens but nine are not uncommon. Other species regularly possess three and nine stamens (Dandy, 1934). All specimens from the Philippines examined by me had at least nine stamens and many had ten or eleven. In those with ten stamens an antisepalous stamen was replaced by two stamens fused by their filaments (Fig. 1). Each member of these pairs has an independent vascular supply. There is a prominent nectary opposite each petal. These structures are not mentioned by Ascherson & Gürke (1889), Hartog (1957) or Dandy (1934). Subramanyam (1962) mentioned rudimentary stamens and Richard (1811) illustrated fleshy tubercles opposite the petals. The antisepalous pairs of stamens arise first. When
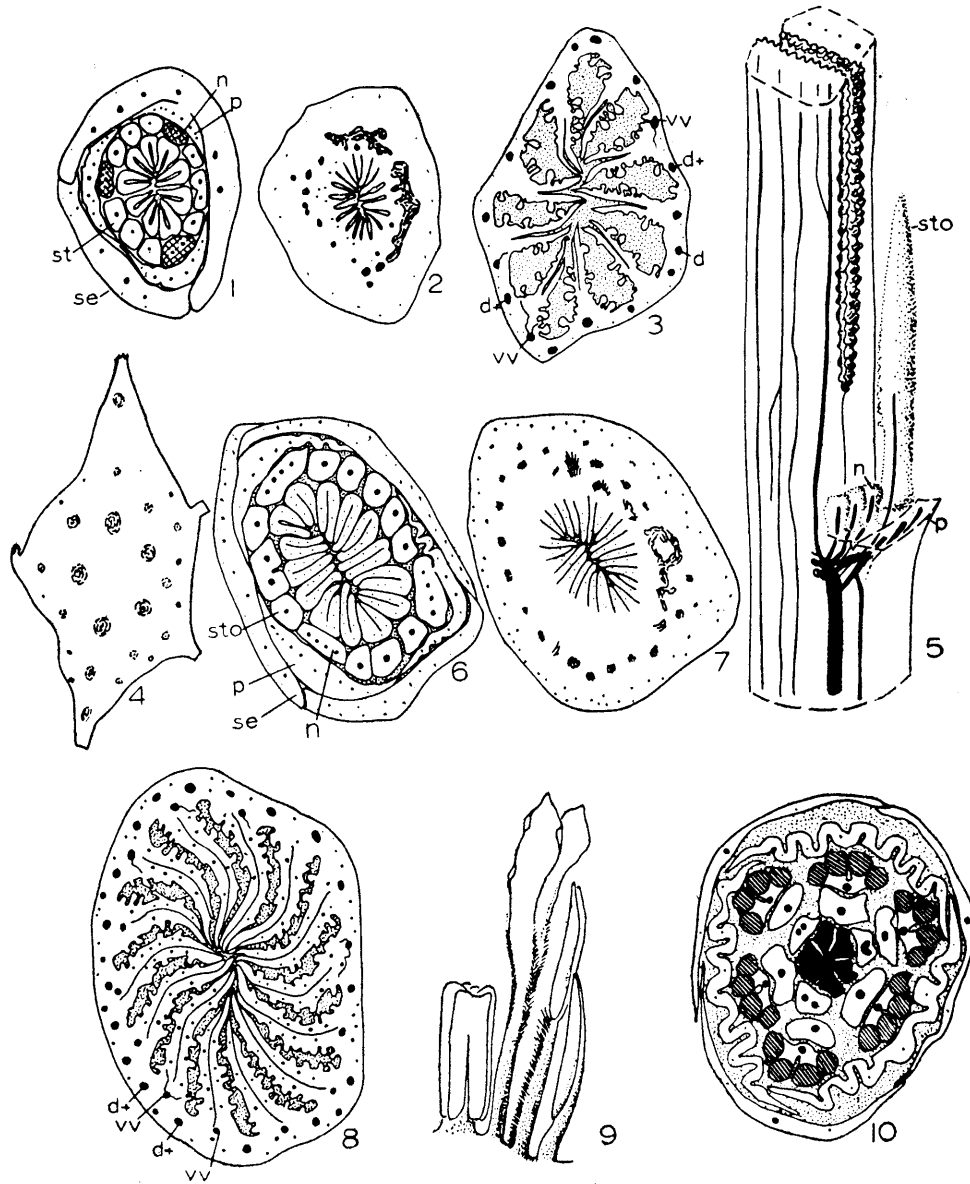
Figs. 1-10 —*Ottelia* and *Boottia* (*d +*, dorsal bundle which also serves perianth and androecium; *n*, nectary; *p*, petal; *se*, sepal; *st*, stamen; *sto*, staminodium; *vv*, ventral bundle serving adjacent carpels). **Figs. 1-4.** *Ottelia alismoides*, transverse sections of flower and peduncle. × 8. **Fig. 1.** Through styles and perianth. **Fig. 2.** Lower stylar region showing vascular plexus. **Fig. 3.** Ovary. **Fig. 4.** Peduncle of inflorescence. **Figs. 5-10.** *Boottia cordata*. **Fig. 5.** Portion of style of female flower with nectaries and staminodium. × 14. **Fig. 6.** Transverse section through perianth of female flower. × 20. **Fig. 7.** Stylar region with vascular plexus. × 10. **Fig. 8.** Ovary. × 10. **Fig. 9.** Portion of androecium of male flower with outer stamens fertile, penultimate expanded staminodium, and central fused staminodia. × 8. **Fig. 10.** Cross section of male flower, paired bundles shown in expanded staminodia, central staminodia black. × 15.

present, the single antisepalous stamens arise next; they are sometimes double. The antipetalous nectaries arise last.

Eichler (1875) and Ascherson & Gürke (1889) observed six carpels in *Ottelia* but Hartog (1957) listed six to nine carpels. The writer has not observed as few as six in Indian and Philippine specimens; most of those examined had ten or more carpels. The ventral margins are free from each other (Fig. 3) but adjacent carpels are partly fused by their abaxial walls.

In the center of the peduncle, below the attachment of the fused bracts, there are six collateral bundles arranged in a ring (Fig. 4). Outside of this ring there are several alternating rings of smaller bundles. At the level of attachment of the bracts the six inner bundles are successively fused, branched, and expanded. At the base of the gynoecium, just above the level of attachment of the bracts, approximately twice as many bundles as there are carpels depart from the vascular ring and pass up the ovary wall to the stylar plexus where their identities are lost (Fig. 2). Usually there is one bundle opposite the locule of each carpel, the dorsal bundle, and one bundle opposite the point of fusion of adjacent carpel walls. These latter bundles are sometimes displaced laterally. They are interpreted here as fused ventral bundles of adjacent carpels because they provide some of the placental bundles to both adjacent carpels (Fig. 3).

At the point of departure of the bundles of the ovary wall from the receptacular plexus a small meshwork of tiny bundles also departs from this plexus into each carpel wall. Many of these tiny bundles, which are the placental bundles, appear to arise directly from the receptacular vascular tissue. The placental bundles are connected at numerous points with both the dorsal and ventral bundles. A similar situation obtains in the female flower of *Boottia cordata* and the reader is referred to the illustration of that species in Fig. 31.

Above the level of the stylar plexus several bundles depart for the adaxial surface of each sepal. The abaxial surface of each sepal is served by numerous tiny bundles derived directly from the peripheral peduncle bundles. These peripheral bundles are not involved in the stylar plexus.

About five bundles from the stylar plexus serve each petal. Each stamen receives one bundle and each nectary two or three bundles from the stylar plexus. That the nectary is composed of reduced stamens is attested to by the fact that the vascular supply is like that to the stamens.

The placental bundles do not become involved in the stylar plexus but pass directly into the style and stigmatic branches where they end. A few bundles from the stylar plexus also enter each style and examination of younger material shows them to be derived from the dorsal bundle only. A similar situation is found in *Boottia* and the reader is referred to the illustrations of that plant in Figs. 5 and 28.

BOOTTIA CORDATA WALL.— The female flower of this species is similar to the flower of *Ottelia alismoides*. It is borne singly within the inflorescence. The androecium is represented by at least nine staminodia, and numbers up to 15 are common. There is a pair of staminodia opposite each sepal and often the

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Figs. 11-27 — *Enhalus, Limnobium* and *Thalassia* (d, dorsal bundle; p, petal median bundle; se, sepal bundle; st, stamen bundle; sto, staminodium bundle; v, ventral bundle). Figs. 11-15. *Enhalus acoroides*. Fig. 11. Section through stylar region. × 9. Fig. 12. Section through ovary. × 9. Fig. 13. Section through receptacle at level of departure of carpel bundles. × 9. Fig. 14. Male flower. × 11. Fig. 15. Female flower, ovary and styles invested with hairs. × 3. Figs. 16-21. *Limnobium spongia*. Fig. 16. Section across perianth. × 15. Fig. 17. Stylar region. × 15. Fig. 18. Ovary. × 15. Fig. 19. Receptacle. × 15. Fig. 20. Pedicel. × 15. Fig. 21. Male flower; each bundle serves a stamen; filaments monadelphous. × 15. Figs. 22-27. *Thalassia hemprichii*, female. × 12. Fig. 22. Section across perianth. Fig. 23. Stylar region. Fig. 24 Fertile portion of ovary. Fig. 25. Sterile portion of ovary. Fig. 26. Receptacle. Fig. 27. Pedicel.

