EVOLUTION AND ADAPTATION OF INFLORESCENCES IN THE HYDROCHARITACEAE[1]

ROBERT B. KAUL

Department of Botany, University of Nebraska, Lincoln

A B S T R A C T

Inflorescence evolution in the Hydrocharitaceae has involved modification of a complex sympodial system by condensation, loss of bracts, fusion of pedicels in some cases, adnation of branches to the peduncle in others, and progressive loss of later-formed flowers resulting in one-flowered inflorescences in many instances. These changes are associated with the transition from entomophily to more specialized water pollination schemes and from the terrestrial to marine and fresh-water habitats.

AMONG THE Hydrocharitaceae are found some of the most primitive floral structures in the monocotyledons, but in many species the flowers are very specialized. Inflorescences throughout the family are moderately to highly specialized. All taxa are aquatic, including three marine genera, and they show the transition from entomophily to hydrophily, including pollinating mechanisms unique in the angiosperms. Most are dioecious, but some are monoecious (in the sense of having unisexual flowers of both sexes on the same plant), and a few have perfect flowers. The flowers and inflorescences are distinctly sexually dimorphic in most cases, but the vegetative organs are not.

There are a few accounts of inflorescences in the literature, but there has been no comprehensive study. Rohrbach (1873) examined *Hydrocharis* and *Stratiotes*, Kubin and Müller (1878) studied *Vallisneria*, Balfour (1879) described *Halophila* thoroughly, and Cunnington (1912) and Troll (1931, 1964) examined *Enhalus*. St. John (1962, 1963, 1964, 1965) has monographed *Elodea* and illustrated many of its inflorescences, and recently Tomlinson (1969) has studied *Thalassia testudinum*. Hartog (1957) and Sculthorpe (1967) have reviewed the pollination mechanisms and other aspects of floral biology. This paper reports morphological, developmental, and vascular data from inflorescences of 13 of the 15 genera. Some of the strange and highly modified types are more readily understood when compared with others in the family.

MATERIALS AND METHODS—Table 1 lists the plants surveyed, their pollination schemes, sex distribution, habitats, and sources. I have collected and in some cases grown these myself, except for the seed of *Boottia*, which was collected by A. L. Bogle. I have cleared some of the inflorescences by a previously described technique (Kaul, 1969) and others have been sectioned and stained with fast green.

OBSERVATIONS—*Bracts*—All inflorescences studied except those of female *Hydrocharis* are subtended by a spathe of two enveloping bracts. These can be congenitally connate forming a closed tube (Fig. 7–11, 13, 19, 20, 23–27) which is forced open apically by the developing flowers, or they can be partially or entirely free from the beginning (Fig. 3–6, 14, 15, 21, 22, 28, 29). The bracts of male *Thalassia* are fused more on one side than the other (Fig. 6; Tomlinson, 1969). The sessile female inflorescence of *Hydrocharis* has a single spathe bract, a condition reported for the bisexual inflorescence of *Halophila decipiens* (Hartog, 1957), which I have not seen.

The spathes lack conspicuous ornamentation except in *Boottia* (Fig. 19), *Ottelia* (Fig. 20), *Enhalus* (Fig. 21), and male *Hydrilla* (Fig. 8). They are persistent around the developing fruits, and even the male spathes may persist long after anthesis.

The freed apices of the two fused spathe bracts show clearly in *Elodea* (Fig. 7, 9, 24), *Nechamandra* (Fig. 13), *Ottelia* (Fig. 20), female *Hydrilla* (Fig. 23), female *Vallisneria* (Fig. 25, 26), male *V. neotropicalis*, and *Blyxa* (Fig. 27). In *Boottia* the spathe in both sexes is ruptured irregularly (Fig. 19) whereas the male spathe of *Vallisneria americana* (Fig. 10) curls back and tears irregularly before the flowers are liberated. The spathe of male *Hydrilla* (Fig. 8) splits open across the terminal knob, and the entire male flower breaks off and floats to the surface before opening, a habit found also in male *Elodea nuttallii* (Fig. 9).

