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AN APPROACH TO THE TAXONOMY OF *VALLISNERIA* L. (HYDROCHARITACEAE)

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ABSTRACT

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Taxonomic decisions presented in this study of *Vallisneria* are founded on the consistency of comparable staminate and pistillate floral structures considering the geography and dioecious nature of the genus. Field studies, realized in southern Europe, eastern North America, Central America, northern South America and the Greater Antilles, formed the basis for the development of the present knowledge of characters. Umbel and spike-like inflorescences were discovered from three localities in the Americas. Staminodia were encountered in the female flowers of *Vallisneria spiralis*. Two species including four varieties are recognized, mapped and illustrated. Infraspecific taxa are *V. spiralis* L. var. *spiralis*, *V. spiralis* var. *denseserrulata* Makino, *V. americana* Michaux var. *americana* and *V. americana* var. *biwaensis* (Miki) Lowden, **comb. nov.** These taxa are delineated according to the degree of connation of fertile filaments in the staminate flower and adnation of staminodia to stigma—style surfaces in the pistillate flower. Both species converge along what appears to be a continuous gradient in floral variation.

INTRODUCTION

Two centuries have elapsed since Linnaeus (1753) described *Vallisneria spiralis* from its native habitat in southern Europe. Toothing of leaf apices and flower colour were used by Linnaeus to distinguish male and female plants. Roumeguère (1874) accounted for *V. spiralis* from southern France, while Kerner (1891, 1902) described and illustrated both sexes from Lake Garda in northern Italy. In the female flower, Kerner found bilobed stigmas with finely fringed margins and scapes tightly coiled at maturity. His illustration of the male flower shows a pair of stamens projecting obliquely up into the air.

Michaux (1803) described the American plant, *V. americana*, stating that the female scapes do not spiral. On the other hand, Nuttall (1818) found the American plant to have spiralled peduncles and toothed leaf margins. Even

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though Nuttall used Michaux's name (*V. americana*), he evidently thought the American plant fitted the Linnaean description, overlooking the fact that Michaux's statement ('pedunculis non spiralibus') was a contradiction. Accordingly, Nuttall concluded that the American plant is 'apparently a mere variety' of the European *V. spiralis*. Torrey (1826) confirmed Nuttall's observations on the American plant and named the variety *V. spiralis* L. var. *americana* (Michaux) Torrey.

Prior to the early 1900s the presence of *V. spiralis* in North America was firmly established in the botanical literature. Roumeguère (1874) considered the American species to be identical with the European. *V. spiralis* was reported from both hemispheres in Engler and Prantl's "Pflanzenfamilien" (Ascherson and Gürke, 1889). The leading manuals of regional floras for eastern North America (Gray, 1848, 1874; Chapman, 1883; Small, 1903, Britton and Brown, 1913; Urban, 1920, 1924) cited the American plant as *V. spiralis*. There is no doubt that common usage had convinced botanists that *V. spiralis* was a component of the aquatic vascular flora in North America. Consequently, the American plant has received adverse responses concerning its true identity and indigenous nature in the Americas.

Rydberg (1909) revived Michaux's original description of *V. americana* as the species name for the American plant found from Florida to Mississippi in the south-eastern United States. Assuming the northern species to be *V. spiralis*, Rydberg (1909) and Small (1913) associated the southern plant having pistillate scapes 'scarcely spiral twisted' with *V. americana*. Stigmas cleft nearly to the base, thickish leaves and long sepals were used to distinguish the southern robust plant from its less gross northern counterpart.

At East Okoboji Lake in north-western Iowa, Wylie (1917) observed male and female flowers of *Vallisneria* and compared them with Kerner's description of *V. spiralis* from southern Europe. In the male flowers he found the fertile stamens to be united, never free and extended as shown in Kerner's drawing. Wylie questioned the morphological difference between the American and European *Vallisneria* concluding that they should be distinct species differing in their inclination of fertile stamens. It was evident that the 'European plant is essentially different from ours of the same name'.

The initial opposition to the presence of *V. spiralis* in North America was presented by Fernald (1918) who formed the supposition that *V. americana* is unique to eastern North America. He considered Rydberg's data 'thoroughly inconstant'. In view of scape dimensions in staminate inflorescences the American *V. americana* 'differs very definitely' from the European *V. spiralis*, even though 'definite diagnostic characters' were unknown to him for the pistillate plants. Wylie's findings were not cited by Fernald. The absence of critical morphological data only permitted Fernald to form a premature argument for *V. americana* as a distinct species. Consequently, the uncertainty of morphological characters forced him to reconsider Torrey's varietal status, *V. spiralis* var. *americana*, for the name of the American plant.

Svedelius (1932) held the opinion that there is a direct relationship be-

tween the united stamens pointed out by Wylie in staminate flowers and the binomial *V. americana*. No mention was made of Fernald's work, but his findings revealed that *V. americana* has a more northern extension into northern North America than just the southern range proposed by Rydberg and Small.

The giant specimens of *Vallisneria* collected from the Río Negro in Cuba persuaded Marie-Victorin (1943) to reconsider species identities in the genus. In his treatise, "Les Vallisnéries Américaines", a type was chosen for *V. americana* under the consideration that the specimen selected was representative of *Vallisneria* throughout the northern range of the genus in North America. Assuming the vicarious *V. spiralis* does not exist in North America, Marie-Victorin believed the *V. spiralis* of Rydberg to be really the *V. americana* of Michaux common to north-eastern North America. Since sepal length, stigmatic clefting, leaf width and coiling of scapes in pistillate flowers of the Cuban plant (Río Negro, Ciénaga de Zapata) corresponded precisely with Rydberg's description of the southern plant, Marie-Victorin named this new taxon from Florida and Cuba, *V. neotropicalis*.

In contemporary floras (Fernald, 1950; Gleason, 1968), only *Vallisneria americana* is cited in eastern North America south to Florida and Texas (Gulf States). More recently (Correll and Correll, 1972) it has been reported from Texas, New Mexico and Arizona in the south-western United States. The large robust plants from central and south Florida, identified as *V. neotropicalis* (Marie-Victorin, 1943; Long and Lakela, 1971), were treated as giant variants of *V. americana* by Godfrey and Wooten (1979). They suggest that 'the large size of plants is a consequence of the factors favoring continuous growth' and that size differences are correlated with the age of individual plants or clones.

DISCUSSION

It is certain that taxonomic judgements have been made in *Vallisneria* without the concurring presence of both sexes. Often the male plant has been missing. For example, Rydberg's characterization of *Vallisneria* in North America treated only female plants. Fernald considered himself incompetent to deal with the taxonomic importance of pistillate characters, such as the stigma characters indicated by Rydberg. Male plants were unknown to Marie-Victorin when he selected a type for *V. americana* and described *V. neotropicalis*. As a result, existing type material is inadequate for the determination of taxa that are above all dioecious plants in nature.

My field studies of populations containing both sexes reveal that the male flowers from Cuba and localities dispersed throughout North America are identical with those originally described by Wylie from Iowa. Rydberg's *V. americana* and Marie-Victorin's *V. neotropicalis* belong to the same floral form of *V. americana* Michaux. The present study treats this distinct floral form which is found commonly throughout North America and East Asia as

V. americana Michaux var. *americana.* This variety has staminodia fused to the stylar bases (Witmer, 1937) of adjacent stigmatic lobes in the female flower and filaments of stamens partially united in the male flower.

In Haiti and Venezuela free staminodia characterize the pistillate plant of *V. americana* var. *biwaensis* (Miki) Lowden. Vigorous male plants with filaments of stamens completely united were found in the Dominican Republic. The disjunct distribution of this variety in Japan was confirmed by Miki's drawings (1934) of male and female flowers showing the same comparative morphology found in *Vallisneria* flowers from Hispaniola and Venezuela.

Vallisneria spiralis is a distinct species. The staminate flowers with freely extended stamens were originally illustrated by Kerner and exactly described by Svedelius (1932) and Kausik (1939). Ascherson and Gürke (1889) stated that there are no staminodia ('keine Staminodien') in the female flowers. No mention of staminodia was made by Kerner (1891, 1902) in the female plant of *V. spiralis* from Lake Garda in northern Italy. In India, Kausik (1939) reported 'no staminodia are seen'.

Contrary to former opinions, there are staminodia in the pistillate flower of *V. spiralis.* Staminodia were encountered in flowers of *V. spiralis* collected in France (Canal Languedoc) and Italy (Lake Garda). They were observed in dried herbarium specimens from throughout the known range of the species. The apices of these staminodia are discernible from their bases which are fused to the adjoining fringed stigmatic lobes. Obviously, staminodia in *V. spiralis* have been overlooked because of their inconspicuous nature. On the other hand, staminodia are more conspicuous in *V. americana* due to the lesser degree of fusion between staminodia and stylar bases, or to the presence of free staminodia which is the case in *V. americana* var. *biwaensis.*

From the present floral evidence, Torrey's variety (1826), *V. spiralis* var. *americana* alluded to by Nuttall (1818), Fernald (1918), Rangasamy (1934), Kausik (1939) and Standley and Steyermark (1958), cannot be accepted since both sexes of *V. americana* are morphologically distinct from those of *V. spiralis.*

Nomenclatural priority has been given to Makino's variety, *V. spiralis* var. *denseserrulata.* The author's morphological interpretation of this variety, based on the study of dried herbarium specimens, was reconfirmed by Miki's drawings (1934) of male and female flowers. This variety is distinct in that the staminodia in the female flower are fused to the base of stigmatic lobes and not near the tips of stigmatic lobes as in *V. spiralis* var. *spiralis.*

Hara's publication (1974) of two varieties under *V. natans* (Lour.) Hara establishes the autonym *V. natans* var. *natans,* of the type named *Physkium natans* Lour. The actual determination of *P. natans* is questionable, since the type specimen from Indochina (Cochin China) is without flowers. Furthermore, the fact that staminate plants are so far unknown in Indochina and Malaysia (Den Hartog, 1957) inhibits a conclusive treatment of *Vallisneria* in south-east Asia. Tentatively, I have placed *P. natans* in synonomy with *V. spiralis* var. *denseserrulata.* A pistillate plant of this variety was examined from Hanoi, Vietnam (Tonkin). To my knowledge, *V. americana* does not occur in Indochina.

FLORAL STRUCTURES OF DIOECIOUS PLANTS

Vegetative and reproductive characters were evaluated for their taxonomic relevance in *Vallisneria*. Width of leaves including the condition of leaf margins, either entire or toothed, had to be discarded as indecisive characters. In the same manner, flower colour, sepal length, coiling of the female scapes, curvature of fruits, width of male scapes and number of fertile stamens proved inadequate. Relevant taxonomic characters emerged from a comparative study of staminodial conditions in pistillate flowers and staminal positions in staminate flowers.

The solitary female flower (Fig. 1a) has an outer whorl of three sepals which alternate with the three petal rudiments in the inner perianth whorl. The next whorl consists of three staminodia alternating with the petal rudiments. These staminodia (opposite the sepals) are free (Fig. 2a) or adnate to stigma–style surfaces (Figs. 2b and 3a). Three pairs of matching stigmatic lobes (opposite the petal rudiments) form the innermost floral whorl (Fig. 1a). Taxonomic decisions were based on the degree of adnation of staminodia with stigmas and styles.

Svedelius (1932) suggested that *V. americana* with 'stigmas cleft nearly to the base' is more primitive than *V. spiralis* with stigmas 'cleft for less than half their length'. It is assumed that 'stigmas cleft' refers to the incision between discordant stigmatic lobes located opposite the sepals. This being the case, the fused stigmatic lobes cleft for less than half their length (Figs. 3a and e) represent a highly derived trait in the solitary pistillate flower of *V. spiralis* var. *spiralis* (Fig. 3d). The partially fused stylar bases of adjacent stigmas in *V. americana* var. *americana*, cleft nearly to the base (Figs. 2b and c), are thought to be less advanced. On the other hand, the freely extended stigmatic lobes and the free staminodia in *V. americana* var. *biwaensis* (Figs. 2a and d) are believed to be more primitive.