single antisepalous staminodium is re-
presented by two incompletely fused
staminodia. Similar fused pairs may
be found in any position including that

of a member of the outer, antisepalous
pair. Further, apparently single stami-
nodia are found in any position and
contain two, three, four, or even five
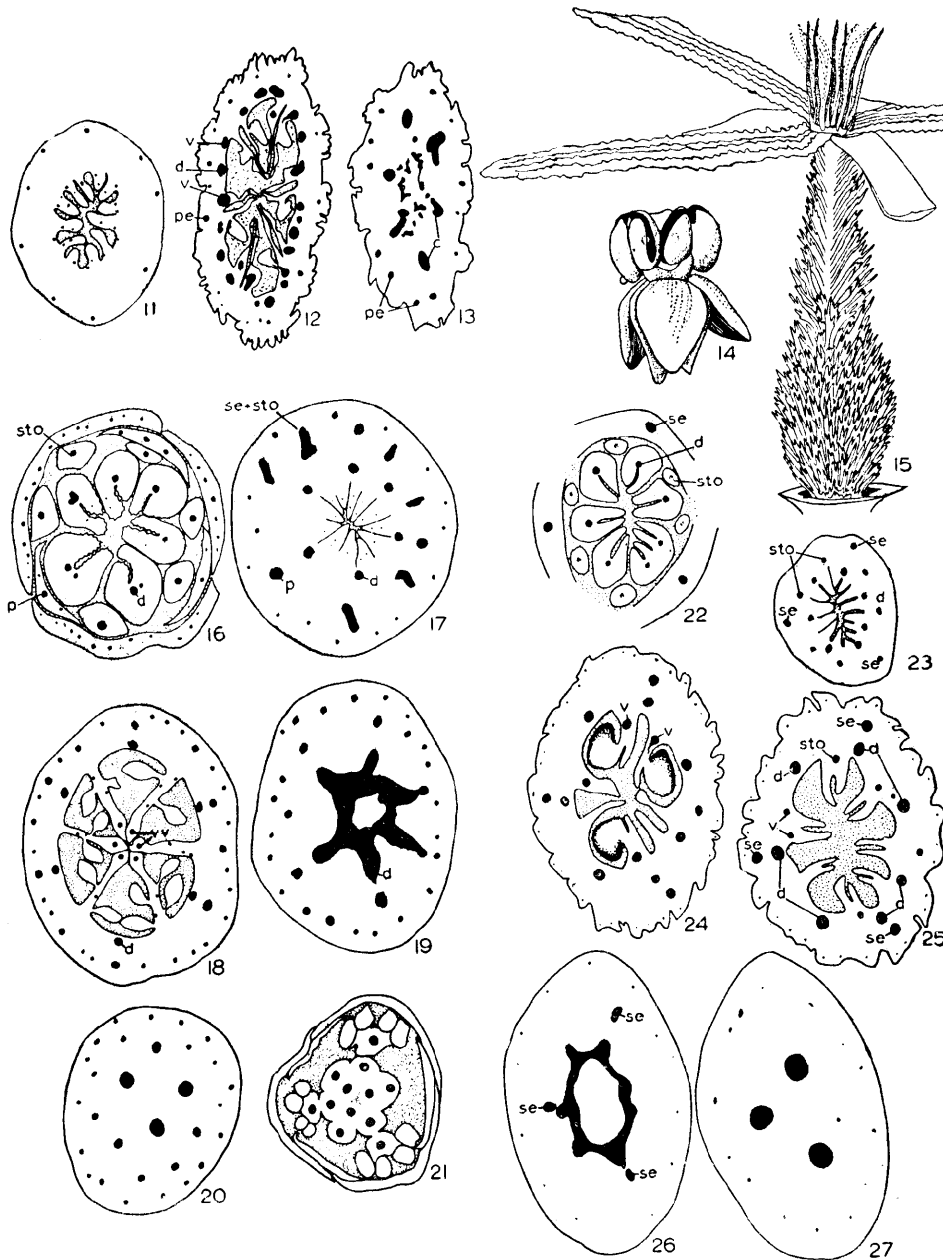
Figs. 11-27

independent bundles. There is a large nectary at the base of, but not fused with, each petal. The order of development of the staminodia and the nectaries is now being investigated.

The number of carpels ranges from 9 to 15. In all specimens examined by the writer there were as many styles as carpels. The ventral margins of the carpels are not fused nor are the projecting carpel walls (Fig. 8). The various interpretations of the gynoecium are considered in the ' Discussion '.

Nine to 12 large vascular bundles can be seen within the aerenchymatous peduncle of the female inflorescence. There is a larger number of smaller bundles toward the periphery. All of the larger bundles and some of the smaller ones make up a confused plexus at the level of attachment of the bracts. The other smaller ones proceed into the abaxial surfaces of the bracts and sepals.

Within the receptacle, slightly above the attachment of the bracts, approximately twice as many bundles as there are carpels depart from the plexus. One bundle is seen opposite the locule of each carpel (Fig. 8); this is the dorsal bundle. One bundle is found opposite the point of fusion of adjacent carpel walls; it represents the fused ventral bundles of adjacent carpels. Some placental bundles to both carpels are derived from it. There are numerous vascular connections between it and the dorsal bundle (Fig. 31). The dorsal and ventral bundles enter into a stylar plexus (Figs. 7, 28).

At the level of departure of the bundles of the ovary wall from the receptacular plexus a meshwork of tiny bundles departs directly from the plexus into the carpel walls. These are also placental bundles (Fig. 31).

From the stylar plexus several bundles pass to the adaxial surface of each sepal and several pass into each petal. The petal median bundle is united in the stylar plexus with a dorsal bundle and the petal lateral bundles are united with the fused ventral bundles. Each staminodium receives one bundle and each nectary receives three or four (Fig. 5). One bundle passes into the dorsal portion of each style and is possibly a continuation

Fig. 28 Boottia cordata. Drawing made from cleared specimens and serial sections of female flower. Dorsal, fused ventral, and placental bundles shown leaving the receptacular plexus. Supply to perianth, staminodia, and nectaries shown leaving stylar plexus. Peripheral bundles serving sepals not shown. Bracts removed and their vascular supply not shown. × 4.

of the dorsal bundle which has maintained its identity in the stylar plexus. The placental bundles are independent of the stylar plexus and pass directly into the ventral portions of the styles and of the stigmatic branches (Fig. 5).
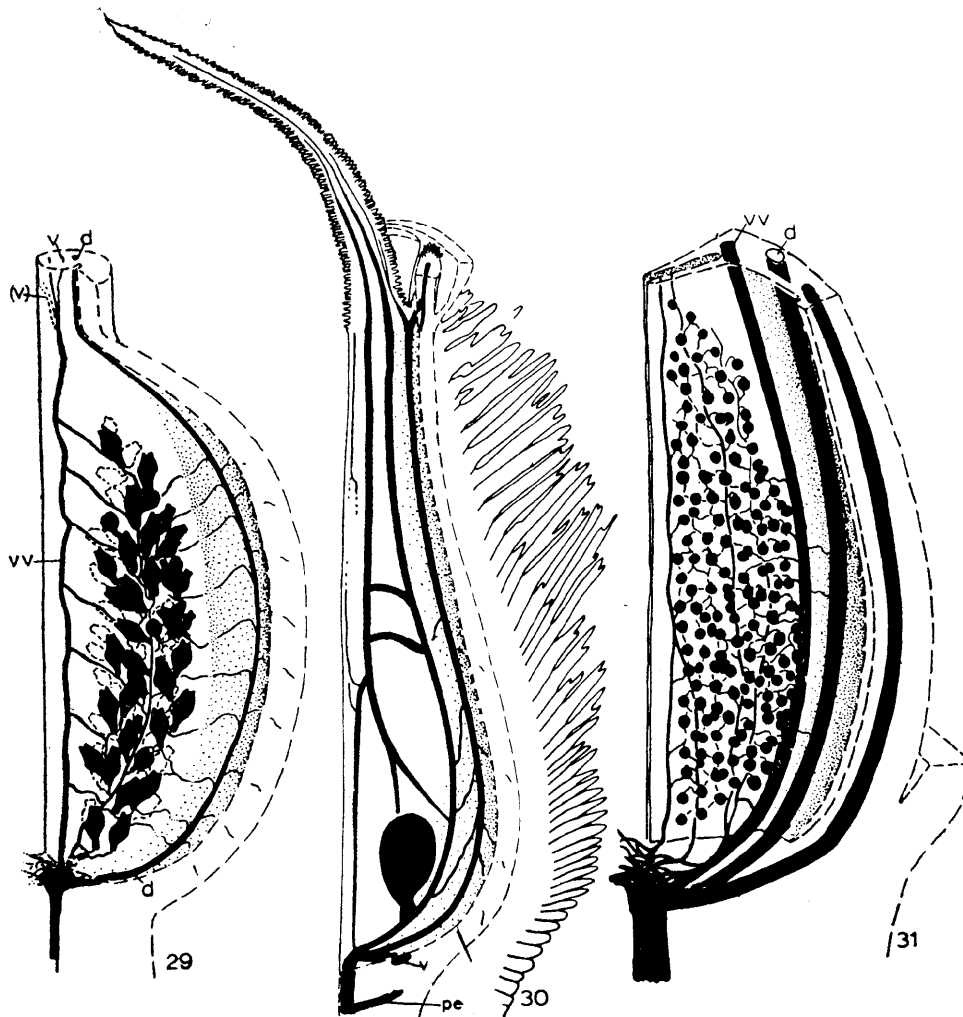
Figs. 29-31 — *Limnobium, Enhalus* and *Boottia*, single carpel wall; drawings made from cleared material. **Fig. 29.** *Limnobium spongia*, ovules and ventral bundle of adjacent carpel shown by dashed lines. × 11. **Fig. 30.** *Enhalus acoroides*, with one stigmatic arm shown. × 8. **Fig. 31.** *Boottia cordata*, bundles serving non-carpellary tissue not shown. × 7.