I have found bracts subtending the flowers within the spathe only in male *Stratiotes* (Fig. 4), male and female *Limnobium* (Fig. 16, 17, 28), and female *Hydrocharis*. In these cases there is a single bract subtending each flower except the

TABLE 1. *Pollination, sexuality, habitat, and source of the plants studied*

Taxon	Pollination	Sexuality	Habitat	Source
Ottelia alismoides	insects	perfect	freshwater	Ceylon
Boottia cordata	insects	dioecious	freshwater	Burma
Limnobium spongia	insects	monoecious	freshwater	Louisiana
Hydrocharis morsus ranae	insects	monoecious	freshwater	Germany
Stratiotes aloides	insects	dioecious	freshwater	Germany
Enhalus acoroides	surface[a]	dioecious	marine	Singapore
Thalassia hemprichii	underwater	dioecious	marine	Philippines
Halophila ovalis	underwater	dioecious	marine	Singapore
Vallisneria americana	surface[a]	dioecious	freshwater	Minnesota
V. neotropicalis	surface[a]	dioecious	freshwater	Florida
V. spiralis	surface[a]	dioecious	freshwater	commercial
Nechamandra alternifolia	surface[a]	dioecious	freshwater	India
Blyxa alternifolia	?	perfect	freshwater	Singapore
B. auberti	?	perfect	freshwater	Singapore
Elodea densa	insects	dioecious	freshwater	commercial
E. nuttallii	surface[a]	dioecious	freshwater	Minnesota
E. canadensis	surface[b]	dioecious	freshwater	Nebraska
Hydrilla verticillata	surface	dioecious	freshwater	Singapore

[a] Entire male flower detaches and rises to the surface.

[b] Pollen is liberated from attached male flowers and floats to the female.

so-called terminal one. Rohrbach (1873) noted that in male *Stratiotes* the middle flowers sometimes had a bract and sometimes didn't.

The fact that one bract envelops the other in many cases (Fig. 3–5, 14–17, 21, 22, 28) suggests that they arise at different levels, but this is not so evident where they are connate. Nevertheless I have found a distinct lopsidedness in the insertion of the spathes of male *Vallisneria* which indicates different levels of origin for the component bracts. Rohrbach (1873) observed consecutive origin at different levels of the bracts of *Hydrocharis* and *Stratiotes*.

Male inflorescences—The male inflorescence of *Boottia* (Fig. 1) is one of the most complex in any of the entomophilous taxa. It has apparently terminal flowers which develop and open first (Fig. 1, 2), followed by a slightly basipetal sequence of flowers on 2–8 radii. Each radius represents a condensed branch, adnate to the peduncle, with acropetally developed flowers. More robust plants produce more complicated inflorescences, and Fig. 2 is an early stage of a depauperate plant having only two branches.

In *Limnobium spongia* (Fig. 16, 17) each bract subtends at least one flower and a branch, and the inflorescence is thus made of two rather condensed sympodial systems. *Stratiotes* (Fig. 4) is similar but the branches are so condensed that the flowers appear to arise directly from the peduncle. Rohrbach (1873) found that in some cases one or both of the sympodia are vegetative. The 3–5 flowers of *Hydrocharis* (Fig. 3) and *Elodea densa* (Fig. 7) are further reductions of these branch systems, and they are without bracts. The inflorescences of *Halophila* (Fig. 5), *Thalassia* (Fig. 6), *Hydrilla* (Fig. 8), and *Elodea nuttallii* (Fig.

9) represent the ultimate reduction to a single flower.

The many flowers of *Vallisneria*, *Nechamandra*, and *Enhalus* break from their pedicels on the submerged inflorescences and float to the surface before anthesis. They develop and abscise in basipetal order, and Fig. 10 and 14 show inflorescences with about half of their flowers left, while Fig. 11 shows a young *Vallisneria* with upper primordia developed. The *Nechamandra* inflorescence (Fig. 13) is shown with the first flower departing.

Outwardly the *Vallisneria* and *Enhalus* inflorescences are similar but vascular anatomy shows important differences. In *Vallisneria americana* (Fig. 12) and *V. neotropicalis* the flowers are supplied with bundles which depart in acropetal order from a large central bundle and its branches, but in *Enhalus* (Fig. 15) they are supplied from downturned bundles departing from the terminal plexus which is, in turn, derived from two large receptacular bundles. This vascular evidence suggests that the core of the *Vallisneria* inflorescence is formed of fused pedicels while that of *Enhalus* is mostly receptacular. *Nechamandra* (Fig. 13) is a simpler version of the *Vallisneria* type, and here it is clear that the core is made of fused pedicels. Further, each flower is vascularized independently from the receptacle and there is no central bundle.