Male flowers (Figs. 1h and i) have three sepals in the outer perianth whorl, accompanied with one rudimentary petal between the two larger sepals. Only one staminodium is found opposite the smallest sepal. There are two fertile stamens (Figs. 3f and g) which appear as one (Figs. 4d and e) when filaments are united to the apex. Taxonomic decisions were based on the degree of connation between filaments and the presence or absence of hairs at the base of the androecium. The connate filaments in *V. americana* (Fig. 4e) might represent a derived trait. The contrasting trait is found in *V. spiralis* (Fig. 3g) where the two stamens are freely extended.

In pistillate and even more so in staminate plants (Figs. 4a and 5a) there is a tendency towards apetalous flowers. In both sexes the inner perianth whorl has been reduced to petal rudiments. Three petal rudiments are found in the female flower (Fig.1a), whereas in the male flower the number of petal rudiments has been reduced to one (Figs. 1h and i).

Evolutionary trends indicate that the common unisexual flowers and the dioecious condition of the genus have been derived from a primitive bi-

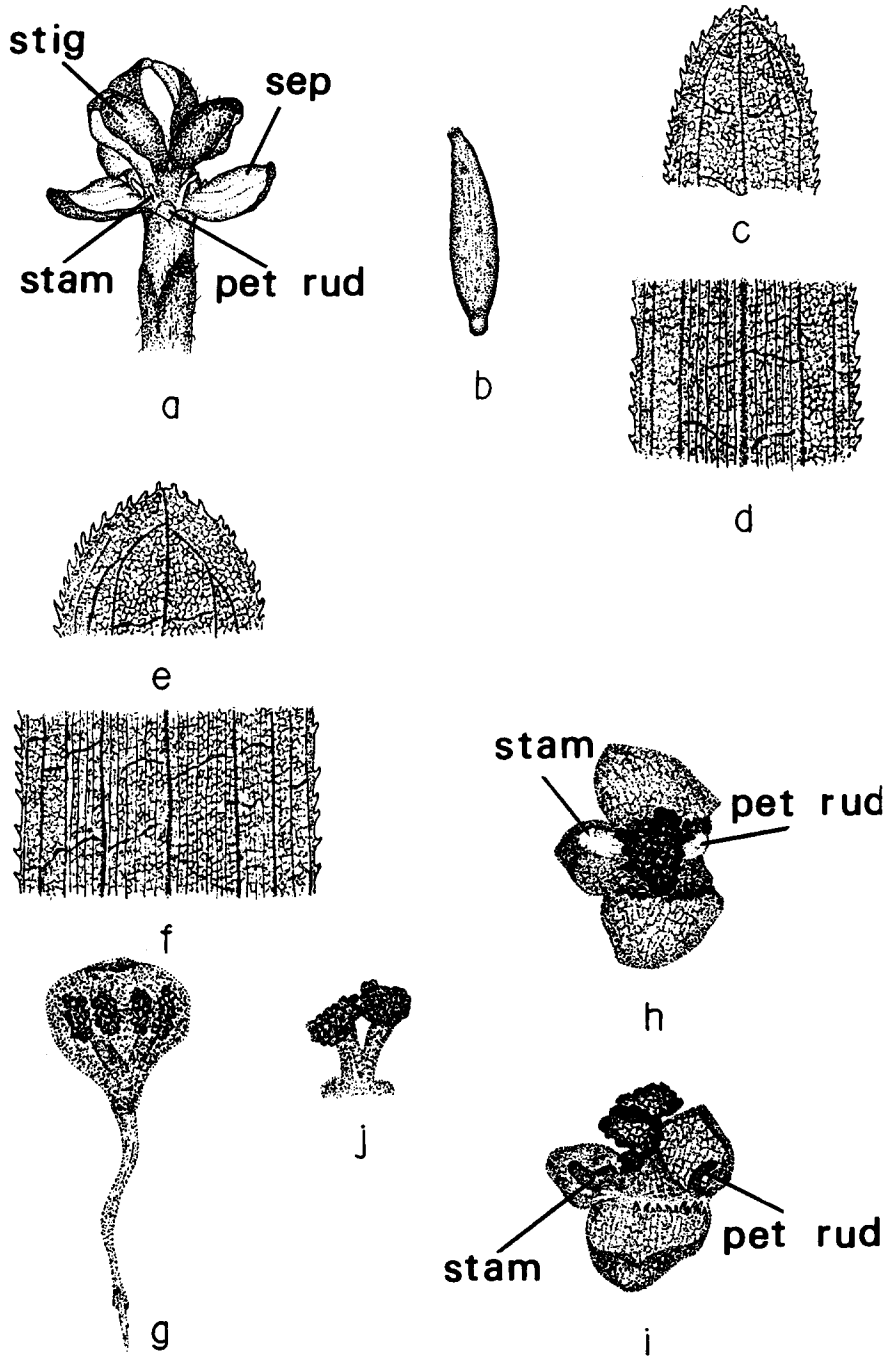
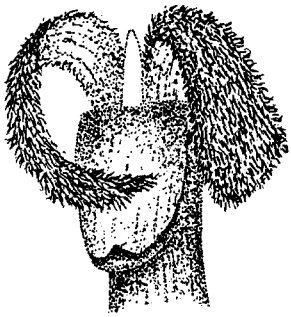


Fig. 1. See caption on p. 279.



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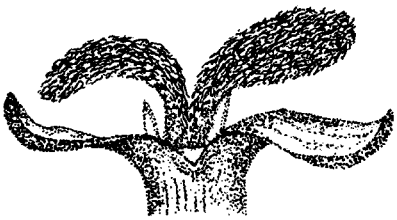

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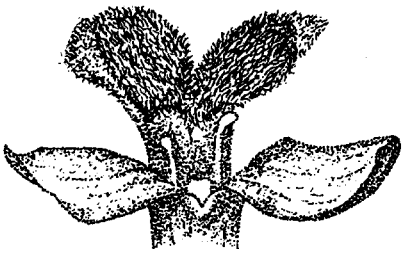

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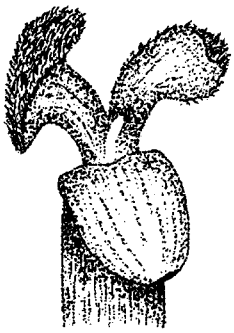

c

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Fig. 2. See caption on p. 279.

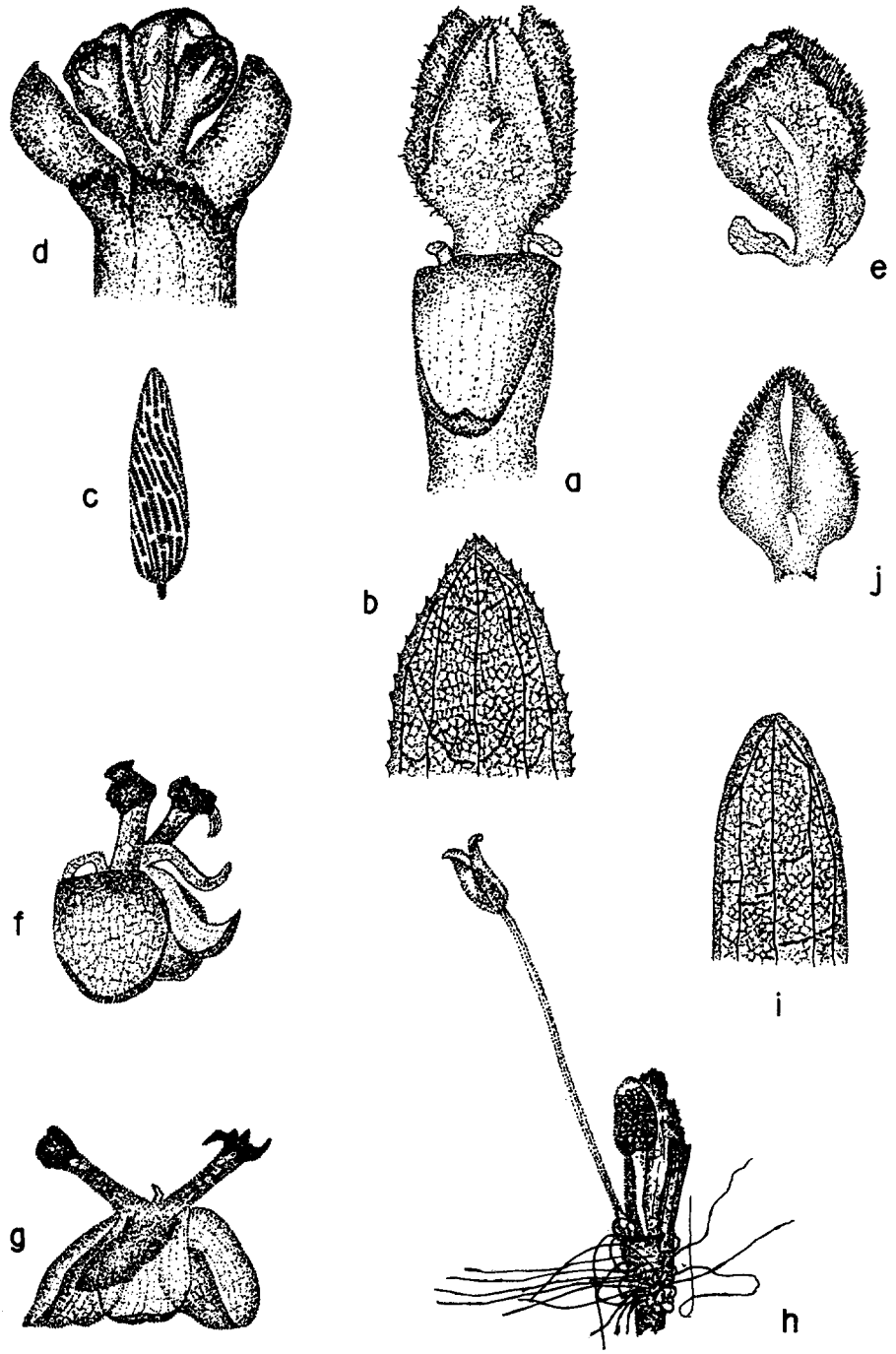


Fig. 3. See caption on p. 279.