Nine to 15 male flowers are borne in the inflorescence of the male plant. The nature of the male inflorescence has not been reported in the literature. It appears to be a reduced cyme.

The writer observed 12 fertile stamens in each flower, whereas Ascherson & Gürke (1889) mentioned 6-12 stamens. The outer six stamens are about one-half as long as the inner six (Fig. 9). The

innermost androecial whorl is made up of three long and bifurcate staminodia; they are alternate with the innermost fertile whorl. The order of maturation is acropetal.

At the base of the receptacle of the male flower all the pedicellar bundles, except the peripheral ones, unite and form a ring of vascular tissue within which the identity of the bundles is lost.

From this confused plexus three bundles depart for each sepal and three for each petal. Each stamen receives one bundle and each staminodium receives a single bundle which branches into the arms (Fig. 10).

Above the departure of the bundle to each staminodium a single bundle enters the fleshy central body where it branches weakly and rapidly becomes diffuse. This central structure (Figs. 9, 10) is considered in the ' Discussion '.

LIMNOBIUM SPONGIA (BOSC) STEUD.— In this species the female flower is sessile within the inflorescence, which usually contains but one flower. Ascherson & Gürke (1889) reported only three staminodia, as did Richard (1811). Eichler (1875) reported three split antisepalous staminodia. Modern taxonomic manuals give the number as three to six. The writer has not observed fewer than six and he found 7 or 8 not uncommon. There is a pair of staminodia opposite each sepal and often one or two single antipetalous staminodia. No fusion was seen among the staminodia. The order of development is centripetal, with the paired members arising first.

The number of carpels varies from six to nine. The ventral margins are not fused although adjacent carpel walls are fused almost to their margins (Fig. 18). The ovules are borne on the projecting carpel walls but not toward the ventral margins. There are no ovules along the dorsal region.

Three large vascular bundles occupy the central portion of the pedicel of the female flower. Three smaller bundles are alternate with them and are slightly farther from the center. Toward the periphery there are numerous smaller bundles regularly disposed around the inner six. The outermost bundles are the smallest (Fig. 20). Within the receptacle the six inner bundles are expanded and form a ring of vascular tissue (Fig. 19). The first bundles to depart from this ring serve the staminodia and the perianth. Above the departure of those bundles the dorsal and ventral carpel bundles depart. At this level a few small bundles leave the receptacle for the carpel walls. These are the placental

bundles (Fig. 29). The reticulum of placental bundles is connected to both the ventral and the dorsal bundles.

The walls of adjacent carpels are completely fused except for the extreme ventral margins and the placental bundles of adjacent carpels are also fused. Therefore, the same reticulum supplies the ovules of adjacent walls of adjacent carpels (Fig. 29).

Each dorsal bundle continues through the style and into the stigmatic arms where it branches. The ventral bundle, which is a double bundle formed by the fusion of adjacent ventral bundles, also continues through the style and then branches into the walls of adjacent carpels which, from the level of the upper styles, are not fused (Fig. 29).

There is no plexus of vascular tissue formed in the stylar region. The bundles to the perianth, except for the abaxial sepal bundles and the staminodial bundles, are derived directly from the receptacular plexus. Bundles of staminodia and perianth segments which are opposite each other are often fused from the receptacular plexus to the upper portion of the style, where they separate (Fig. 17, se+sto). Each staminodium receives a single bundle which does not branch, and each petal receives three bundles.

Each male flower is simply constructed of 3 sepals, 3 petals, and 12 stamens in 4 alternating whorls of 3 members each. There is no evidence of paired stamens, or of staminodia, or of a rudimentary gynoecium. The stamens are monadelphous (Fig. 21). The order of maturation, and presumably of origin, is acropetal. Hartog (1957) reported six partly connate stamens in *L. stoloniferum*.

The three large bundles in the center of the pedicel of the male flower of *L. spongia* are surrounded by a ring of six smaller bundles, three of which are opposite, and three alternate, with them. These nine bundles form a receptacular plexus. The three large bundles become completely fused with the three smaller ones opposite them while the three small alternate bundles are only weakly united to the plexus. These latter supply the petals. All of the sepal bundles are derived from the plexus.

Each of the four whorls of stamens is supplied from successively higher levels of the plexus. Each stamen receives a single bundle which departs from the plexus individually; there is no fusion or branching of the stamen bundle. There is no vascular suggestion of a rudimentary gynoecium (Fig. 21).

HYDROCHARIS MORSUS-RANAE L. — The genus *Hydrocharis* is similar to *Limnobium*. There is a single female flower in each female inflorescence. There are six subulate, free staminodia arranged in antisepalous pairs, and there is a large bilobed nectary at the base of each petal. Six carpels are present. In all specimens examined by the writer adjacent carpel walls within the ovary were fused almost to their margins. This interpretation is contradictory to that of Ascherson & Gürke (1889) and others. Saunders (1929) and Eber (1934), however, saw such fusion.

According to Rohrbach (1871) the paired staminodia arise as a single primordium which soon bifurcates. The carpels arise in two whorls of three each, the outer whorl opposite the petals and the inner whorl opposite the sepals. After the appearance of the carpels a nectary arises between each petal and the carpel opposite it.

There is a system of small peripheral bundles in the pedicel of the female flower. These serve the abaxial surfaces of the sepals. Above the departure of the bundles to the bracts the confused receptacular plexus rapidly sorts itself out. About a dozen small bundles leave the plexus and proceed up the ovary wall. These branch variously and serve the sepals, staminodia, and nectaries directly. The dorsal, ventral, and placental bundles depart just above the departure of the perianth bundles. The single dorsal bundle of each carpel continues unbranched into the style where it branches and serves both stigmatic arms. The ventral bundle continues into the lower stylar region and then branches into the styles of two adjacent carpels. The placental bundles are attached to both the dorsal and the ventral bundles. Further, each reticulum of placental bundles, and each ventral bundle, provides the

vascular supply to the ovules in adjacent carpels. The ventral bundle is therefore interpreted here as representing the fused ventral bundles of adjacent walls of adjacent carpels.

The vascular anatomy of the female flower of *H. morsus-ranae* is well illustrated with transverse views by Saunders (1929). The reader is referred to the illustrations of *Limnobium spongia* (Figs. 16-20, 29) in which the vasculature is similar.

The interpretations of the androecium in the male flower of *H. morsus-ranae* are various. Rohrbach (1871) considered it to represent four centripetally arising whorls of three members each. Richard (1811) saw only six stamens, each split into two members on the same radius. He interpreted the outer stamen as bearing two anthers and the inner stamen as bearing a single anther on its outer branch; he interpreted the inner branch as an appendage. Rohrbach (1871), Eichler (1875) and Ascherson & Gürke (1889) called the sterile branches staminodia. Rohrbach (1871) presented convincing ontogenetic evidence that there is no branching of the stamens. He showed that each member of a so-called branched stamen arises independently and that ontogenetic fusion of members on the same radius produced the apparently forked stamens. He demonstrated that the androecium arises in four alternating whorls of three members each, with the inner whorl being staminodial. Daumann (1931a) believed the fleshy central body of the male flower to represent the innermost androecial whorl fused with three antipetalous rudimentary carpels. He observed some specimens in which stigmatic branches could be seen in the middle of the male flower. These branches were surrounded by fused staminodia.

STRATIOTES ALOIDES L.— The six carpels of the female flower have been shown to arise in two whorls of three each, the lower whorl being antisepalous (Rohrbach, 1871). The projecting walls of adjacent carpels are not fused, and the ovules are borne on the projecting walls except at the margins. There are no ovules along or near the dorsal bundle. About 15 to 30 staminodia occur between the perianth

and the carpels. They are united laterally into groups of three or more. According to Rohrbach (1871) they arise in two whorls, the upper whorl antisepalous and the lower antipetalous, with the lower arising first. Salisbury (1926) concluded, after examining transverse sections, that it is the upper whorl that is antipetalous.

Each carpel has a single dorsal bundle. The ventral bundles are on the same circumference as the dorsal bundle and they are not fused with those of adjacent carpels. A diagrammatic illustration of the gynoecium is given in Fig. 70. The numerous placental bundles form a complex network attached to both the dorsal and the ventral bundles in numerous places. The placental bundles of adjacent carpels are not at all fused. The ventral bundles and some of the placental bundles pass directly through the style and serve the stigmatic arms with numerous bundles. The supply to the perianth and the staminodia is derived from the bundles located in the outer portion of the ovary wall. These bundles depart independently of the dorsals and ventrals from the receptacular plexus. Each of the staminodia receives two or three tiny bundles from the single trunk bundle which supplies a group of three or more of them.

The male flower of *Stratiotes* possesses 12 stamens and about 24 nectary-staminodia. Rohrbach (1871) studied the ontogeny of the male flower and found that, after the initiation of the petal primordia, the paired antisepalous stamens arise as a single primordium. A single antipetalous stamen arises later and above the paired stamens, and finally a single antisepalous stamen arises above each antipetalous stamen. Thus, there is a regular centripetal development of alternating whorls of fertile stamens, the outer one of which consists of six paired stamens. After the last whorl of stamen primordia has arisen, about 24 primordia form between the perianth and the outer whorl of stamens. They arise in two whorls, just as in the female flower (Rohrbach, 1871).