The female inflorescences and those with bisexual flowers (*Ottelia*, *Blyxa*) are one-flowered (Fig. 19–29). The flowers are sessile or nearly so except in *Limnobium* (Fig. 28) and *Hydrocharis*, where they are elevated well above the spathe and the water surface. In these two genera the pedicel bends after anthesis and pushes the maturing fruit under water and into the mud,
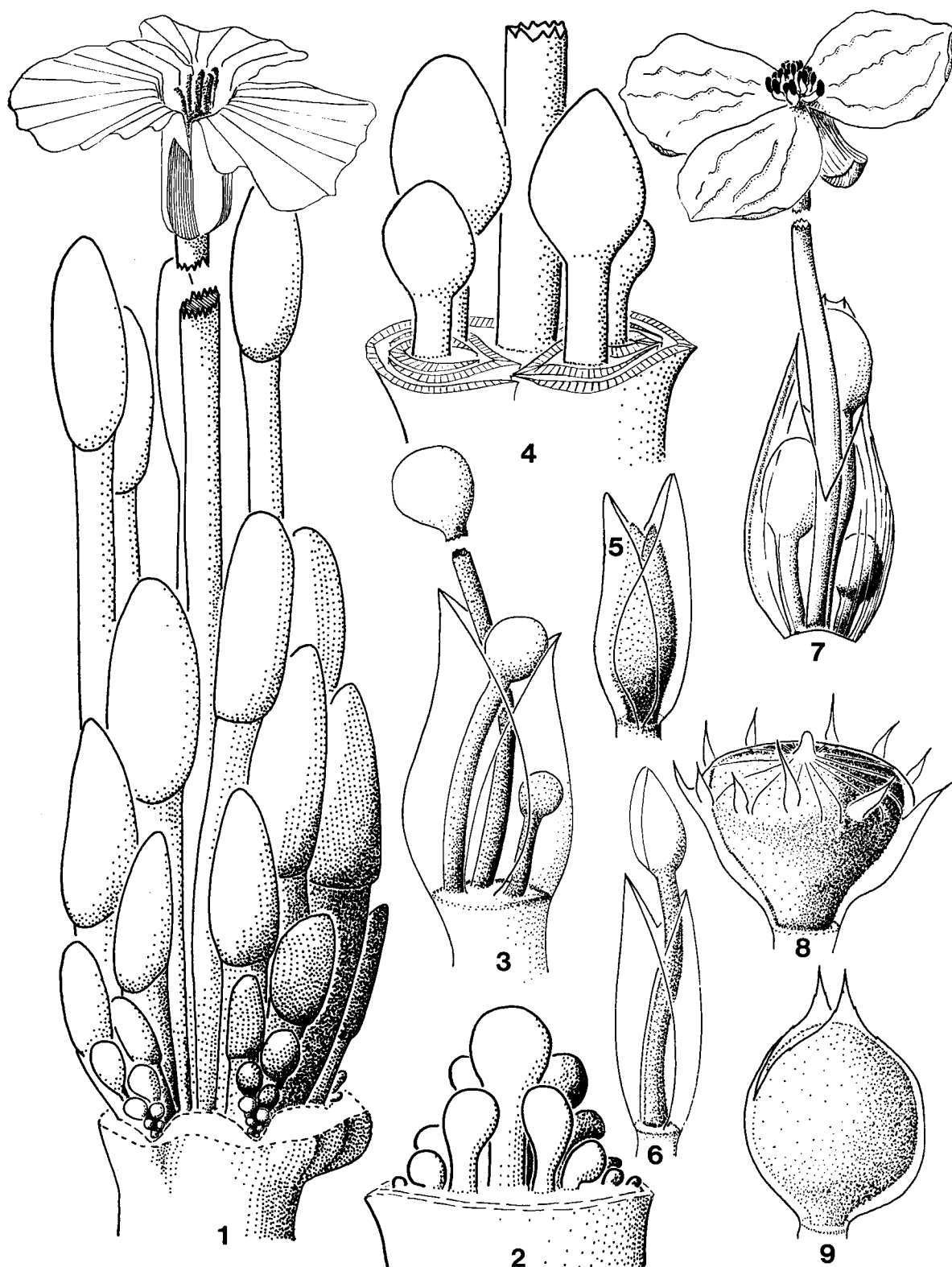
Fig. 1–9. Male inflorescences.—Fig. 1. *Boottia cordata*. ×3. —Fig.2. Young *Boottia cordata*. ×20.—Fig. 3. *Hydrocharis morsus ranae*. ×3.