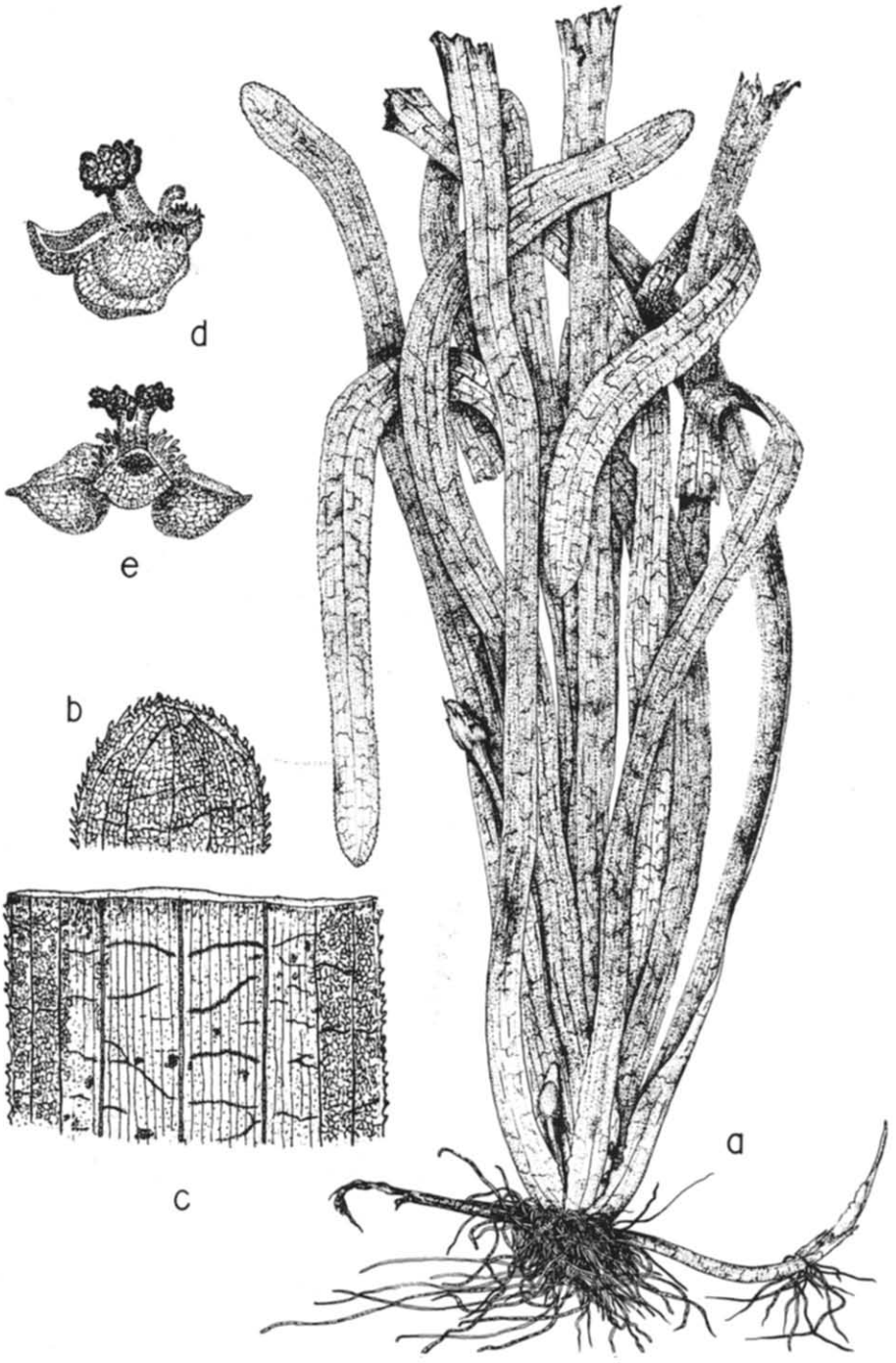


Fig. 4. See caption on p. 279.

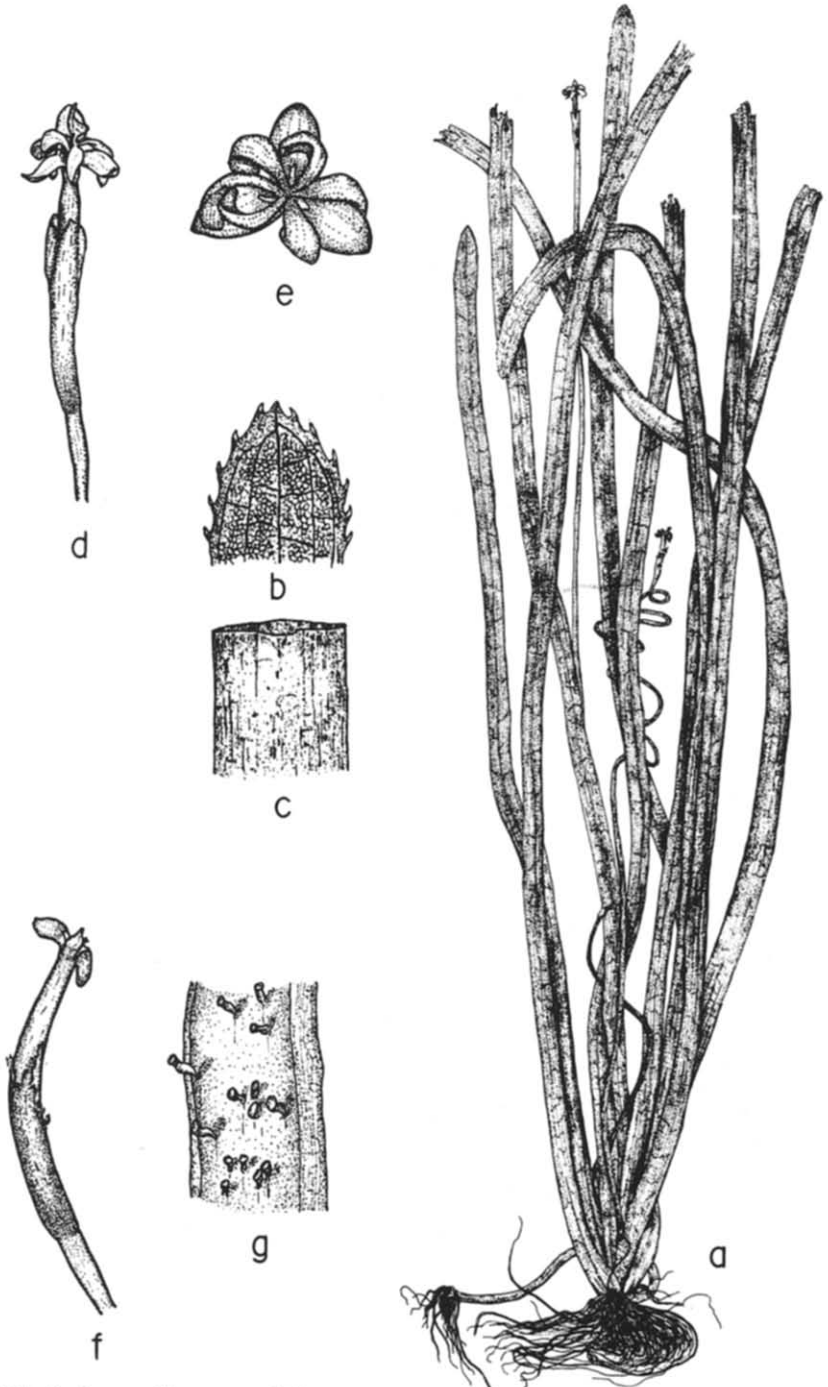


Fig. 5. See caption on p. 279.

sexual flower. The vitality of this bisexual flower is intimated by the similarity of floral whorls found in both sexes and evidenced by the presence of stamen vestiges in all solitary pistillate flowers (Fig. 5e).

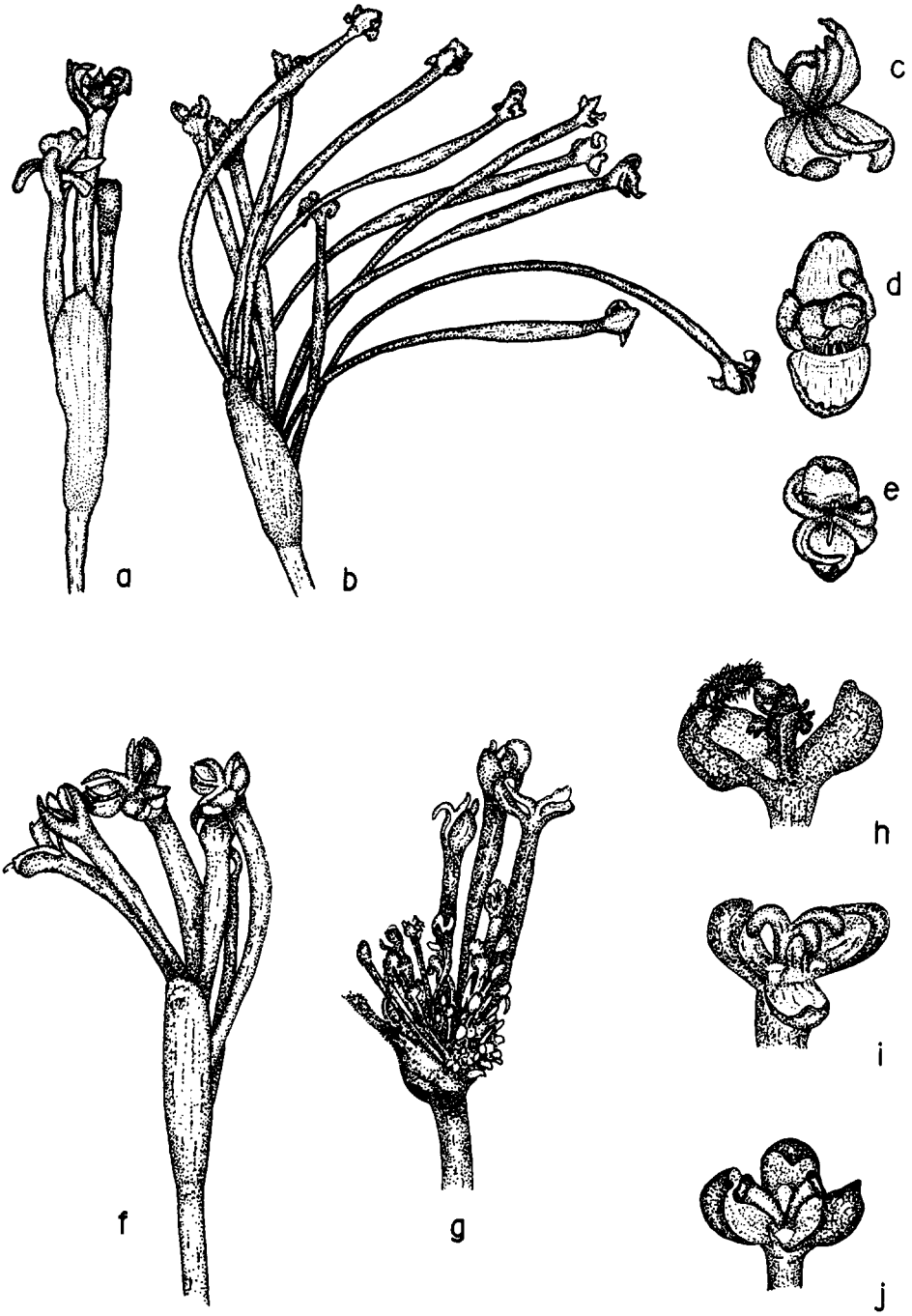
Fig. 1. Leaf, flower and seed organs of *Vallisneria americana* var. *americana*, illustrating pistillate (Ohio (a) and (b) *Lowden 3806*) and staminate (Ohio (g)—(j) East Harbor State Park, *Wehrmeister*) floral structures. (a) A solitary pistillate flower at anthesis showing sepals — petal rudiments — staminodia fused to styles — bifid stigmas — bases of styles united; (b) a young seed, 0.5 mm wide by 2.0 mm long; (c) and (d) a dentate leaf apex and margin (Ohio, *Lowden 3806*); (e) and (f) a conspicuously toothed leaf apex and margin with numerous transverse pigmented striations between prominent longitudinal veins (Texas, *Lowden 3807*); (g) an immature male flower having two bilobed stamens enclosed by calyx lobes; (h) and (i) staminate flowers at anthesis showing sepals — petal rudiments — staminodia (stam) — upright stamens — hairs at androecium base; (j) two basally united filaments with separate pollen masses.

Fig. 2. Pistillate floral portions from solitary flowers of *Vallisneria americana* var. *biwaensis* from Haiti ((a) and (d) *Lowden 3658*), and var. *americana* from Texas ((b) and (e) *Lowden 3807*) and Ohio ((c) and (f) *Lowden 3806*), showing variability in stigma—style surfaces in relation to positions of sepals (a)—(f), staminodia (a)—(f) and petal rudiments (d)—(f); degrees of incision between discordant pairs of stigmatic lobes (a)—(c); bifiding of matching stigmatic lobes (d)—(f); and adnation of staminodia to fused stylar bases (b) and (c), (e) and (f).

Fig. 3. Floral and leaf structures of *Vallisneria spiralis* from France ((a) and (b) *Lowden 3834*, (c) canal Castel-Sarrazin Garonne), Italy ((d) *Lowden 3836*, (e) Porto Toscolano *Landolt & Hauser*, (f)—(i) *Lowden 3835*) and India ((j) *Saldanha 15555*). (a)—(i) *V. spiralis* var. *spiralis*: (a) and (d) solitary female flowers showing sepals — petal rudiments — staminodia apically fused to pairs of fringed stigmatic lobes; (c) a mature striated seed; (e) a staminodium fused near the summit of fringed stigmatic lobes subtended by two petal rudiments; (h) a partially dissected male plant showing a young spadix and a short scape of a dehisced spathe; (f) and (g) staminate flowers with freely extended stamens; (b) a finely serrated leaf apex with visible transverse striations; (i) an entire leaf margin with striations hardly visible; (j) *V. spiralis* var. *denseserrulata* showing a pair of slightly fringed stigmatic lobes fused basally by a staminodium.