Each stamen receives a single bundle and each nectary-staminodium receives

three bundles, the central one of which passes almost to the tip of the structure. The author has been unable to positively identify trunk bundles serving groups of stamens or nectary-staminodia.

THALASSIA HEMPRICHII (EHRENB.) ASCHERSON — The female flower of this marine plant possesses three perianth segments. The position of each opposite a pair of staminodia suggests that they are sepals. There are six small subulate staminodia in the female flower. Staminodia appear not to have been recorded previously in this genus. The flower has six carpels and six styles, each of which branches into two very long stigmatic arms. Adjacent walls of adjacent carpels are not fused within the ovary (Fig. 25).

Thalassia testudinum is the only other species in the genus. It is reported by Hartog (1957) to have 9 to 12 undivided styles. The author has not seen specimens of this plant.

The three large bundles of the pedicel of the female flower of *T. hemprichii* are expanded into a continuous ring of vascular tissue within the receptacle (Figs. 26, 27). Three bundles depart at the same level from the lower part of this ring. Each of these bundles continues unbranched through the ovary wall and enters a sepal (Figs. 22-25). Above the departure of the sepal bundles the bundles serving the carpels and the staminodia leave the receptacle. Some of these bundles serve both as carpel dorsal bundles and as staminodium supplies but others serve a staminodium directly (Figs. 22-24, *sto*). A weakly developed system of ventral and placental bundles is derived from the receptacle (Fig. 24). Some of the ovules are also supplied by tiny branches from the ventral bundles. In the five specimens studied by the writer no two adjacent carpels bore ovules. The stylar region is served not only by the dorsal bundles and the perianth-staminodia supplies, but also by the weak ventral bundles. There is no stylar plexus.

ENHALUS ACOROIDES (L.) RICH. EX. STEUD — Each female flower of this marine plant has three green sepals and three very long and crinkled white

petals (Fig. 15). There are six carpels and six styles which bear two long stigmatic branches. Toward the base of the ovary adjacent carpel walls are fused by their abaxial surfaces and their ventral margins are united at the center of the ovary. A 6-chambered ovary is thus produced at this level by these fusions. A similar condition was seen in *Limnobium spongia*. Cunnington (1912) reported a small vascular column in the center of the base of the ovary. The writer has been unable to discover such a column in any of his material from Singapore.

Two large bundles occupy the center of the aerenchymatous peduncle of the female inflorescence, which possesses but one flower. Around these two bundles there are numerous smaller peripheral bundles which serve the abaxial surfaces of the bracts. Each of the two large bundles of the peduncle provides each bract with three main bundles. Above the departure of the main bract bundles the two large peduncular bundles form a weakly developed receptacular plexus (Fig. 13). From this plexus about 12 bundles run almost horizontally to the periphery of the receptacle where they turn upward and, passing unbranched along the ovary wall, serve the perianth. There are no staminodia.

Immediately above the departure of the perianth bundles the six carpellary bundles leave the plexus. At the base of each carpel each bundle divides into one dorsal and two ventral bundles (Fig. 30). The ventral bundles continue into the stigmatic arms but the dorsal bundle branches and becomes diffuse in the style (Figs. 11, 13). The dorsal and ventral bundles are connected by several small but well-defined bundles (Fig. 30). The placental bundles are connected at several places with the ventral bundles and some of them originate below the point of divergence of the dorsal and ventral bundles. Ordinarily only two ovules are formed in each carpel. Each is attached on or near a ventral bundle and at a different level from that of the other ovule. The ventral bundles of adjacent carpels are not fused with each other (Fig. 12). These bundles were termed " marginal bundles " by Cunnington (1912).

Hundreds of tiny male flowers are borne in each submerged male inflorescence. Each is simply constructed of three sepals, three petals, and three stamens (Fig. 14). There are no staminodia or rudimentary carpels.

The vasculature of the male flower is equally simple. A single pedicellar bundle branches in the receptacle and provides each stamen with a single bundle. There is no vascular tissue in the perianth.

VALLISNERIA AMERICANA MICHX.— The genus *Vallisneria* is variously interpreted as including 6 to 10 species. A single sessile female flower is borne in the inflorescence of the female plant. The flower has three tiny scarious petals alternate with the larger sepals. Three tiny staminodia are alternate with the petals (Fig. 32). The writer has observed occasional antisepalous pairs of staminodia (Fig. 34). Subramanyam (1962) reported bifid staminodia in *V. spiralis*.

The ovary of *V. americana* consists of three carpels whose margins project a short way into the locule (Fig. 36). These margins are rapidly crushed and obscured by the developing ovules. The numerous ovules are borne in the area of bending of the carpel walls (Figs. 33, 36). The identity of the carpel is maintained in the style. The stigmatic arms are short and blunt; at anthesis they are greatly reflexed.

A single bundle occupies the center of the peduncle of the female inflorescence. A single large bundle is at the periphery and two smaller bundles are also at the periphery alternate with the central and the larger peripheral bundles (Fig. 39). At the level of attachment of the bracts these four bundles form a plexus in which their identities are lost (Fig. 38). From this plexus four large bundles serve the bracts. Above the departure of the bract bundles the plexus becomes organized into three large bundles of similar size. These three bundles occupy the same radii as the sepal median bundles (Figs. 34-37) and they are located at the point of fusion of adjacent carpels. One or all of these bundles may be inverted. From each of these bundles a branch departs and fuses with a similar branch of an adjacent bundle (Fig. 37,d). The product

of this union occupies a median position in the carpel wall and is, therefore, the dorsal bundle. The dorsal bundle forks again towards the upper part of the ovary and each branch then reunites with its parent bundle in the stylar region (Fig. 32). The vascular supply to the ovules is derived mainly from the three large bundles opposite the point of fusion of adjacent carpels (Fig. 33). These bundles are the fused ventral bundles of adjacent carpels. Each of these bundles supplies
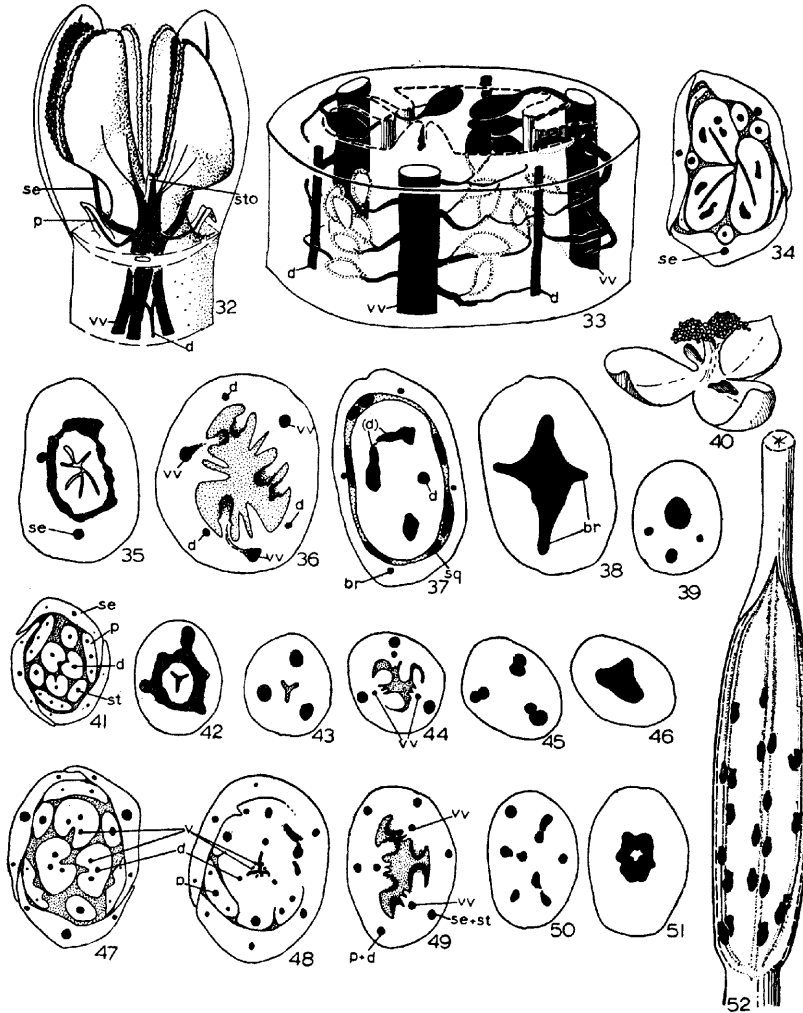
Figs. 32-52

the ovules of adjacent walls of adjacent carpels. There are occasional vascular connections between the ovules and the dorsal bundle (Fig. 33). At the upper part of the ovary the bundles of the ovary wall are approximate. The sepal bundles, one to each sepal, depart quickly from the converged bundles (Fig. 32). The identities of the bundles serving the petals, staminodia, and styles are obscured briefly in the congress of bundles but they depart quickly (Fig. 32). There is no dorsal bundle in the upper portion of the style.