—Fig. 4. *Stratiotes aloides*, bracts cut away. ×3.—Fig. 5. *Halophila ovalis*. ×4.—Fig. 6. *Thalassia hemprichii*. ×3.—Fig. 7. *Elodea densa*. ×6.—Fig. 8. *Hydrilla verticillata*. ×26.—Fig. 9. *Elodea nuttallii*. ×28.
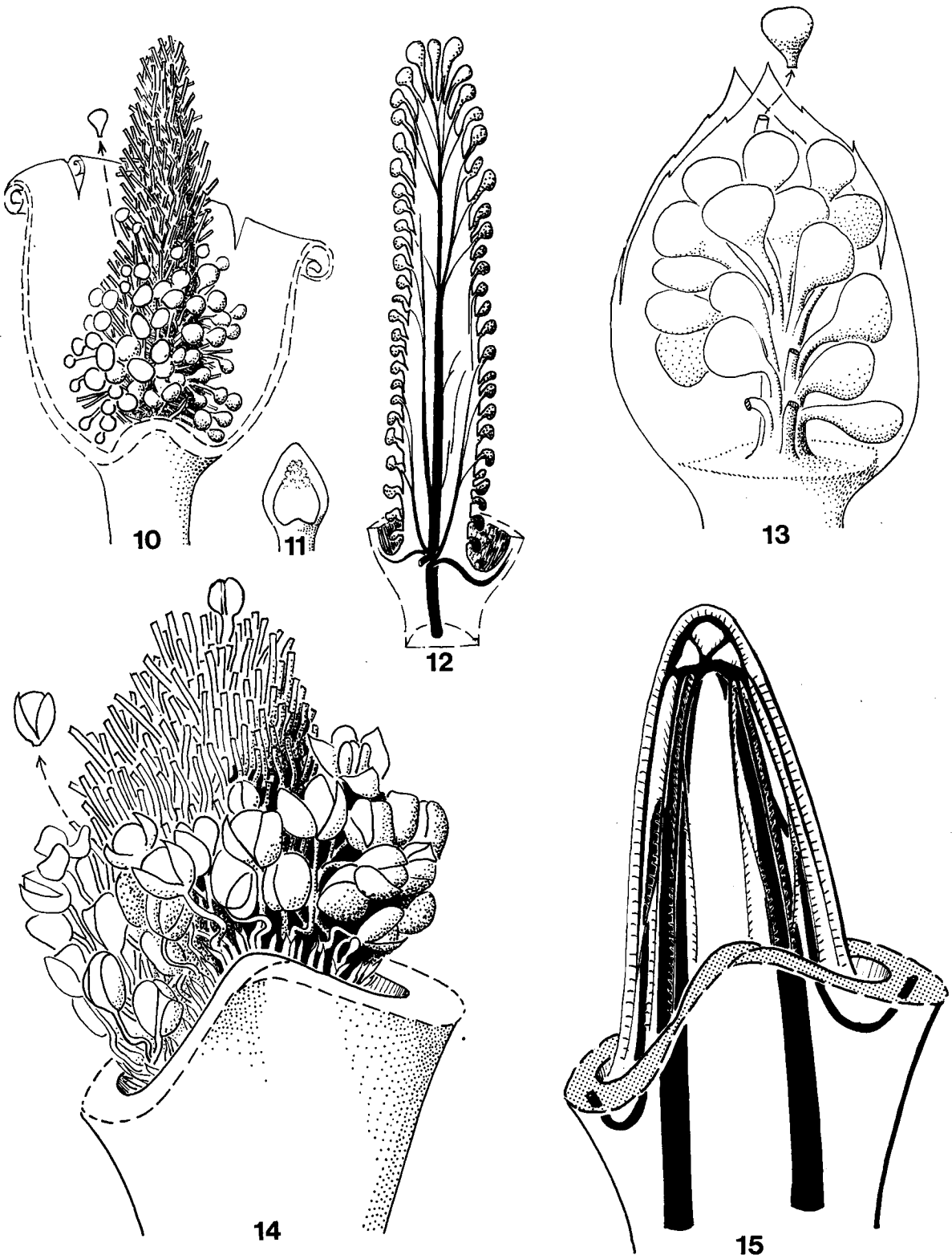
Fig. 10–15. Male inflorescences.—Fig. 10. *Vallisneria americana.* ×5.—Fig. 11. Young *V. americana* with flower primordia appearing in basipetal order. ×15.—Fig. 12. *V. americana*, longitudinally halved inflorescence showing vasculature. ×8.