Fig. 4. Staminate plant of *Vallisneria americana* var. *biwaensis* from the Dominican Republic (*Lowden 3305*). (a) Habit showing stolons and thick scapes of spadices; (b) a dentate leaf apex; (c) a dentate leaf margin with prominent longitudinal veins and transversal pigmented striations; (d) and (e) staminate flowers at anthesis with united filaments terminating in separate pollen masses and hairs at androecium base.

Fig. 5. Pistillate plant of *Vallisneria americana* var. *biwaensis* from Haiti (*Lowden 3658*). (a) Habit showing coiled and uncoiled scapes of solitary flowers; (b) a toothed leaf apex; (c) the entire margin of a lower leaf segment; (d) a solitary flower subtended by a bivalved spathe; (e) an actinomorphic flower with basally bifid stigmas alternating with awl-shaped staminodia; (f) a curved fruit with remains of perianth and spathe; (g) a portion of an ovary wall showing parietal placentation of ovules.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AN UMBELLATE PROTOTYPE

Umbel and spike-like inflorescences (Fig. 6) were discovered from three distinct geographical localities in the Americas (Figs. 7 and 8). Floral data exist for inflorescences collected at Lake Miragoâne (Haiti) and Lake Petén Itza (Guatemala), whereas the umbels (2, 6, 9 flowered) from Biloxi (Mississippi) were examined superficially at the Paris Museum. These inflorescence types are known on *V. americana* in which their presence accentuates the close affinity existing between varieties of this species. The Miragoâne plant (Figs. 6a—e), *V. americana* var. *biwaensis*, has free staminodia, while the plants from Lake Petén Itza (Figs. 6f—j) and Biloxi, *V. americana* var. *americana*, have staminodia adnate to stylar bases. Identical staminodial conditions were observed in the solitary flowers of female plants growing in the same aquatic ecosystems.

A reduction in the actual floral size and number of parts in floral whorls is quite noticeable in umbel inflorescences (Fig. 6). Perhaps there is some correlation between the formation of inflorescence types and the transition in flower sizes through the formation of unisexual flowers. Umbels from Lake Miragoâne (Figs. 6a and b) have few large normal flowers (Fig. 5e) mixed with smaller female flowers (Figs. 6c—e). These smaller flowers show a change in sexual tendency resulting from a reduction in the number of bilobed stigmas and petal rudiments. Likewise, the number of normal pistillate flowers is few in the umbel to spike-like inflorescences from Lake Petén Itza. As individual flowers become progressively smaller (Fig. 6g) the stigmas are absent (Figs. 6i and j) or reduced to pistillodia (Fig. 6h), and the staminodia are replaced with apparent fertile stamens. A flower (Fig. 6j) was encountered with all the floral parts corresponding to a male flower. This change in the sexual expression of individual flowers within the same inflorescence suggests a monoecious condition.

Apparently, the dioecious state in *Vallisneria* has been derived from an umbellate inflorescence type (Fig. 6) evolving along divergent evolutionary lines in separate plants. The solitary female flower (Fig. 5d) has been formed

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Fig. 6. Variation in the inflorescence structure of *Vallisneria americana* var. *biwaensis* from Haiti ((a)—(e), *Lowden 3671*) and *V. americana* var. *americana* from Guatemala ((f)—(j), *Lowden 3838B*): (a) a 3-flowered umbel with short pedicels enclosed by subtending spathe; (b) a 12-flowered umbel with exserted flower pedicels; (c)—(e) flowers of umbel inflorescences having (c) 2 sepals — 2 petal rudiments (not shown) — 4 staminodia (not shown) — 4 stigmas (two deeply and two slightly bifid), (d) 2 sepals — 2 petal rudiments (not shown) — 4 staminodia (only three shown) — 2 bifid stigmas (segments lobular), (e) 2 sepals — 1 petal rudiment (not shown) — 3 staminodia — 2 bifid stigmas; (f) a 6-flowered umbel with shortened pedicels enclosed by subtending spathe; (g) a numerous flowered spike-like inflorescence; (h)—(j) flowers of spike-like inflorescence having (h) 2 sepals — 1 petal rudiment — 2 staminodia — 1 stigmatic extension with 4 stigmatic lobes (i.e., 2 stigmas), (i) 3 sepals — 3 petal rudiments (only two shown) — 3 staminodia — no stigmas, (j) 3 sepals — 1 petal rudiment — 2 stamens — 1 staminodium — no stigmas.

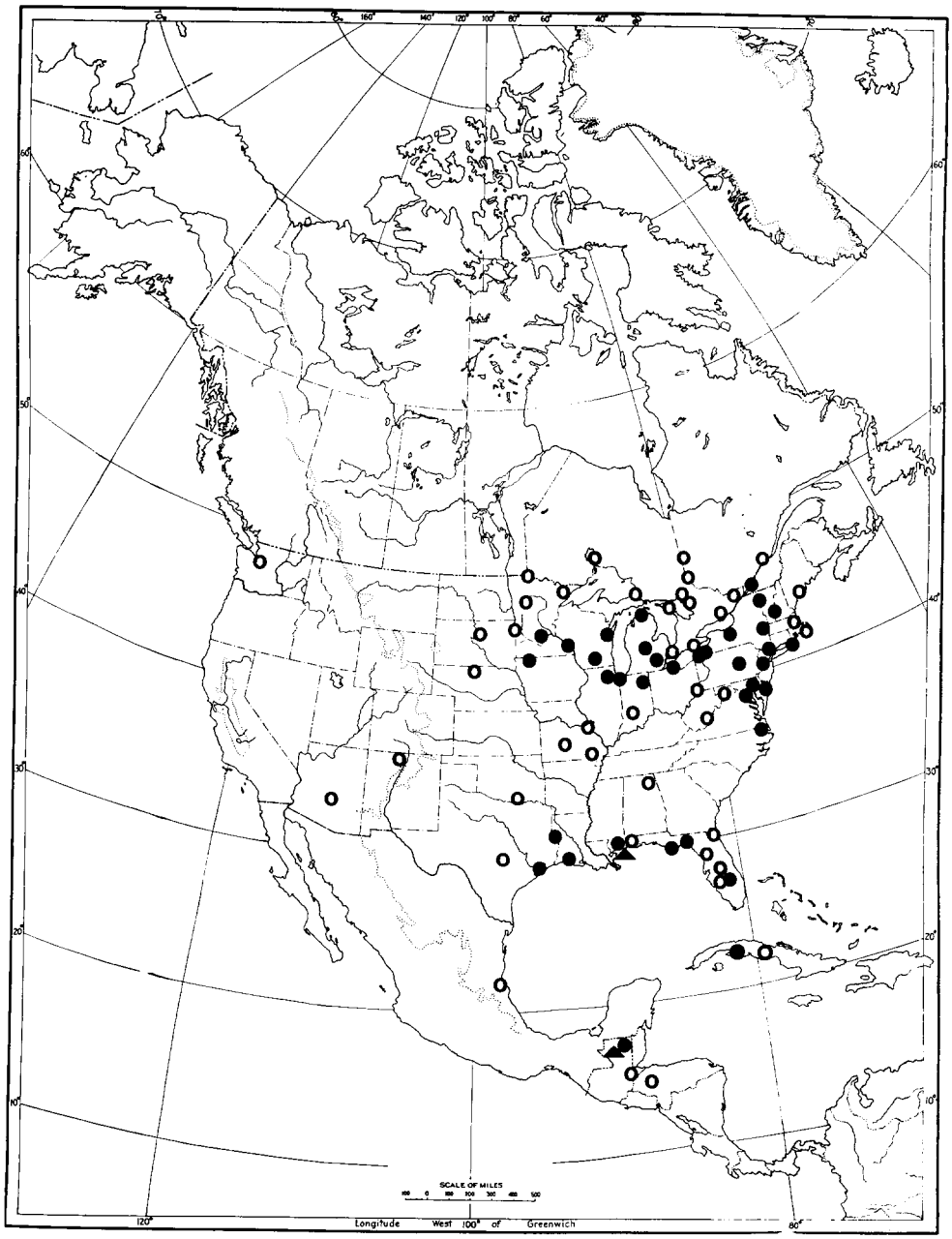


Fig. 7. Distribution of *Vallisneria americana* var. *americana* in North America and the Greater Antilles (Cuba): bisexual populations with solitary female flowers (solid circles), umbel or spike-like inflorescences (triangles; Mississippi, United States and El Petén, Guatemala), and representative unisexual or sterile collections (open circles) to show geographic extension.