Numerous tiny male flowers are produced in the submerged inflorescence. In *V. americana* the male flowers have three sepals, a single petal, two stamens, and one staminodium (Fig. 40). Hartog (1957) reported three petals in the male flower of *V. gigantea.* Richard (1811) illustrated a single organ alternate with the petals in *V. spiralis*; presumably it is a petal. He also showed three organs opposite the sepals; their nature is unknown to the writer. Subramanyam (1962) observed that the structure of the male flower of *V. spiralis* is the same as that of *V. americana.*

The writer was unable to discover any vascular tissue in the male flowers of *V. americana.*

BLYXA THOUARS — The genus *Blyxa* comprises about ten species. Ascherson & Gürke (1889) divided the genus into two sub-genera: *Saivala* (dioecious, 6-9 stamens), and *Diplosiphon* (monoecious, 3 stamens). Hartog (1957) pointed out

that this is an artificial division because the male flower of dioecious species possesses three stylodia and the female flower sometimes possesses one or more stamens.

The writer has examined only monoecious species which show a single flower in the inflorescence. Each flower possesses three sepals, three petals, and three, six, or nine stamens (Figs. 41, 47). In the species examined here, *B. auberti* Rich. and *B. alternifolia* (Miq.) Hartog, there are three stamens.

The ovary consists of three carpels whose walls project a short distance into the locule (Figs. 44, 49, 52). The ovules are borne in the region of bending of the carpel walls. There are three styles which do not branch but bear filiform stigmas.

B. ALTERNIFOLIA (Miq.) HARTOG — There are two large bundles in the peduncle of *B. alternifolia.* Each of these supplies a bract with one bundle. Above the departure of the bract bundles the two peduncular bundles become expanded and lose their identities (Fig. 46). From the plexus formed by them three bundles depart on the sepal radii (Fig. 44). Each of these bundles soon branches to form two bundles of unequal size located on the same radius (Figs. 44, 45). The outer and larger of these courses up through the ovary wall without branching until it disappears in the stylar plexus. The inner, smaller bundle runs parallel with the outer bundle and is the source of the vascular supply to the ovules (Figs. 44, 53). This bundle is located opposite

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←——

Figs. 32-52 — *Vallisneria* and *Blyxa* (*d*, dorsal bundle; *p*, petal bundle; *se*, sepal bundle; *st*, stamen bundle; *sto*, staminodium; *vv*, fused ventral bundles of adjacent carpels). **Figs. 32-40.** *Vallisneria americana.* **Fig. 32.** Drawing from cleared specimen and serial sections of upper portion of female flower; stigmatic branches still appressed before anthesis. × 50. **Fig. 33.** Mid-portion of ovary at anthesis showing dorsal and fused ventral bundles (slightly exaggerated for emphasis) and slightly projecting carpel walls. × 75. **Figs. 34-39.** Serial sections through female inflorescence. × 20. **Fig. 34.** Perianth. **Fig. 35.** Stylar region showing vascular plexus. **Fig. 36.** Ovary. **Fig. 37.** Receptacle, fused bracts shown. **Fig. 38.** Upper peduncle. **Fig. 39.** Peduncle. **Fig. 40.** Male flower. × 20. **Figs. 41-46.** *Blyxa alternifolia,* serial sections through flower. × 35. **Fig. 41.** Perianth. **Fig. 42.** Stylar region with vascular plexus. **Fig. 43.** Stylar region below plexus. **Fig. 44.** Ovary. **Fig. 45.** Base of ovary at level of separation of ventral bundles from bundles to perianth and androecium. **Fig. 46.** Pedicel. **Figs. 47-51.** *Blyxa auberti,* serial sections of flower. × 50. **Fig. 47.** Perianth. **Fig. 48.** Upper stylar region. **Fig. 49.** Ovary. **Fig. 50.** Base of ovary at level of separation of ventral bundles and supply to sepals and androecium; petal and dorsal bundles have already departed. **Fig. 51.** Pedicel. **Fig. 52.** *Blyxa* sp., ovary slit open to show arrangement of ovules along the slightly projecting carpel walls. × 2.5.

the point of fusion of adjacent carpels and, because it supplies the ovules of both adjacent carpels, represents the fused ventral bundles of those adjacent carpels. There is no dorsal bundle in the ovary.

The three double ventral bundles and the three larger outer bundles unite in a weak plexus at the top of the ovary (Figs. 42, 43). The bundles do not completely lose their identities. From this plexus three bundles proceed to each sepal and three bundles enter each petal. One bundle enters each stamen and each style, where it occupies the median position (Fig. 53). It is likely that this median stigmatic bundle represents the carpel dorsal bundle even though there is no dorsal bundle in the ovary.

B. AUBERTI RICH. – Two large bundles occupy the center of the peduncle of *B. auberti*. Each of these bundles sends one branch into one of the bracts. Above the departure of the bract bundles the peduncular bundles form a receptacular plexus of vascular tissue (Fig. 51). The plexus immediately gives rise to six bundles which run up the ovary wall. Just above the departure of these six bundles three more bundles depart opposite three of the lower bundles (Fig. 50). Thus, there are nine bundles in the ovary wall, six of them in pairs on the same radius. The inner bundle of each pair provides the vascular supply to the ovules of adjacent carpels and represents the fusion of ventral bundles of adjacent walls of neighbouring carpels (Fig. 49, *vv*). When these fused ventral bundles reach the level of separation of styles they separate and each branch proceeds into the style of one carpel. The outer bundle of each pair, as seen in the ovary branches in the stylar region and sends three bundles to a sepal and one bundle to a stamen (Figs. 47-49, 53, *se+st*). Each of the single bundles in the ovary wall, upon reaching the upper stylar region, branches and provides a petal with a single bundle and also provides the style with a dorsal bundle (Fig. 53). Therefore, the single bundle, as seen in the ovary, represents the fusion of the carpel dorsal bundle and the petal bundle. There is no stylar plexus.

HALOPHILA OVALIS (R. BR.) HOOK. F.— *Halophila* is a marine genus of nine species, according to the most recent study (Hartog, 1959). Vegetative differences among the species are pronounced but, as far as is known, the floral morphologies are quite similar. I examined only *H. ovalis* in detail.

The female flower of *H. ovalis* is sessile and has a perianth of three segments. The ovary consists of three carpels whose fused adjacent walls project very slightly into the ovarian cavity (Fig. 58). Balfour (1879) correctly interpreted the structure of the ovary although he considered the plant to belong to the Naiadaceae. He described three parietal placentae, each bearing two rows of ovules. These placentae are easily detected in young specimens (Fig. 58) but they are quickly distorted by the growth of the ovules (Fig. 55). There is a very long stylar region composed of the fused styles of the three carpels. The styles separate at the level of the perianth and each bears a long filiform stigma (Fig. 56). The stigmas are receptive on their inner grooved surfaces for their entire lengths.

Above the departure of the bundles to the bracts the peduncle of *H. ovalis* contains a single large central bundle. Within the receptacle this bundle produces six branches. Each of the three lower branches, which depart at the same level, provides the vascular supply to one of the three perianth segments and to the dorsal region of the style (Fig. 57, *pe+d*). The three upper branches of the peduncular bundle provide the vascular supply to the ovules. Each of these branches serves ovules in adjacent carpels and represents the fusion of ventral bundles of adjacent walls of adjacent carpels (Fig. 58, *vv*). The ventral bundles end in the stylar region.