—Fig. 13. *Nechamandra alternifolia* with three lower flowers cut away; the terminal flower is shown breaking from its pedicel. ×25.—Fig. 14. *Enhalus acoroides* with spathe cut away. The flowers abscise in basipetal order. ×6.—Fig. 15. *E. acoroides*, vascular system of inflorescence slightly simplified. ×6.
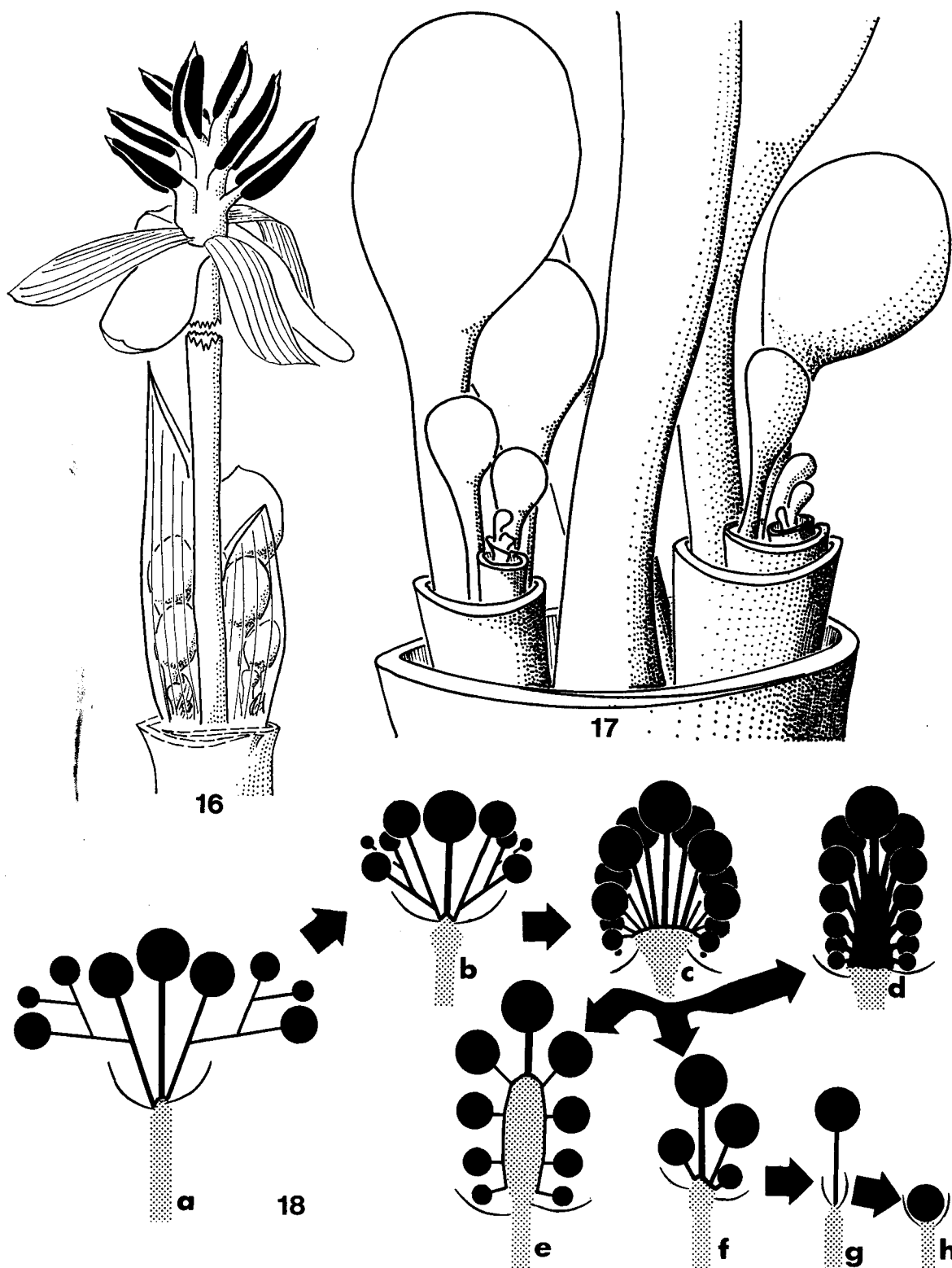
Fig. 16–18.—Fig. 16. *Limnobium spongia*, male inflorescence with spathe removed. ×4.—Fig. 17. *L. spongia*, detail of young male inflorescence with bracts removed. ×16.—Fig. 18. Possible evolution of inflorescences. Further explanation in text.