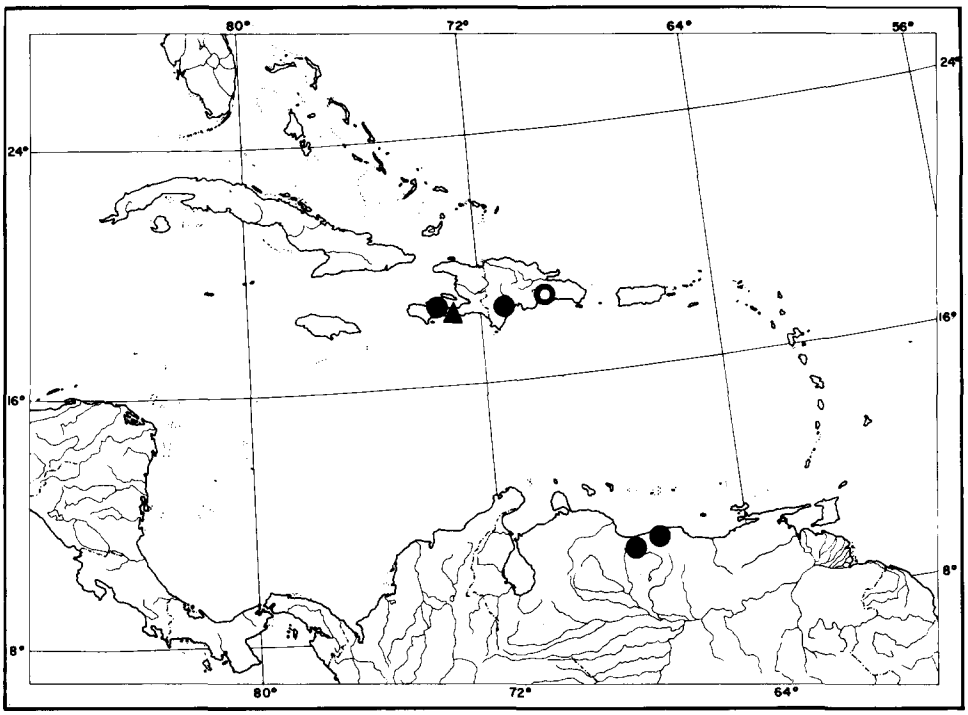


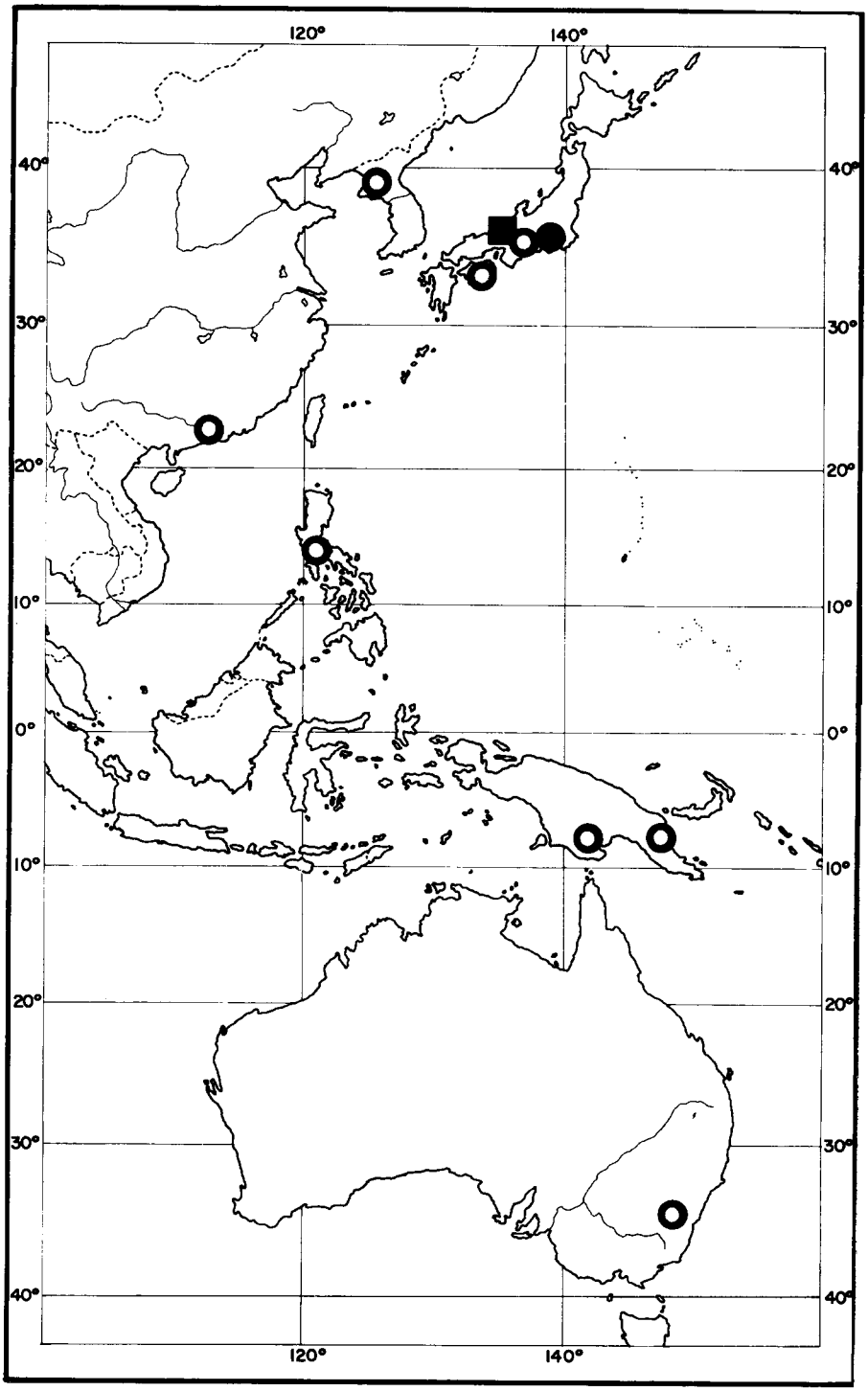
Fig. 8. Distribution of *Vallisneria americana* var. *biwaensis* in the West Indies (Hispaniola) and northern South America: solitary female flowers (solid circles; Haiti, Dominican Republic, Venezuela), female umbel inflorescences (triangle; Haiti) and a male population (open circle; Dominican Republic).

by a complete reduction in number of flowers, meanwhile the spadix inflorescence in the male plant (Fig. 4a) has suffered little reduction in flower number other than a reduction in floral size and pedicel length.

TAXONOMY AND GEOGRAPHY

Vallisneria L., Sp. Pl. 1015. 1753
Physkium Lour., Fl. Cochinch. 662. 1790; Moore, J. Bot., 63: 290—291. 1925.

Dioecious, freshwater perennial aquatic plants. Roots fibrous (Fig. 5a). Leaves submerged or floating, longest 214 cm, linear, strap to tape shaped. Vertical stem axis short, bearing runners (Fig. 4a). Staminate Plant: Spadix with numerous, minute imperfect flowers enclosed by a dehiscing two-valved, reflexed spathe (Fig. 3h); scapes short (Fig. 4a); flowers (Figs. 1h and i) with three sepals (two larger, one smaller), one minute petal rudiment, one staminodium and two stamens (sometimes filaments united and stamens thus appearing to be one) (Figs. 1j and 3g). Pistillate Plant: Inflorescence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30°
40°

subtended by a bivalved spathe (Fig. 1a); scapes long, extended to spirally coiled (Fig. 5a). Flowers solitary (Figs. 1a and 5d and e) with three sepals, three minute transparent petal rudiments, three staminodia and three bifid stigmas borne on short or highly reduced styles; or flowers numerous in umbel to spike-like inflorescences, floral parts varying in number and form (Fig. 6). Ovary inferior (Fig. 5d), unilocular; fruit elongate, approx. 9.5—10.0 cm long, ellipsoid, indehiscent (Fig. 5f); placentation parietal (Fig. 5g); seeds numerous, ellipsoid, striate, 1.3—2.0 mm long (Figs. 1b and 3c); endosperm absent.

Type species: *Vallisneria spiralis* L.

Distribution: Widely distributed in eastern North America, Greater Antilles, Europe, Africa, Asia, Oceania and Australia (Figs.7—10). There are two closely related species, each having two varieties.

Key to species and varieties

(1A) Stamens of staminate flowers free and obliquely extended; hairs absent at base of androecium (Fig. 3g); floral incision of pistillate flowers deepest between matching stigmatic lobes (opposite the petal rudiments), stigmas fringed (Figs. 3a, d and j). (1) *V. spiralis*
- (2A) Staminodia of pistillate flowers adnate to the shallowly cleft apex of the fused stigmatic lobes (Fig. 3a) . . . (1a) *V. spiralis* var. *spiralis*
- (2B) Staminodia of pistillate flowers adnate to the deeply cleft base of the fused stigmatic lobes (Fig. 3j) . . . (1b) *V. spiralis* var. *denseserrulata*

(1B) Stamens of staminate flowers upright with partially or totally united filaments; hairs at base of androecium (Fig. 4e), floral incision of pistillate flowers deepest between discordant stigmatic lobes (opposite the sepals) (Fig. 2c and f), or equal to incision between matching stigmatic lobes (Figs. 2a and d), stigmas not fringed. (2) *V. americana*
- (3A) Staminodia of pistillate flowers adnate to styles (not to stigmas) (Figs. 2e and f) . . . . . (2a) *V, americana* var. *americana*
- (3b) Staminodia of pistillate flowers free between stigmas with reduced styles (Figs. 2a and d) . . . . . .(2b) *V. amerixana* var. *biwaensis*

1. **V. spiralis** L., Sp. Pl. 1015, 1753.

Leaves (Figs. 3b and i) narrow, generally less than 10 mm wide, with three to five nerves, margins entire to finely toothed, blades with perceivable to in-

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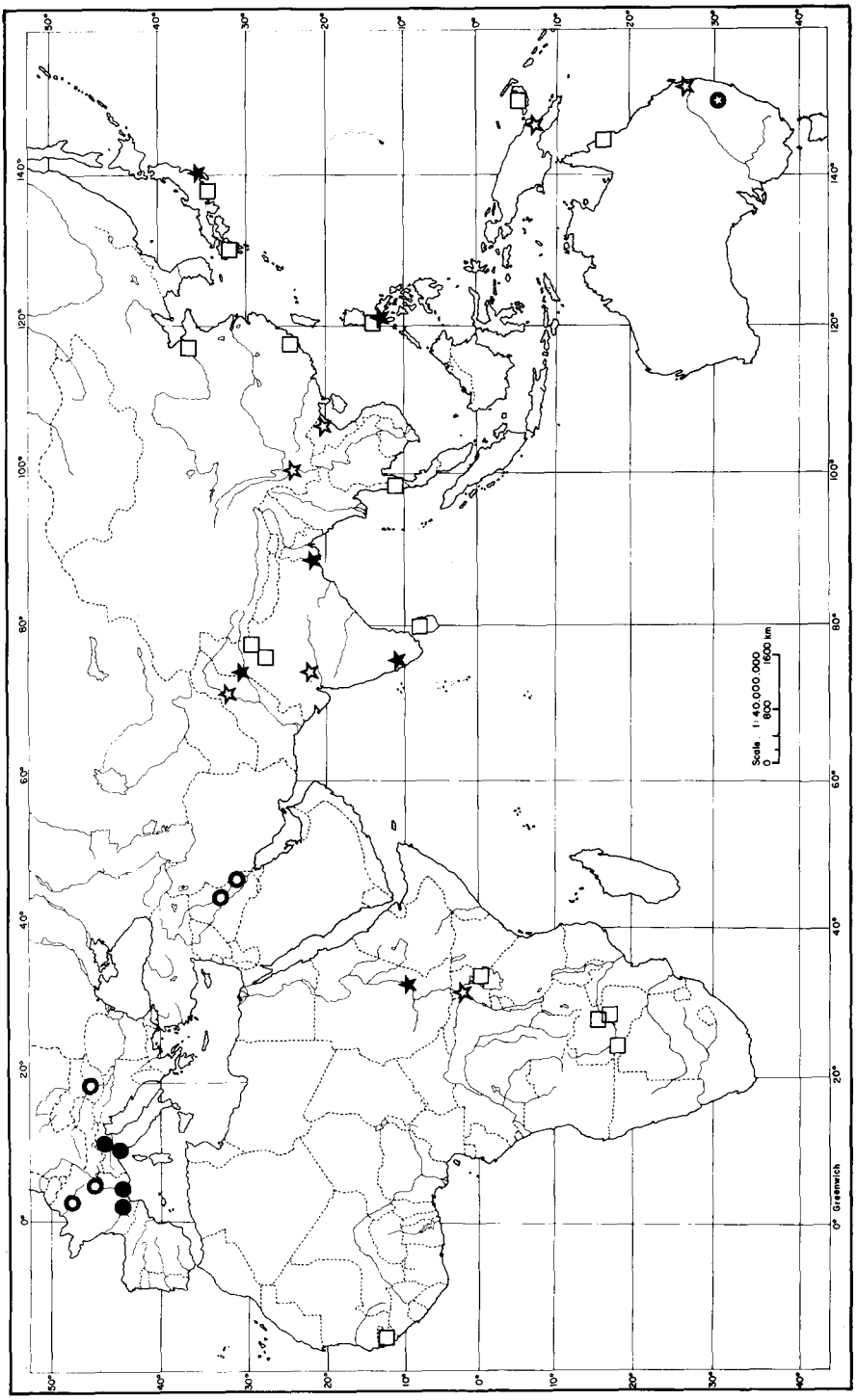
Fig. 9. Distribution of *Vallisneria americana* in east and south-east Asia, Oceania and Australia: *V. americana* var. *americana*, bisexual (solid circle; Japan) and female collections (open circles; Japan, Korea, China, Philippines, Papua New Guinea, Australia); *V. americana* var. *biwaensis*, a bisexual population (square; Japan).


Scale 1:40,000,000
0 800 1600 km
0° Greenwich

visible transverse pigmented striations (of freshwater inland waterways and lakes). Staminate Plant: Scapes (Fig. 3h) thin, 1.0—1.3 mm wide, 10—30 mm long; flowers (Figs. 3f and g) slightly zygomorphic, 0.9—1.1 mm wide (spread of two larger sepals), with obliquely extended stamens, hairs absent at base of androecium (Figs. 3f and g). Pistillate Plant: Staminodia (Fig. 3a) small-inconspicuous, adnate to fused discordant stigmatic lobes; stigmas fringed (Figs. 3a, e and j); floral incision (Figs. 3a and d) deepest between matching stigmatic lobes; flowers solitary (Fig. 3d), slightly zygomorphic, sepals 2.0—3.5 mm long (spread at anthesis 3.0—3.5 mm).

Distribution: The species has two varieties, one occurring in Europe and south-west Asia and the other in Africa, Asia, Oceania and Australia (Fig. 10).

(1a) **Vallisneria spiralis** L. var. **spiralis**

Probable synonyms:

V. michelii Savi, Oss., 11. 1816.
V. jacquini Savi, Oss., 12. 1816.
V. micheliana Spreng., Syst., 3: 900. 1826.
V. jacquiniana Spreng., Syst., 3: 900. 1826.
V. pusilla Barbieri, ex Bertol. Fl. Ital., 299—300. 1854.