The male flowers of *H. ovalis* are pedicelled and consist simply of three perianth segments and three stamens alternate with them (Fig. 54). The single pedicellar bundle sends one bundle to each of the three perianth parts. Above the departure of the perianth bundles a single bundle passes into each of the three stamens. There are no bundles which might suggest a vestigial gynoecium.
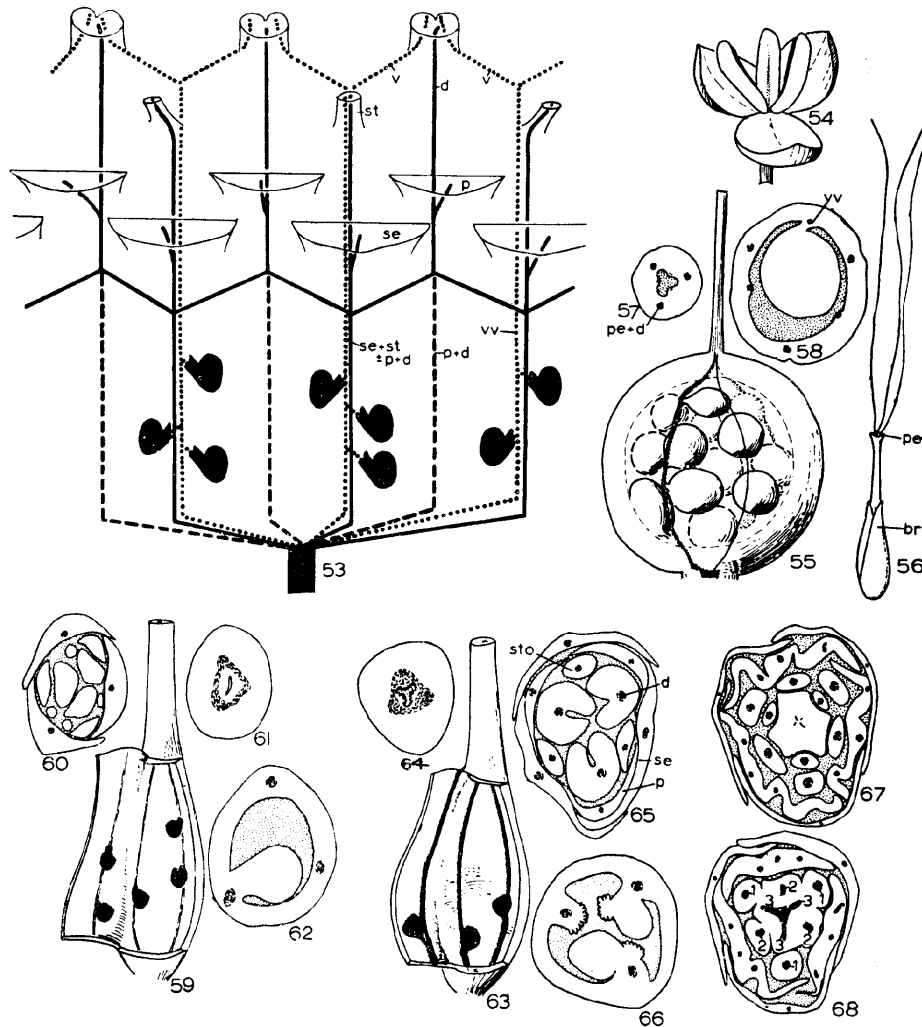
Figs. 53-68 — *Blyxa, Hydrilla, Elodea* and *Halophila* (*d*, dorsal bundle; *p*, petal bundle; *pe*, perianth bundle; *se*, sepal bundle; *st*, stamen bundle; *sto*, staminodium; *vv*, fused ventral bundles). **Fig. 53.** Diagrammatic representation of vascular supply in the flowers of *Blyxa auberti* and *B. alternifolia*; drawn as if the flowers were split open and flattened above the receptacle. In *B. auberti* the dotted line represents *se + st* only; in *B. alternifolia* it represents *se + st + p + d*, and there is no *p + d*; not drawn to scale. **Figs. 54-58.** *Halophila ovalis.* **Fig. 54.** Male flower. × 6. **Fig. 55.** Large mature fruit showing attachment of seeds (stippled line) and bundle serving dorsal portion of carpel and perianth. × 10. **Fig. 56.** View of female flower at anthesis. × 4. **Fig. 57.** Stylar region showing tricarpellate nature of gynoecium. × 14. **Fig. 58.** Fertile region of ovary. × 14. **Figs. 59-62.** *Hydrilla verticillata.* **Fig. 59.** Ovary opened showing attachment of ovules along fused ventral bundles. × 20. **Fig. 60.** Section through perianth; a pair of staminodia is seen in one position. × 20. **Fig. 61.** Stylar region with vascular plexus. × 20. **Fig. 62.** Section across fertile region of ovary. × 20. **Figs. 63-68.** *Elodea.* **Fig. 63.** *E. canadensis*, ovary opened to show attachment of ovules along ridges formed by fusion of adjacent carpel walls. × 20. **Fig. 64.** Section across stylar neck region showing slight fusion of bundles. × 65. **Fig. 65.** Section across perianth region showing staminodia. × 65. **Fig. 66.** Section through ovary showing attachment of ovules at sides of ridges; note the slime gland cells on ridges. × 65. **Fig. 67.** *E. densa*, male, showing disposition of stamens. × 15. **Fig. 68.** Section slightly lower than Fig. 67 showing slight monadelphy. × 15.

ELODEA MICHX.—*Elodea* is a New World genus variously interpreted as containing 5 to 10 species. The female flowers possess three sepals and three petals and often three, and sometimes six, staminodia (Fig. 65). These staminodia are occasionally fertile (Wylie, 1904). The ovary is composed of three carpels, a feature correctly recognized by Van Tieghem (1891) but generally overlooked before and since. The lateral portions of each carpel are fused with adjacent lateral portions of adjacent carpels and the products of these fusions are three slight ridges on the inner surface of the ovary (Figs. 63, 66). The ovules arise at the sides of these ridges and as they grow they assume a pseudo-terminal position on them. The terminal portion of each ridge is occupied by mucilage cells (Fig. 66).

Above the level at which the single central peduncular bundle of *E. canadensis* provides each of the two fused bracts with a single bundle, three bundles pass into the ovary wall. Each of these three bundles is located within the ridge formed by the fusion of carpel walls, and each is the source of the vascular supply to the ovules on adjacent walls of neighbouring carpels (Fig. 66). There are no dorsal bundles. In the stylar region these three bundles form a ring of vascular tissue (Fig. 64). From this ring one bundle passes into each of the three sepals and, just above, into each of the three petals. Then a single bundle passes into each staminodium and a single bundle into the dorsal position of each style. The stylar bundle then forks and a branch proceeds to each stigmatic arm.

The male flowers of *Elodea* possess three sepals, usually three petals, and three or nine stamens. In *E. canadensis* the nine stamens are slightly monadelphous (Fig. 68), but in *E. densa* they are free. In some species, e.g. *E. canadensis*, the male flower is tiny and breaks from the inflorescence before anthesis. Wylie (1904) reported well-developed stigmas in some staminate flowers of *E. canadensis*; Eichler (1875) called them staminodia. The large fleshy structure at the center of the male flower of *E. densa* (Fig. 67) was interpreted by Caspary (1858) as a rudimentary gynoecium.

The vascular anatomy of the male flower of *E. densa* is as simple as its gross morphology. A single bundle passes from each of the three pedicellar bundles into a sepal. Above the sepal bundles, and alternate with them, a single bundle passes into each petal where it branches into three. At successively higher levels within the receptacle the three whorls of these stamens each is provided with bundles. Tiny bundles pass into each lobe of the central body; each of these bundles is opposite a petal. The extremely reduced nature of the central body obscures its true character. However, I interpreted similar but more fully developed structures in *Boottia* as fused staminodia.

HYDRILLA VERTICILLATA (L.) ROYLE — *Hydrilla* is a monotypic monoecious or dioecious genus with unisexual flowers. The female flower is borne singly within the inflorescence and possesses three sepals, three petals, and three slightly bifid styles. Neither Caspary (1858), Hartog (1957), nor Subramanyam (1962) mentioned the presence of staminodia but Ascherson & Gürke (1889) said there are sometimes three but more often none. All specimens examined by me had at least three staminodia, and often one of these was replaced by a pair (Fig. 60). The ovary consists of three carpels whose margins are not at all protruded into the locule (Figs. 59, 62). The ovules are borne at the point of fusion of adjacent carpels.

The single central pedicellar bundle produces the three bundles seen in the ovary wall in Fig. 62. Tiny branch bundles serve the ovules from these large bundles. The three bundles form a ring of vascular tissue in the stylar region (Fig. 61) and six bundles pass upward from this ring. Three of these six serve the sepals. Each of the other three, alternate with the sepal bundles, provides a petal with a single bundle and provides the style opposite that petal with a tiny dorsal bundle. The three bundles seen in the ovary represent the fused adjacent ventral bundles as well as the entire supply to the perianth. The dorsal bundle is reconstituted above the stylar plexus. The staminodia lack vascular tissue.

The tiny male flower is also borne singly in each inflorescence. It is simply constructed of three sepals, three petals, and three stamens, all in alternating whorls. The vasculature of the male flower is extremely simple. From a single pedicellar bundle single bundles pass, in alternating whorls of three and at successively higher levels, to the sepals, petals, and stamens respectively.

NECHAMANDRA ALTERNIFOLIA (ROXB.) THW.— The female flower of *Nechamandra* possesses three perianth parts and three bilobed stigmas. The ovary consists of three carpels whose fused walls project a slight distance into the locule. The ovules are borne at the region of turning of the carpel margins. A single bundle passes through the small ridge formed by fusion of adjacent carpel walls. The ovules are borne directly on these bundles, which represent the fused ventral bundles of adjacent carpels. There is no dorsal bundle within the ovary.

The author has not seen male flowers of *Nechamandra*. According to Subramanyam (1962) they are very similar to the male flowers of *Vallisneria*.

LAGAROSIPHON HARVEY — I did not study the vasculature of the flowers of *Lagarosiphon* but the illustrations provided by Harvey (1842) in his original description of the genus suggest that the basic pattern is the same as that of *Nechamandra*, at least as far as the female flower is concerned. According to his illustrations, the ovary is interpreted here as composed of three carpels whose fused adjacent walls project very slightly into the locule. Wager (1928) studied the morphology and anatomy of the genus and his illustrations of the female flower agree with those of Harvey.

The male flowers also possess three sepals and three petals. There are three fertile stamens and three filiform staminodia (Harvey, 1842). Structures similar to these staminodia are seen in the male flowers of dioecious species of *Blyxa*; Hartog (1957) called them stylodia.

MAIDENIA RUBRA RENDLE — This is a little-known monotype from north-western Australia. Rendle's illustration of a cross-section of the ovary shows that no trace remains of the projecting carpel walls. He showed the ovules arising all over the inner surface of the ovary.

According to Rendle (1916) the male flowers are each reduced to a single stamen, with no trace of a perianth. If the male flowers are truly as he depicted them, they then represent the most reduced flower in the entire family. Rendle, however, examined only dried material and my experience with dried material of tiny male flowers of other genera shows that the perianth readily falls away.

Rendle believed the genus to show great affinity with *Vallisneria*, and Dandy (1959) placed it in that genus.