while in *Enhalus* and *Vallisneria* the peduncles coil and pull the fruits well below the surface. In others, except possibly *Stratiotes*, the fruits remain where they were at anthesis.

There are 0–3 abortive branch systems in the female *Limnobium* inflorescence (Fig. 28), each containing 1–3 bracts and female buds arranged like those of the male inflorescence. These systems are axillary to the spathe bracts. There is one such branch in female *Hydrocharis*, located between the single spathe bract and the flower.

DISCUSSION—Hydrocharitaceous inflorescences and flowers show a spectrum of adaptations for specialized pollination. Most inflorescences are so modified that their fundamental nature is at first glance obscure, but male *Boottia* and *Limno-* *bium* are simple enough to provide clues and I have used them in devising a prototype (Fig. 18a). In this each spathe bract subtends a sympodium bearing flowers, and the spathe is therefore made up of the lowest two floral bracts. Some inflorescences (Fig. 1–4, 7) have apparently terminal flowers, but it is not really clear whether these flowers are terminal on the peduncle or basal on a sympodium. The latter seems to be the case in *Limnobium* (Fig. 17), where the first two flowers are subtended by the spathe bracts. I suspect that all "terminal" flowers in the family are really pseudoterminal. Regardless of the morphological position of the first flower, inflorescence evolution in the Hydrocharitaceae has involved loss of all bracts except the lowest one or two, condensation of the sympodia, adnation of the sympodia to
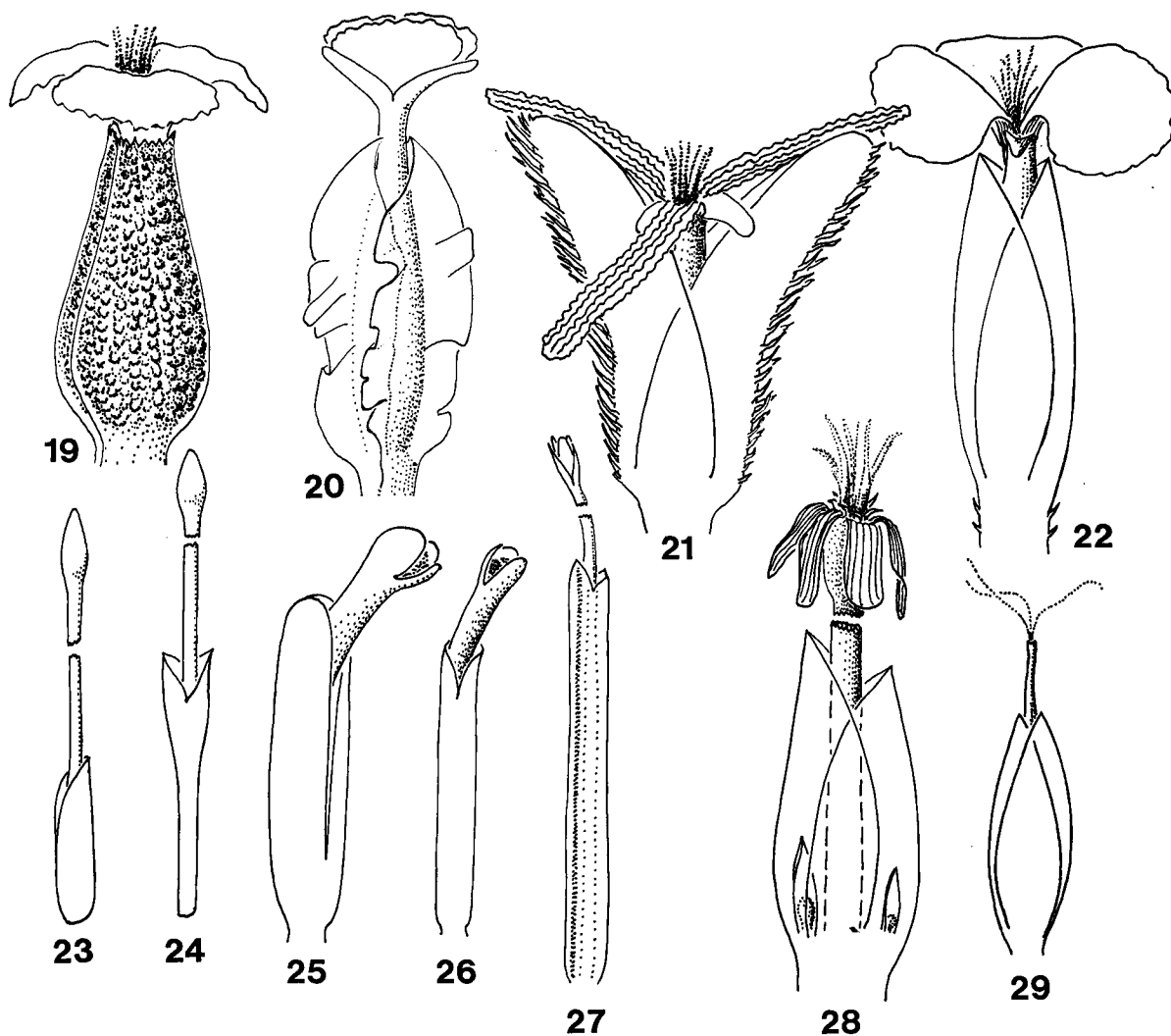