Pistillate Plant: Staminodia adnate near the apex of fused stigmatic lobes (Fig. 3a). Fused discordant stigmatic lobes shallowly cleft and conspicuously fringed (Figs. 3d and e).

Distribution: See Fig.10.

Reports of *Vallisneria* from Denmark (Jørgensen, 1927; Winge, 1927) and England (Harris and Lording, 1973) probably represent the alien extension of this variety in northern Europe. In the West Indies the female plant has been introduced.

Representative specimens: **EUROPE. France.** Arles (female MO; male MO, NY).* Toulouse vicinity, Canal Languedoc, south-east of Castelnaudary, 31 Aug. 1978, *Lowden 3833—3834* (female and male UCMM). Saône River: Lyon, *Jordan* (female US) and 18 Aug. 1849, *Chabert* (female NY); Seurre, Aug. 1861, *Moniez* (female F); Doubs, 29 Sept. 1867, *Paillot* (female NY). Paris: Bois de Boulogne, 13 Sept. 1897, *Jeanpert* (female F); Vigneux, 15 Oct. 1911, *Jeanpert* (female F). **Hungary.** Budapest: Aquincum, 1 Oct.

*For explanation of herbarium abbreviations, see Acknowledgements.

Fig. 10. Distribution of *Vallisneria spiralis* in the Eastern Hemisphere: *V. spiralis* var. *spiralis* in Europe and south-west Asia — bisexual populations (solid circles; France, Italy) and female collections (open circles; France, Hungary, Iraq); *V. spiralis* var. *denseserrulata* in Africa, Asia, Oceania and Australia — bisexual populations (solid stars; White Nile (Sudan), India, Philippines, Japan), female collections (open stars; Uganda, Pakistan, India, China, Vietnam, Papua New Guinea, Australia) and a male collection (circled star; Australia). (Squares represent the geographic extension of the genus based on indeterminate collections from Africa (Uganda, Botswana, Zambia, Rhodesia, Senegal), India, Sri Lanka, Burma, China, Japan, Philippines, Papua New Guinea and Australia.)

1910 and 31 July 1911, *Kümmerle, Jávorka & Szurák 89* (female F, GH, MO, US) and 5 Aug. 1922, *Vestergren* (female GH, MO); Thermas Romanas, June 1914, *Lengyel* (female GH). **Italy.** Pisano, Aug. 1816 (female GH, NY; male F, GH, NY) and 1860, *Savi* (female MO, US); Pisa, 1840—1841 (female and male GH). Lake Garda, Gardone Riviera, 2 Sept. 1978, *Lowden 3835—3836* (female and male UCMM). **SOUTHWEST ASIA. Iraq.** Bagdad, June 1850 (female P); Howear Canal, Amara liwa, 21 Sept. 1964, *Barkley, Khanam & Sabbar 89* (female GH). **WEST INDIES. Cuba.** Province Ciudad de la Habana: Estación Experimental Agronómica, cultivated, 2 May 1955, *Acuña* (female HAC). **Jamaica.** Parish Hanover: Lucea, cultivated, 10 Apr. 1955, *Proctor 10002* (female IJ, NY).

(1b) **V. spiralis** L. var. **denseserrulata** Makino, Bot. Mag. Tokyo, 28: 27. 1914; Miki, Bot. Mag. Tokyo, 48: 330, Fig. 4Q—W 1934. Type: Japan, Prov. Shimoosa, Sakura, 10 Sept. 1895, T. Makino.

Probable synonyms:

Physkium natans Lour., Fl. Cochinch., 663. 1790. Type: Indochina, 'Cochinchinâ' (British Museum, London).

V. physcium Juss. ex Spreng., Syst., 3: 900. 1826.

V. spiraloides Roxb. in Roxburgh, Fl. Ind., 3: 750. 1832.

V. minor Royle, Illustr. Bot. Himal., 377. 1839.

V. aethiopica Fenzl, Flora, 19: 311. 1844; Sitzb. Akad. Wien, Math.-Nat., 51 (abt. 1): 139. 1865.

V. numidica Pomel, Nouv. Mat. Fl. Atl., 386. 1874.

V. denseserrulata (Makino) Makino, J. Jpn. Bot., 2: 19. 1921.

V. natans (Lour.) Hara [var. *natans*], J. Jpn. Bot., 49: 136. 1974.

Pistillate Plant: Staminodia adnate near the base of fused stigmatic lobes (Fig. 3j). Fused discordant stigmatic lobes deeply cleft and inconspicuously fringed (Fig. 3j).

Distribution: See Fig. 10.

Leaves are conspicuously toothed in African and Japanese specimens.

Voucher Specimens: **AFRICA. Sudan.** White Nile, *Schweinfurth 1017* (male GH) and *1043* (female GH). **Uganda.** Junction of Victoria Nile and Lake Albert, 10 Feb. 1935, *Taylor 3357* (female MO). **ASIA. Bangladesh.** Jessore, 8 Nov. 1896, *Mokim* (male US). **China.** Province Yunnan: K'un-ming, Apr. 1935, *Wang 62748* (female GH); Lac de Yunnan sen (Yunnansheng), 9 Sept. 1903, *Ducloux 2219* (female P). **India.** State Karnataka, Hassan District: Nagpuri, 18 Nov. 1969, *Saldanha 15555* (female MO, US); Hole Narsipur, 9 Apr. 1970, *Saldanha 16714* (female US); Bindenahalli, 9 Mar. 1971, *Ramamoorthy HFP1418* (female MO, US) and *HFP1419* (male US); Halbag, 26 Nov. 1971, *Hooper & Saldanha HFP2563* (female MO, US). State Punjab: Gurdaspur, 3 Mar. 1917, *Stewart 1362* (female MO, US). State West Bengal: Calcutta, Botanical Garden (male NY), 24 Nov. 1884 (female NY) and 28—29 Nov. 1884 (female NY). **Pakistan.** Province Punjab: Sialkot, 20 Dec. 1916, *Stewart 586* (male NY); Campbrelpur (Campbellpore) District, 2 May 1925, *Stewart 7763* (female NY). **Philippines.** Luzon Island, Province Laguna: Los Baños, 17 Mar. 1906, *Merrill 5117* (male US); Santa Maria Mavitac, Feb. 1908, *Curran 8854* (female US) and Feb. 1910, *Curran 19274* (female US). **Vietnam.** Tonkin: Hanoi, Grand Lac, Dec. 1921, *Pételot 305* (female NY, P). **Japan.** 'Prov. Shimoosa: Sakura' (Makino, 1914); (H. Hara, University of Tokyo, personal communication, 1980). **OCEANIA. Papua New Guinea.** District Morobe, near Lae, 18 and 20 Aug. 1958, *Henty*

10558 (female GH, US). **AUSTRALIA. New South Wales.** Mechi River, Moree, 27 Feb. *Cheel 573* (male GH). Queensland. Moreton District, Laidley Lagoon, 27 Mar. 1960, *Thorne & Trapnell 25630* (female MO, NY).

2. **V. americana** Michaux, Fl. Bor. Am., 2: 220. 1803. Type: United States, 'flumine Mississipi' (Lectotype P!, Herb. Michaux).

Probable synonyms:

V. minor K. Ito, Nippon Shokubutsu Dzusetsu, I., fol. 23 verso. 1874.

V. gigantea Graebn., in Engl. Jahrb., 49: 68. 1912 Type locality: Papua New Guinea.

V. asiatica Miki, Bot. Mag. Tokyo, 48: 329. 1934.

V. gigantea Graebn. sensu Kitamura, Acta Phytotax. Geobot., 22: 74. 1966.

P. natans Lour. sensu Hara, J. Jpn. Bot., 49: 136. 1974.

Leaves narrow (Figs. 1c and d), less than 10 mm wide, from three to five nerves, margins entire to finely toothed (Figs. 5a—c), blades with perceivable to invisible transverse pigmented striations (of freshwater inland waterways, lakes and lagoons); or leaves broad (Figs. 1e and f and 4a—c), 10—25 mm wide from five to nine nerves, margins conspicuously toothed, blades with many visible transverse pigmented striations (of coastal freshwater inlets or waterways subject to year round constant temperatures of underground springs with possible brackish water movement at high tide). Staminate Plant: Scapes thick (Fig. 4a), 1.5—5.0 mm wide, 30—160 mm long; flowers (Figs. 1g—i) zygomorphic, 1.0—1.4 mm wide (spread of two larger sepals); upright stamens with united filaments (Figs. 1j and 4e); inconspicuous transparent hairs at base of androeccium (Fig. 4e). Pistillate Plant: Staminodia (Figs. 2a—c) large, conspicuous, free from stigmas with reduced styles (Figs. 2a and d) or adnate to fused stylar bases of discordant stigmatic lobes (Fig. 1a); floral incision deepest between discordant stigmatic lobes (Fig. 2f) or clefts equal between stigmatic lobes (Figs. 2a and d). Flowers solitary (Fig. 5d) or in umbel- to spike-like inflorescences (Fig. 6); sepals 3.5—6.5 mm long (spread at anthesis 5.5—9.5 mm).

Graebner (1912) distinguished between *V. gigantea* and *V. spiralis*. He considered the Indian plant to be *V. spiralis* (i.e. *V. spiralis* var. *denseserrulata*) and specified that *V. gigantea* does not occur in India (Coromandel). Some collections were cited by Graebner from the Philippines (Luzon) and Papua New Guinea (Huon Gulf). Curran's specimen no. 8854 from the Laguna Province (Luzon) comprises a mixed female collection of *V. spiralis* var. *denseserrulata* and *V. americana* var. *americana*. Female plants of both varieties have been examined from the Morobe District, near Lae (Papua New Guinea).

In Flora Malesiana, Den Hartog (1957) recognized *V. gigantea* based on styles split into broad flattened non-fringed lobes to near the base, leaves

wide with five to nine nerves and margins faintly dentate. These characters are in contrast with *V. spiralis* having styles fringed, leaves relatively narrow with five nerves and margins entire. Allusion was made to a size resemblance between *V. gigantea* and *V. neotropicalis* (i.e. *V. americana* var. *americana*).

Apparently, no decisive morphological relation exists between *V. spiralis* and *V. gigantea*. Nonetheless, *V. americana* agrees with the descriptions of pistillate Papuan and Malaysian plants. This relation is confirmed in female plants having styles split to near the base into non-fringed lobes and broad leaves.

Distribution: The species has two varieties, one occurring in the Americas, East and Southeast Asia, Oceania and Australia; the other occurs in Japan, Hispaniola and Venezuela (Figs. 7—9).

(2a) **Vallisneria americana** Michaux var. **americana**

Probable synonyms:

V. spiralis L. var. *americana* (Michaux) Torrey, Compendium Flora Northern and Middle States, 365. 1826.

V. spiralis L. forma *minor* Makino, Bot. Mag. Tokyo, 28: 26. 1914.

V. spiralis L. var. *wylii* Chodat, Les Plantes Aquatiques, 255 (Fig. 146). 1917.

V. spiralis L. var. *subulispatha* Makino, J. Jpn. Bot., 7: 6. 1931.

V. spiralis L. var. *subulispatha* Makino, forma *minor* (Makino) Makino, J. Jpn. Bot., 7: 6. 1931.

V. asiatica Miki [var. *asiatica*], Bot. Mag. Tokyo, 48: 329, 330 (Fig. 4A—F), 332 (Fig. 5A). (May) 1934.

V. asiatica Miki var. *higoensis* Miki, Bot. Mag. Tokyo, 48: 330 (Fig. 4L—P), 331, 332 (Fig. 5C). (May) 1934. Type: Japan, Kiushu Prov. Higo, Edzuko, 29 Apr. 1927, S. Miki.

V. subulispatha (Makino) Koidzumi, Acta Phytotax. Geobot., 3: 147. (Oct.) 1934.

V. neotropicalis Marie-Victorin, Contrib. Inst. Bot. Univ. Montréal, 46: 34. 1943. Type: West Indies: Cuba: Province Matanzas: Cienaga de Zapata, Río Negro, 24 Feb. 1941, *F. Marie-Victorin, F. León, F. Alain & L.R. Rivas 19552* (Holotype MT!; isotypes GH!, NY!).