Discussion

The perianth of the Hydrocharitaceae shows several specializations. The most conspicuous of these is a tendency toward reduction in size and number of segments. The basic pattern in the family is the possession of three sepals and three petals but this is sometimes reduced by loss of entire whorls, as in *Halophila ovalis* and *Thalassia hemprichii*, or parts of whorls, as in the male flowers of *Nechamandra* and *Vallisneria*. At least five, and often more, bundles serve the sepals of *Ottelia alismoides*, female *Boottia cordata*, *Enhalus* and *Limnobium spongia*, but in the tricarpellate genera, except for *Blyxa*, the sepals receive but one bundle. The perianth of *Halophila ovalis* lacks vascular tissue altogether. A similar variability is found in the petals where one, three, five, or no bundles can be found. A single bundle serving each petal can be seen in female *Limnobium spongia*. This bundle passes independently from the receptacular plexus through the ovary wall and into the petal. It is likely that all the genera have similar single-trace petals but in most of them this trace has become obscured by fusion or by branching within a stylar plexus, or has been lost altogether. The loss of the corolla of *Thalassia* and *Halophila* is probably correlated with underwater pollination and not with the marine habitat. *Enhalus*, the third marine genus, is pollinated at the surface and has one of the showiest corollas in the family.

No evidence of more than one bundle in a stamen is seen in the fertile stamens but there are three bundles in the staminodia of *Hydrocharis morsus-ranae* and *Stratiotes*. In male *Hydrocharis* flowers some of the stamens, particularly those of the penultimate whorl, are bisporangiate. That this bisporangiate condition is not the primitive condition but is brought about by the failure of two sporangia to develop, rather than by an ontogenetic or phylogenetic splitting of a stamen, is suggested by the frequent development of partially or completely developed third and fourth sporangia in stamens in which but two would be expected.

The reduction of the androecium in both male and female flowers is roughly correlated with an increase in specialization of pollination mechanisms and with a decrease in size of flower. The entomophilous genera generally have more and larger stamens and staminodia, and well-developed perianth, while the hydrophilous members have fewer stamens and rather inconspicuous perianths.

The androecium of the tricarpellate genera comprises fewer members, generally, and the ultimate in reduction is reported in male *Maidenia* in which the flower consists solely of a single stamen. In most of the tricarpellate genera the male flowers contain three functional stamens and some have what appear to be staminodia. In *Nechmandra* and *Vallisneria* the single remaining whorl of stamens is partly sterile.

The tendency toward sterilization of stamens is pronounced in the Hydrocharitaceae. The bisporangiate condition of the male *Hydrocharis morsus-ranae* flower, and the complete lack of sporangia on the innermost stamens of the same flower, suggests that it is the innermost stamens which are sterilized first. Further evidence of this is seen in male *Boottia cordata* where the innermost whorl of definable androecial structures is represented by large and forked staminodia, and in male *Stratiotes* where the innermost whorl is sometimes represented by rudimentary stamens.

Daumann's (1931a, b) study of *Hydrocharis morsus-ranae* and *Stratiotes*, however, suggests that the outer whorls of stamens are also sterilized in some cases. His study of numerous flowers led him to conclude that there are three general types of staminodia and that some of them are outside the fertile stamens, with numerous transitional forms existing among the types and between the staminodia and fertile stamens and nectaries. He concluded that these structures could not be interpreted as anything but androecial in nature. Rohrbach (1871) interpreted them as axial structures not related to the androecium. My observations on the vascularization of these structures in *Stratiotes* add further credence to Daumann's interpretation of them as staminodia. It must be emphasized that the features attendant upon the inferior ovary have somewhat obscured the pattern of vascularization to the perianth and androecium in the female flower.

Other transformations of stamens into nectariferous staminodia can be seen in female *Boottia cordata* and *Ottelia alismoides*. In these the nectaries occur in groups but each nectary has an independent vascular supply from the stylar plexus (Fig. 5). These structures arise below and after the stamens (*Ottelia*) or staminodia (*Boottia*). A tendency toward fasciation can occasionally be seen in the fertile stamens or non-nectariferous staminodia of these genera (Figs. 1, 6).

The morphological nature of the 6-armed fleshy structure at the center of the male flowers of *Boottia cordata* and *Hydrocharis morsus-ranae* is obscure. Rohrbach (1871) thought it represents, in *Hydrocharis*, two or three undeveloped staminodia. He based his conclusion on its origin below the floral apex but above the last-formed whorl of well defined staminodia. Daumann (1931a) found several specimens in which this central body appeared to envelop a rudimentary gynoecium. He concluded that it represents the fused members of the inner androecial whorl and sometimes also a rudimentary gynoecium. These interpretations suggest that, with the development of unisexuality, the nectaries of the incipient male flowers retained, or possibly assumed, an uppermost position within the androecium but that in the

female flower they remained crowded toward the outside. Further evidence in support of this interpretation is the fact that these structures, regardless of their position, always arise after all other stamens or well-defined staminodia have arisen. Furthermore, I observed that the vascular supply to the nectaries of female *Boottia cordata*, and *Ottelia alismoides* is derived from the stylar plexus slightly above the supply to the stamens or to other staminodia. I am, therefore, led to conclude that these nectaries are actually the uppermost portion of the androecium.

Meristic reductions in the male and female flowers have generally paralleled each other. Those genera with the most numerous fertile stamens in the male flowers tend to have female flowers with numerous staminodia, e.g. *Stratiotes*. Reduction in the number of androecial members has produced constant but rather a large number of stamens and staminodia in *Boottia*, *Limnobium* and *Ottelia*. In these and other genera continuing basipetal sterilization and loss of stamens are seen. The result is that in the tricarpellate genera there are three or no staminodia in the female flowers and four, three, one or none in the male flowers. Further modifications, such as sterilization of one or two of the remaining fertile stamens, have produced such forms as male *Vallisneria*.

Antisepalous pairs of stamens or staminodia are seen in *Ottelia alismoides* and in the female flowers of *Boottia cordata*, *Hydrocharis morsus-ranae*, *Limnobium spongia*, *Thalassia hemprichii* and in male *Stratiotes*. They also occur occasionally in the female flowers of *Hydrilla* and *Vallisneria*. There are no staminodia in the female flower of *Enhalus*, and the arrangement of the stamens in the male flower of *Thalassia hemprichii* is unknown. A comparison of the male and female flowers of *Stratiotes* with those of *Boottia cordata* and *Limnobium spongia*, and with the bisexual flowers of *Ottelia alismoides*, suggests that antisepalous stamen pairs are an intermediate condition and that, with the development of unisexual flowers, the normal (unpaired) condition is attained in the male flower.

Under this interpretation transitional conditions can be seen in *Hydrocharis morsus-ranae* in which both sexes possess paired androecial organs, and in male *Stratiotes* flowers with their paired anti-sepalous stamens. The female *Stratiotes* flower, with its numerous grouped staminodia, is then interpreted as a primitive type.

On the basis of my observations in the Hydrocharitaceae and in the related Butomaceae I suggest that the solution to the problem of the origin and significance of paired stamens is to be found in the progressive reduction of stamen fascicles and not in the addition of new organs through phylogenetic splitting. There is external evidence of fasciation in the female flowers of *Stratiotes*. Other evidence of fasciation is seen in the androecia of *Boottia cordata* and *Ottelia alismoides*, with their fused nectaries, stamens, and staminodia.

Until 1930 the standard interpretation of the hydrocharitaceous gynoecium was that it is syncarpous and unilocular with split parietal placentae. Rohrbach (1871), Ascherson & Gürke (1889), Svedelius (1904), and Cunnington (1912), among others, espoused this interpretation. In 1931 Troll, in the first comprehensive survey of the gynoecium in the family, interpreted the gynoecium as apocarpous and the so-called split placentae as wings of adjacent carpels. He postulated the development of the hydrocharitaceous from a butomaceous type of gynoecium by a termination of apical growth accompanied by continuation of growth of a torus. In this process an ovary would be produced in which the carpels are united by the central portions of their abaxial surfaces to axis tissue. The lateral portions of the carpels and their ventral margins are not fused according to this interpretation. Therefore, the carpels are free from each other, although each is united to a common wall, and an apocarpous but inferior gynoecium exists.

My observations on the morphology and the vasculature of the gynoecia of most genera, while agreeing in many ways with Troll's, suggest that some modifications of his interpretations

are necessary. Evidence from vascular anatomy suggests that the fusion of abaxial carpel surface to non-carpellary tissue of the ovary wall is more complete in some genera than in others. For example, in *Limnobium spongia* and *Thalassia hemprichii* the bundles which supply the perianth and staminodia are not fused with the dorsal and ventral bundles of the carpels as they are in *Boottia cordata* and *Ottelia alismoides*. In *Blyxa alternifolia* the bundles to the perianth and androecium are not fused with those of the carpels, but in *B. auberti* the dorsal and petal bundles are fused and the sepal bundles are independent. In *Elodea* and *Hydrilla* the vascular supply to the perianth and staminodia is derived from three bundles, each of which represents the fusion of two ventral bundles and the perianth and androecium supplies.

In *Boottia cordata*, *Ottelia alismoides* and all the tricarpellate genera, the vascular supply to the ovules of one carpel wall is also the supply to those of the adjacent carpel wall. On this basis the ventral bundles of adjacent carpels are presumed to be fused and thus to indicate a partially syncarpous gynoecium in these genera. In young specimens these fused ventral bundles divide once just below the separation of the fused styles. Each branch continues to a style of an adjacent carpel. Further evidence of syncarpy can be seen in *Ottelia alismoides* where adjacent carpel walls are obviously fused for a short distance, and in *Elodea canadensis* where adjacent carpel walls form low ridges on the ovary wall. In *Enhalus* and in *Stratiotes* the ventral bundles are not fused and the gynoecium is apparently apocarpous (Fig. 12). The gynoecium of *Thalassia hemprichii* appears to be an intermediate form in which some ventral bundles are free and others are fused.