Fig. 19–29. Female inflorescences.—Fig. 19. *Boottia cordata.* ×1.—Fig. 20. *Ottelia alismoides*, with perfect flower. ×1.—Fig. 21. *Enhalus acoroides.* ×1.7.—Fig. 22. *Stratiotes aloides.* ×2.5.—Fig. 23. *Hydrilla verticillata.* ×7.—Fig. 24. *Elodea canadensis.* ×4.—Fig. 25. *Vallisneria americana.* ×2.—Fig. 26. *V. spiralis.* ×4.—Fig. 27. *Blyxa alternifolia.* ×1.5.—Fig. 28. *Limnobium spongia.* Flower pedicellate, abortive branches present. ×3.—Fig. 29. *Halophila ovalis.* ×10.

the peduncle in some cases and fusion of the pedicels in others, and progressive loss of later-formed flowers ultimately leaving a single flower.

Figure 18 is one of several possible schemes, but it is the one which seems to correlate best with evolutionary changes in the flowers (cf. Kaul, 1968), with pollination mechanisms, and with vegetative morphology. I have shown terminal flowers in these figures, although their existence is questionable; without them the scheme would be similar except that the first flower on the lower sympodium would be pseudoterminal. Figure 18b is an early stage of sympodium condensation (cf. Limnobium, Fig. 17) while 18c shows further condensation and adnation of the sympodia (cf. Boottia, Fig. 1, 2). Figure 18d illustrates continued modification resulting in pedicel fusion (cf. Vallisneria and Nechamandra, Fig. 10, 12, 13) and the formation of a non-receptacular axis. Still another modification, by loss of later-formed flowers, is shown in 18f (cf. Hydrocharis and Elodea densa, Fig. 3, 7). Figure 18g, a single pedicelled flower (c.f Halophila, Hydrilla, and Elodea nuttallii, Fig. 5, 8, 9), shows the ultimate stage in the phylogenetic disappearance of flowers. Another modification has occurred in Fig. 18d, g, and h in that entire flowers break out of the inflorescence before anthesis and act as pollen vectors—a behavior probably unique in the angiosperms. The single-flowered state has probably arisen several times in the family.