V. higoensis (Miki) Ohwi, Bull. Nat. Sci. Mus. Tokyo, 26: 1. 1949.

V. gigantea Graebn. var. *higoensis* (Miki) Kitamura, Acta Phytotax. Geobot., 22: 74. 1966.

V. natans (Lour.) Hara var. *higoensis* (Miki) Hara, J. Jpn. Bot., 49: 136. 1974.

Staminate Plant: Filaments of stamens partially connate (Fig. 1j), few transparent hairs at base of androecium (Fig. 1i). Pistillate Plant: Staminodia adnate to fused stylar bases (Figs. 2e and f). Flowers solitary, slightly zygo-

morphic (Fig. 1a), or rarely a 3—60 flowered umbel to spike-like inflorescence with regular—irregular flowers varying in size and degree of sexual determination (Figs. 6f—j).

Distribution: See Figs. 7—9.

In North America *V. americana* var. *americana* has been reported recently in the western United States (Fig. 7; Washington, Nebraska, New Mexico, Arizona). The sterile specimens from Lake Yoyoa, Honduras (Central America) are presumed to be this variety. In the Greater Antilles, Cuba is a possible region where biological convergence might occur between *V. americana* var. *americana* and *V. americana* var. *biwaensis*.

Voucher specimens (umbel- to spike-like inflorescences): **UNITED STATES OF AMERICA. Mississippi.** Jackson Co., Biloxi, Sept. 1849, *Trécul* (female P). **MIDDLE AMERICA. Guatemala.** Department el Peten: Lake Petén Itza, Flores, 28—29 Dec. 1978, *Lowden 3838B* (female—male, UCMM).

Representative specimens (dioecious plants): **EAST AND SOUTHEAST ASIA. China.** Kwangtung Province: Canton vic., 12 Dec. 1917, *Levine 1933* (female GH, MO, US). **Korea.** Pyongyang, 7 Oct. 1937, *Smith* (female GH). **Japan.** Honshu Island: Prefecture Kanagawa, Yokohama, 1862, *Maximowicz* (female GH, NY, US; male GH, NY); Prefecture Mie, Nagara river, Kuwana, 3 Oct. 1964, *Shimizu 14616* (female NY, US). Shikoku Island: Prefecture Kochi, Tokano, Tosa, 16 Sept. 1894 (female US). **Philippines.** Luzon Island: Province Bulacan, Calumpit, 15 Jan. 1915, *Ramos-Merrill 667* (female GH, MO, NY, P, US); Province Laguna, Santa Maria Mavitac, Feb. 1908, *Curran 8854* (female US). **OCEANIA. Papua New Guinea.** Lake Daviumbu, Middle Fly River, Sept. 1936, *Brass 7639* (female GH). Morobe District: Kajabit Mission vicinity, Aug.—Dec. 1939, *Clemens 10856* (female GH); Lake Wanum, 2 May 1959, *Brass 29370* (female GH, NY, US). **AUSTRALIA. New South Wales.** Strahorn State Forest, Mungery, north-west of Peak Hill, 30 Sept. 1951, *Constable 17565* (female MO). **CANADA. Province Ontario**: Lake Nipigon, Shakespeare Island (Marie-Victorin, 1943); Lake Superior, Batchawana Island, 10 Sept. 1935, *Taylor 1455* (male GH); Lake Huron, Manitoulin Island, Little Current, 28 July 1932, *Grassl 2050* (female NY); Georgian Bay, Hemlock Island, Parry Sound, 26 July 1942, *McDonald 263* (female US); Lake Crowe, north-east of Marmora, 6 Aug. 1952, *Gillett 6758* (female NY). **Province Quebec.** Chambly Co., St-Laurent: near Montréal, 3 Sept. 1827, *Jacquemont* (female and male P); Montréal-Sud, 6 Sept. 1943, *Rouleau 43020* (female MO, NY, US; male F); Ile Charron, 26 Aug. 1978, *Lowden & Rouleau 3831—3832* (female and male UCMM). Champlain Co.: Batiscan, 19 July 1941, *Raymond 1072* (sterile GH). Temiscaming Co.: Ville Marie, L. Laperriere, 13 Sept. 1952, *Baldwin & Breitung 4521* (female GH). **UNITED STATES OF AMERICA***. **Alabama.** Mobile Co. Jackson Co. **Arizona.** Maricopa Co. **Delaware.** Sussex Co.: Rehoboth City, 17 Aug. 1878, *Parker* (female NY); Burton's Pond, south-west of Rehoboth Beach, 25 June 1942, *McVaugh 6541* (female and male F, GH, NY). **District of Columbia.** Chesapeake and Ohio Canal, near Georgetown, 22 July 1923, *Muenscher 3615* (female and male MO). **Florida.** Citrus Co. Desoto Co. Duval Co. Franklin Co.: Apalachicola, *Chapman* (female and male MO; female F, NY), 1846 (female and male GH). Lee Co. Marion Co. Okeechobee Co.: Kissimmee River, north of Lake Okeechobee, 11—25 Nov. 1913, *Small 4384* (female US, male GH). Polk Co. Wakulla Co.: St. Marks River, above Newport, *Lowden & Godfrey 3812* (female and male UCMM) and Wakulla River, 3813 (male UCMM). **Illinois.** Dupage

*Only specimens representing localities with the two sexes in the United States (Fig. 7, solid circles) are cited here along with state and county names for unisexual—sterile collections (Fig.7, open circles).

Co.: DuPage River, Naperville, 25 July 1896, *Umbach* (female and male US). Kane Co.: Fox River, Aurora, 22 July 1896, *Umbach* (female and male F). **Indiana.** Elkhart Co. Lake Co., Wolf Lake: 3 Sept. 1900, *Chase 1470* (female F); 1 Sept. 1908, *Greenman 2734* (female MO); 1910, *Greenman* (male GH); 18 Aug. 1920, *Peattie* (female GH). Monroe Co. Whitley Co.: Blue Lake, north-west of Fort Wayne, 22 Aug. 1978, *Lowden 3829—3830* (female and male UCMM). **Iowa.** Clay Co.: Trumbull Lake, 19 Aug. 1940, *Hayden 9677—9678* (female and male MO, NY). Dickinson Co.: East Lake Okoboji, 1 Aug. 1896, *Shimek* (female and male F; male MO); Spirit Lake, Aug. 1901, *Shimek* (female and male MO, NY, US). **Louisiana.** Cameron Parish: Lacassine Wildlife Refuge, 12 Aug. 1978, *Lowden 3820—3821* (female and male UCMM). Sabine Parish: south-east of Toledo Bend Reservoir, 11 Aug. 1978, *Lowden 3818—3819* (female and male UCMM). **Maine.** Sagadahoc Co. **Maryland.** Chesapeake Bay Region, south of Mill Creek and west of Northeast River, 31 July 1902, *Shull 139* (male GH) and mouth of Mill Creek, *Shull 142* (female GH, MO, US). **Massachusetts.** Dukes Co. Middlesex Co. Nantucket Co. Norfolk Co. **Michigan.** Cheboygan Co., Douglas Lake: North Fishtail Bay, 8 Aug. 1919, *Ehlers 845* (female MO); 10 Aug. 1942, *Braun* (female US); South Fishtail Bay, 20 Aug. 1953, *Wood 8296* (female GH); (male; R.R. Haynes, University of Alabama, personal communication, 1978). Gratiot Co.: Alma, 11 Aug. 1893, *Davis* (female GH, US; male NY). Washtenaw Co.: Whitmore Lake, north of Ann Arbor, Sept. (female and male; E.G. Voss, University of Michigan, personal communication, 1978). **Minnesota.** Clearwater Co. Hennepin Co.: Navarre, Lake Minnetonka, 18 Aug. 1929, *Oosting 2963* (female F); Christmas Lake (female and male; Hill, 1965). Jackson Co.: Loon Lake, south of Jackson, 2 Aug. 1922, *Metcalf 1939* (female US; male GH, US). Lake of the Woods Co. Nicollet Co. St. Louis Co. Sherburne Co. Winona Co.: Winona, Aug. 1889, *Holzinger* (female and male US). **Mississippi.** Jackson Co., Ocean Springs: 9 Sept. 1895, *Skehan* (female GH, MO); Old Fort Bayou, 14 Aug. 1978, *Lowden 3822—3823* (female and male UCMM). **Missouri.** Butler Co. Phelps Co. St. Louis Co. **Nebraska.** Cherry Co., (Churchill et al., 1976). **New Hampshire.** Sullivan Co., Connecticut River, Charlestown: 23 Aug. 1963, South Charleston, *Seymour 21060* (female MO); 9 Aug. 1965, *Seymour 23085* (male MO). **New Jersey.** Mercer Co., Princeton, *Holton* (female NY); Princeton Depot Canal, 30 Aug. 1847, *Holton* (female and male F). **New Mexico.** Rio Arriba Co. **New York.** Cayuga Co., Cayuga Lake: Farley's Point, 21 Aug. 1922, *Fernald & Wiegand 14549* (male GH, NY, US) and *14550* (female NY, US); Carr's Cove, 19 Aug. 1978, *Lowden 3826* (female and male UCMM); Cayuga Village, 19 Aug. 1978, *Lowden 3824—3825* (female and male UCMM). Chautauqua Co., Bemus Point, Lake Chautauqua, 7—8 Aug. 1896, *Churchill* (female MO; male GH, MO). Oswego Co.: Salmon River, Selkirk, 24 Aug. 1922, *Fernald, Wiegand & Eames 14129* (male NY, US) and *14130* (female GH, US). Suffolk Co., Montauk: Long Island, 12 Sept. 1920, *Ferguson 2* (female NY); Fort Pond, 18 Aug. 1938, *Muenscher & Curtis 6782* (female and male NY). Westchester Co.: Peekskill, 21 Aug. 1879, *LeRoy* (male NY); Roa Hook, Peekskill Creek, Hudson River, 22 Aug. 1936, *Muenscher & Curtis 5581* (female GH). **North Carolina.** Perquimans Co., Perquimans River: west of New Hope, 26 Aug. 1952, *Radford 6526* (male NY, US), near Suttons Creek, *6531* (male GH) and *6533* (female GH, NY, US; male US). (Bourn, 1934). **Ohio.** Sandusky Bay; 21 Sept. 1894, *Moseley* (female MO) and Aug. 1898, *Pieters* (male US). Ottawa Co.: East Harbor State Park, 25 July 1977, *Wehrmeister* (female and male UCMM); Put-in-Bay, 3 Aug. 1977, *Lowden & Wehrmeister 3805* (male UCMM) and 16 Aug. 1977, *3806* (female and male UCMM). **Oklahoma.** Bryan Co. **Pennsylvania.** Erie Co., Presque Isle, Erie; 21 Aug. 1879, *Guttenberg* (female US), Horse Shoe Point, Misery Bay, 20 Aug. 1978, *Lowden 3827—3828* (female and male UCMM). Snyder Co., Penns Creek: Swinging Bridge, Selinsgrove, 21 Oct. 1928, *Moldenke 4201* (female NY); north-east of Centerville, 3 Aug. 1948, *Wahl 5850* (male GH). **South Dakota.** Potter Co. Roberts Co. **Texas** Brazoria Co.: Halls Bayou, south-west of Hitchcock, Aug. 1977, *Lowden 3807* (female and male UCMM). Hays Co. **Vermont.** Addison Co., Lake Champlain: 8 Aug. 1878, *Pringle* (female and male US); Ferrisburgh, 27 Aug. 1881, *Boyce* (female F); near Ferrisburgh, 11 Aug. 1885 (female NY). Chittenden Co.: Winooski River, Burlington, 8 Aug.