Other evidence of syncarpy in the Hydrocharitaceae is seen in *Limnobium spongia* where the total fusion of adjacent carpel walls is obvious (Fig. 18). The fusion is so complete that the placental bundles supplying the ovules in one carpel also supply those of the adjacent carpel wall. I have somewhat tentatively designated the bundles labelled " *vv* "

in Fig. 18 as ventral bundles which are fused. However, their position so close to the carpel margin, unlike the ventral bundles of other genera of the family, suggests that they are merely placental bundles, or perhaps false ventral bundles in the sense of Moseley (1965). The larger size and well defined course of these bundles seems to set them apart from other placental bundles.

Kausik (1940) concluded, on the basis of anatomical studies in *Enhalus*, that the outer portion of the ovary wall is made of the fused basal portions of the petals and sepals. He noted that the outer bundles of the ovary wall serve the perianth and not the carpels and he considered this to be evidence for the appendicular nature of the ovary. My observations on *Enhalus* agree with those made by Kausik. Furthermore, I have observed similar conditions in the other genera. On the basis of currently accepted concepts of the inferior ovary (Douglas, 1944, 1957; Eames, 1961) I consider the inferior ovary of the Hydrocharitaceae to be appendicular in derivation.

In six of the multicarpellate genera and in *Vallisneria americana*, the vascular supply to the ovules is connected in several places with both the dorsal and the ventral bundles. Similar connections have been reported for a few dicotyledons and the author has observed them in *Butomus*. In these genera, except for *Vallisneria*, the main source of the vascular supply to the ovules is not directly from the ventral bundles but directly from the receptacular plexus. It is probable that these placental bundles are derived from a single principal bundle below the level at which that bundle gives rise to the dorsal and ventral bundles but that such a pattern is obscured at anthesis.

The general primitiveness of the multicarpellate genera, and a similar primitiveness in *Limnocharis*, suggests that these genera possess the most basic type of ovule supply in both the Hydrocharitaceae and the Butomaceae. Using this as a working hypothesis it is possible to derive the Vallisneria type by a reduction in number of ovules with a consequent reduction in vasculature but nevertheless

retaining connections to the dorsal bundle. Further reduction could lead to the sub-marginal Blyxa auberti type in which there are no connections to the dorsal bundle and then, finally, to the Blyxa alternifolia type in which the dorsal bundle, as such, has disappeared altogether. In this scheme it is the ventral bundles which gradually assume the function of supplying the entire flower while the other bundles have either dis-appeared or have fused with them. The possibility that the evolution of laminal placentation in the Hydrocharitaceae was by a phylogenetic expansion of the fertile area from the sub-marginal position seems remote when the vasculature and morphology of the carpels in the entire family are considered.

Figures 69-77 represent the various types of gynoecia in the family. They suggest probable patterns of reduction. A basic type consists of free carpels whose walls project almost to the center of the ovary. Each carpel has one dorsal and two ventral bundles. This is the Stra-tiotes type (Fig. 70). The ovules are distributed all over these projecting walls but are not found along the margins or along the midrib. The dorsal and the ventral bundles of each carpel are located on the same circumference, a situation which strongly recalls that of *Limnocharis* in the Butomaceae. Whether this dis-position of bundles is the primitive condi-tion in the families or is merely due to crowding of numerous carpels is impos-sible to say at this time.

A step in reduction of the gynoecium is the slight fusion of adjacent carpels and the total fusion of their ventral bun-dles. This is the Boottia type (Fig. 69).
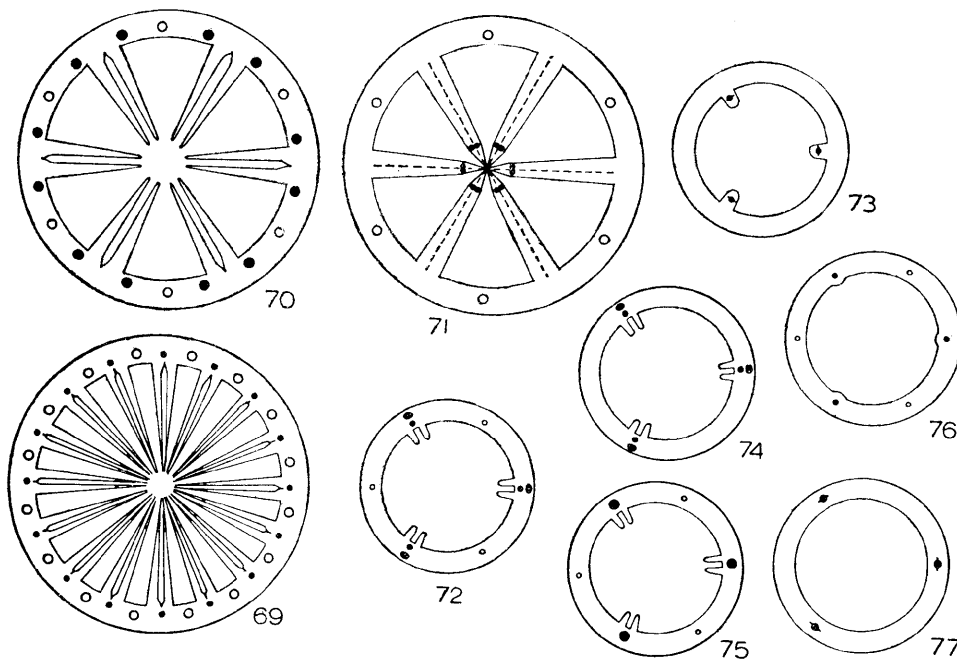
Figs. 69 -77 — Types of gynoecia in the Hydrocharitaceae; clear circles are dorsal bundles, blackened circles ventral bundles, single or fused; hatched circles are bundles to perianth and an-droecium; supply to perianth and androecium not shown for multicarpellate types; all bundles shown for tricarpellate types. **Fig. 69.** *Boottia.* × 10. **Fig. 70.** *Enhalus* and *Stratiotes.* × 12. **Fig. 71.** *Limnobium* and *Hydrocharis.* × 15. **Fig. 72.** *Blyxa auberti.* × 50. **Fig. 73.** *Elodea.* × 65. **Fig. 74.** *Blyxa alternifolia.* × 55. **Fig. 75.** *Vallisneria.* × 18. **Fig. 76.** *Halophila.* × 18. **Fig. 77.** *Hydrilla.* × 25.

Genera with this type may or may not have the perianth and androecium bundles fused with the carpel bundles. Further reduction results in the gradual fusion, toward the margin, of adjacent carpel walls. This is the Ottelia type (Fig. 3). Or, the carpel walls may remain unfused beyond the ventral bundles but may become reduced in size as in the Blyxa-Vallisneria type (Figs. 72, 74, 75). The ovuliferous area is thus greatly reduced. Complete disappearance of the projecting walls could produce the Hydrilla type (Fig. 77).

An alternative pattern is suggested by the Limnobium type (Fig. 71). In this the presumed ventral bundles are near the carpel margins and the carpel walls project to the center of the ovary and are totally fused by their abaxial surfaces. Stages in the reduction of this type could produce the Elodea type (Fig. 73), the Halophila type (Fig. 76) and finally the Hydrilla type, with a corresponding reduction in the number of ovules produced and in the prominence of the projecting carpel walls.

The tricarpellate genera are the most reduced in carpel and ovule number and in vasculature. *Vallisneria* represents a transitional type between the multi- and tricarpellate forms. Of the genera studied in detail here *Hydrilla* possesses the most reduced gynoecium.

The carpels of all genera of the family are always open; the ventral margins are not even closely appressed or held together by hairs. There is no evidence of a tendency toward carpel closure. On the contrary, the tendency is toward greater openness by reduction of projecting walls.

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VASCULARIZATION OF CYCAD LEAFLETS[1]

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Abstract

A detailed investigation of leaflets of cycads, using eight representative species of eight genera, was made to study venation patterns, morphological and anatomical characteristics of the veins and associated tissues, and to point out similarities and differences found in this group.

Vein patterns vary within this group from a completely closed system with all veins anastomosing toward the apex as shown in *Encephalartos lehmanii* to a completely open system with all veins ending blindly as found in *Zamia pumila*. Others have a mixed system with some veins ending blindly and some anastomosing at the apex. Only two species studied have a midrib — *Cycas revoluta* and *Stangeria paradoxa*.

In every species the blade thickness at the vein is greater than the blade thickness between veins. In only one species, *Zamia pumila*, does the blade thickness at the vein exceed the total of the blade thickness between the vein and the vein thickness.

Seven species have an endarch xylem located at the adaxial side of the bundle. One species has a mesarch xylem with the major part of the metaxylem differentiating centrifugally.

The phloem is located on the abaxial side of the bundle with the metaphloem adjacent to the xylem and the crushed protophloem at the periphery of the bundle. The bundles, though primitive in vein patterns and type of veins, have an advanced anatomy.

Very little morphological or anatomical investigation has been done on cycad leaflet venation. Lamb (1923) determines genera and species by gross morphological characters of the leaflets. She also gives brief descriptions of the leaflet anatomy of each genus from observations of free-hand and permanent cross-section preparations.

Gaussen (1944) provides a general description of the anatomy of cycad