Figure 18e is the Enhalus type (cf. Fig. 14, 15) formed by the phylogenetic fusion of the sympodia basipetally on the peduncle. Vascular anatomy and basipetal flower abscission support this interpretation, first made by Troll (1931, 1964) on the basis of the basipetal development of flowers. Vallisneria and Enhalus have acquired similar inflorescences by somewhat different processes, but in both the upper flowers are morphologically the lowest. Their pollination is similar but their floral structure is not (Kaul, 1968). The Boottia inflorescence (Fig. 1) represents a precursor type to those of Vallisneria and Enhalus, and its modification was certainly related to the evolution of underwater inflorescences and surface pollination. Nechamandra (Fig. 13) suggests an intermediate step in this process.

The female inflorescences have probably arrived at the one-flowered condition by similar paths. In female Limnobium (Fig. 28) and Hydrocharis there is a clue to earlier complexity—the presence of abortive branches. All others, and also those few with perfect flowers, are one-flowered and without vestigial branches.

In some respects Limnobium is the least specialized member of the family. It and Hydrocharis are the only non-submerged, and possibly the only monoecious, members, and their flowers and inflorescences are relatively unspecialized for the family. They appear to be transitional phases from the terrestrial to the aquatic habitat, from the perfect condition to dioecism, and from amply branched to highly condensed inflorescences. In neither genus are the female flowers as well protected by the spathe as they are elsewhere in the family. Limnobium, with its secondary bracts and its branched inflorescences, is less specialized than Hydrocharis, however.

Grant (1950) has shown the adaptive value of the inferior ovary as protection of the ovules from pollinating animals. The spathes of Hydrocharitaceae provide additional protection in the entomophilous members, but I believe that the thick bracts are more useful in protecting the ripening fruits and the delicate male flowers from small herbivores and from drying. Snails avoid the spathes and their enclosed flowers of my greenhouse specimens of Boottia, Ottelia, and Blyxa, but they eat everything else available, and I have noticed this immunity in Thalassia and Enhalus in the sea. In some cases the spathe also prevents wide dispersal of the seeds by failing to disintegrate with the ovary, thereby insuring survival of the colony in its location. Limnobium, whose fruits are not protected by a spathe, achieves similar results because its fruits ripen in the mud and the seeds are liberated there when the ovary disintegrates.

Generally, the female inflorescences are more specialized than the male inflorescences in this family, but the opposite is true for the flowers (Kaul, 1968). A result is that a relatively unspecialized male inflorescence (e.g., Boottia) has a specialized female counterpart. Clearly behavioral modifications may be greater than morphological ones, as in Enhalus, where the male and female flowers are not particularly specialized for the family, although the inflorescences are.

The entomophilous taxa have the most primitive flowers (Kaul, 1968, 1969) and the most primitive male inflorescences, while the water and surface pollinated members are more specialized in both respects. The large numbers of male flowers of Vallisneria, Enhalus, and Nechamandra are adaptations to the randomness of surface pollination, and the many one-flowered inflorescences of Hydrilla and Elodea nuttallii achieve the same result. Adaptations for underwater pollination in Halophila and Thalassia are in the flowers rather than the inflorescences and include reduction of the perianth, elongation of the stigma, and liberation of the pollen in chains.

The Hydrocharitaceae probably have been derived from stock resembling the Butomaceae (Kaul, 1969), and their most primitive inflorescences show similarities to Limnocharis and Butomus inflorescences, which are apparently less specialized, however. As the ancestors of the modern Hydrocharitaceae moved into the water they developed the compact inflorescences typical of submerged aquatics. Then, as some made the transition from entomophily to more specialized pollination, they developed extreme reduction

in both flowers and inflorescences. Fortunately, many types remain, and they provide clues that help us deduce their phylogeny.

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