1895, *Grout* (female F, NY; male F, GH, NY, US). Virginia. (Bourn, 1934). Washington. King Co. West Virginia. Greenbrier Co. Hardy Co. Ohio Co. Wisconsin. Brown Co.: Fox River, Green Bay, Aug. 1881, *Schuette* (female and male F, GH, NY; male US). Dane Co.: Lake Mendota, 29 June—3 Aug. 1923, 13—25 Aug. 1934 (female and male; Witmer, 1937). MIDDLE AMERICA. Guatemala. Department el Petén: Lake Petén Itza, Flores, 28—29 Dec. 1978, *Lowden 3837-3838A* (female and male UCMM). Department Izabal: Lago Izabal, Río Polochic, opposite El Estor, 1 Jan. 1979, *Lowden 3844* (male UCMM). Honduras. Department Comayagua, Lake Yojoa: near Agua Azul, Dec. 1946, *Carr 2352* (sterile F); 1 Feb. 1978, *Robinson 2203* (sterile F). Mexico. State Tamaulipas: vic. Tampico, 27—30 Apr. 1910, *Palmer 314* (female F, GH, MO, NY); Laguna de Chairel, near Tampico, 14 Sept. 1967, *Rzedowski 24574* (female F, US). WEST INDIES. Cuba. Province Matanzas: Río Negro, Ciénaga de Zapata, 24—25 Feb. 1941. *Victorin, León, Alain & Rivas 19552* (female GH, HAC, MT, NY); Guama, Laguna del Tesoro, Ciénaga occidental de Zapata, 21 July 1979, *Lowden, Del Risco & Vales 3877—3878* (female and male HAC, UCMM). Province Sancti Spiritus: Sabana de Sti. Spiritus, Sta. Clara, 20 July 1918, *León & Roca 7823* (sterile HAC, NY).

(2b) **V. americana** Michx. var. **biwaensis** (Miki) Lowden, **comb. nov.**

Probable Synonyms:

V. asiatica Miki var. *biwaensis* Miki, Bot. Mag. Tokyo, 48: 330 (Fig. 4G—K), 331, 332 (Fig. 5B). 1934. Type locality: Japan, Honshu, Prov. Ohmi, Lake Biwa.
V. biwaensis (Miki) Ohwi, Bull. Nat. Sci. Mus. Tokyo, 26: 1. 1949.
V. gigantea Graebner var. *biwaensis* (Miki) Kitamura, Acta Phytotax. Geobot., 22: 74. 1966.
V. natans (Lour.) Hara var. *biwaensis* (Miki) Hara, J. Jpn. Bot., 49: 136. 1974.

Leaves frequently ruffled to strongly twisted with apices distinctly serrulate (Figs. 5a—c). Staminate Plant (Fig. 4a): Filaments of stamens connate nearly to apex (Fig. 4e), many transparent hairs at base of androecium (Figs. 4d and e). Pistillate Plant: Staminodia free between discordant stigmatic lobes with reduced styles (Fig. 2a). Flowers solitary, actinomorphic (Figs. 5d and e), or rarely an umbel with 2—13 regular to irregular flowers (Figs. 6a—e).

Distribution: See Figs. 8 and 9.

The location of *V. americana* var. *biwaensis* in Japan (Fig. 9) is based on the description of male and female flowers from Lake Biwa (Miki, 1934). Many old habitats of *Vallisneria* in Japan have been recently destroyed (H. Hara, University of Tokyo, personal communication, 1980).

In Hispaniola *Vallisneria* is extinct at Thomazeau (Haiti) and Lagoon Rincón (Dominican Republic). The aquatic flora in these habitats is undergoing successional changes. Lake Miragoâne (Haiti) is the only known locality of *V. americana* var. *biwaensis* in the Americas that does not suffer immediate environmental endangerment. The inevitable destruction of the staminate population in the Cachón de la Rubia (Dominican Republic) is due to private business and housing expansion in Santo Domingo. Industrial

and agricultural pollution in the vicinity of Maracay-Valencia (Venezuela) has destroyed the aquatic flora in Lake Valencia.

Voucher specimens (umbel inflorescences): **WEST INDIES. Haiti.** Department Sud: Miragoâne, Lake Miragoâne, 15—16 Dec. 1976), *Lowden 3671* (female UCMM).

Voucher specimens (dioecious plants): **EAST ASIA. Japan.** Honshu Island: Prefecture Kyoto, Yamashiro, 31 July 1925, *Shiota 4834* (sterile GH); Prefecture Shiga, Zeze, Otsu-shi, Lake Biwa, 14 Oct. 1972, *Tanimoto 1157* (female MO). **WEST INDIES (HISPANIOLA). Dominican Republic.** National District, Cachón de la Rubia: 21 Sept. 1973, *Lowden 3305* (male UCMM); 23 Feb. 1974, *Liogier, Marcano & Jiménez 21358* (male NY, UCMM); 18 Apr. 1975, *Lowden 3471* (male UCMM) and 23 Nov. 1976, *Lowden 3650* (male UCMM). Province Barahona: Rincón, Aug. 1911, *Fuertes 960* (female F, GH, NY, P, US). **Haiti.** Department l'Ouest: Lake Saumâtre, Manneville, Croix des Bouquets, Plaine Cul de Sac, Thomazeau, 20 Jan. 1925, *Ekman H3058* (sterile IJ, NY). Department Sud, Miragoâne, Lake Miragoâne: 15 Nov. 1926, *Ekman* H7228 (female IJ) and H7238 (female US); 15—16 Dec. 1976, *Lowden 3658* (female UCMM). **SOUTH AMERICA. Venezuela.** Federal District: Caracas, pond in Botanical Institute, 8 Oct. 1975, *Gonzalez 732* (female VEN) and 23 May 1979, *Lowden 3845* (female UCMM). State Aragua: Lake Valencia, 14 July and 14 Dec. 1940, *Chardon 229* (female US, VEN).

Unidentified Taxa

V. nana R. Br., Prod., 345. 1810. Australia and Tasmania.

V. caulescens Bailey & F. Muell., Syn Queensl. Fl. Sec. Suppl., 56. 1888. Australia: Queensland, 60 miles west of Normanton, M. Lagoon, coll. Thos. L. Bancroft.

V. gracilis Bailey, Rep. Exped. Bellend., 62. 1889, Syn. Queensl. Fl. Third Suppl., 70. 1890. Australia: Queensland, Mulgrave River.

CONCLUSIONS

An inventory of 1170 *Vallisneria* specimens (Fig. 11) reveals a higher frequency of pistillate plants than staminate plants. This very high frequency of pistillate plants might be somewhat biased by the collector's preference to collect in nature the more obvious and accessible female plant. There are more bisexual populations (Fig. 11) in temperate localities than in tropical regions. This suggests a possible temperate origin for the genus. The presence of isolated unisexual populations (in Hispaniola, Venezuela and Guatemala) and umbel to spike-like inflorescences of *V. americana*, in subtropical and tropical America (Figs. 7 and 8), are thought to be marginal ancestral stocks whose survival is attributed to a very effective means of stolon propagation.

The two morphologically distinct species of *Vallisneria* have probably evolved from one continuous gradient in floral variation. Speciation (Fig. 11) seems more defined in the staminate plant, meanwhile at the varietal level the pistillate plant shows a conspicuous gradient in its floral morphology.

The extent to which *Vallisneria* species have been introduced as cultivated or aquarium plants is unknown. This study discloses no evidence that *V.*

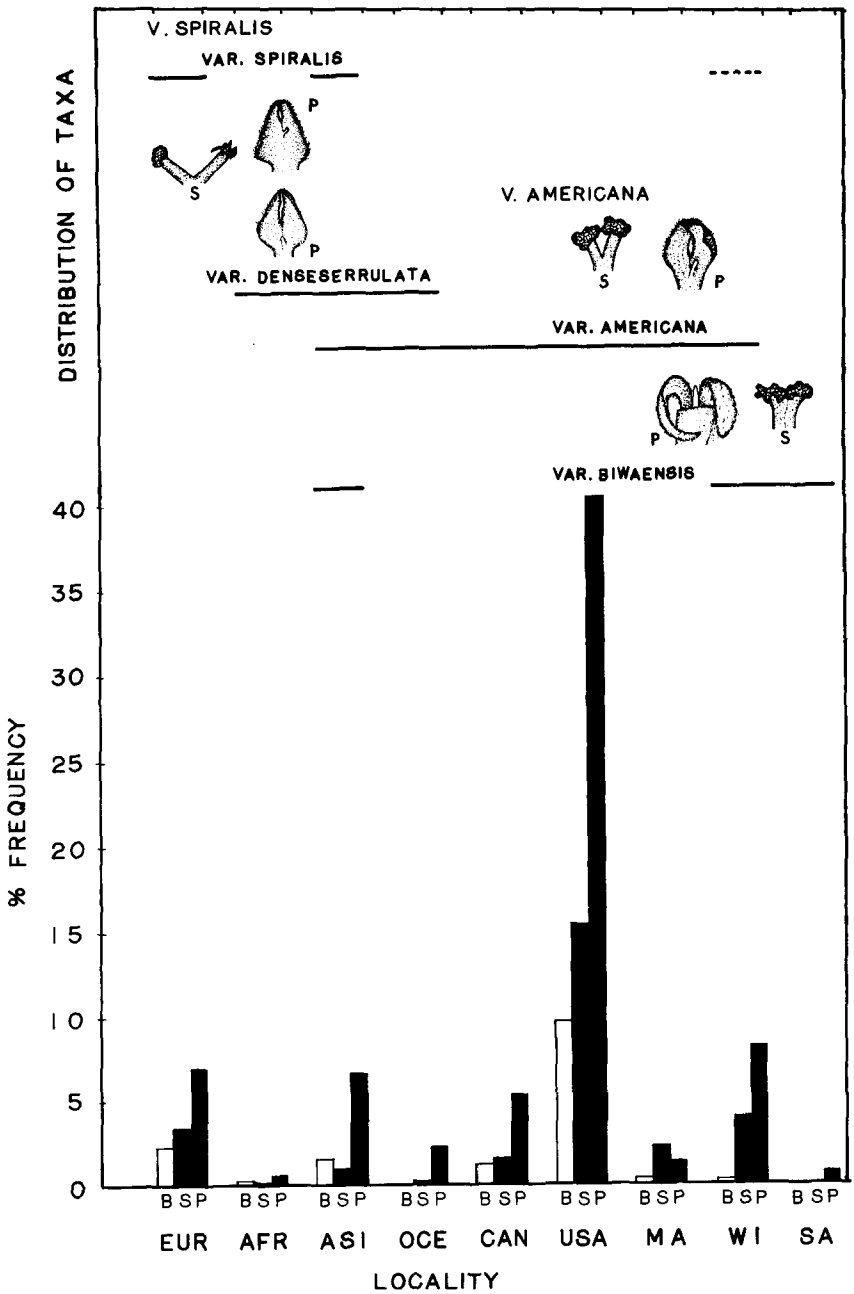


Fig. 11. A graphic presentation of *Vallisneria* taxa correlating the relevant taxonomical characters with bisexual (B), staminate (S) and pistillate (P) population frequencies for Europe (EUR), Africa (AFR), Asia (ASI), Oceania and Australia (OCE), Canada (CAN), United States (USA), Middle America (MA), West Indies (WI) and South America (SA).

spiralis has been naturalized in the Americas, however the possibility is not excluded. In the West Indies (Fig. 11) the pistillate plant of *V. spiralis* var. *spiralis* has had a meagre introduction in Jamaica and Cuba.

Today, *V. spiralis* cannot be thought of as essentially a Mediterranean species of southern Europe (Fig. 10), or *V. americana* as a species that occurs only in North America (Fig. 9). The geographic extension of *V. spiralis* var. *spiralis* into northern Europe must be verified in the light of the present findings. The actual identity of African material (Fig. 10) needs further study. The degree of geographic and biological convergence between *V. spiralis* and *V. americana* (Figs. 9 and 10) in Asia, Oceania and Australia depends on a thorough inspection of male and female populations. In this manner the exact identity of *V. natans* (Lour.) Hara might be determined.

Further comparative studies rely on flower samples collected at anthesis. A close examination of the critical floral structures of both sexes is required, since these structures (Fig. 11) are easily overlooked.

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