

Studies of hybridization and chromosome number variation in aquatic angiosperms: evolutionary implications

D.H. Les^a and C.T. Philbrick^b

^aDepartment of Ecology and Evolutionary Biology, The University of Connecticut, Storrs,
CT 06269-3042, USA

^bRancho Santa Ana Botanic Garden, 1500 North College Ave., Claremont, CA 91711-3157, USA

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ABSTRACT

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Aquatic angiosperms are widely recognized as a biological group sharing attributes associated with adaptations to the aquatic condition. Clonal growth, high vagility of vegetative propagules, and rare to sporadic sexual reproduction are common convergences among aquatic plants, and play central, interacting roles in various evolutionary factors. In this review, two important evolutionary factors, hybridization and chromosome number variation, are discussed with respect to interactions involving clonal growth, vagility, and asexuality. Asexual reproduction emerges as a significant evolutionary catalyst allowing for the perpetuation of hybrid offspring and anomalous cytotypic variants. Inherent phenotypic plasticity in aquatic plants is difficult to discern from both hybrid individuals and cytotypic variants. Detailed studies of putative 'hybrids' in some groups may reveal a higher incidence of cytotypic variants at the basis of morphological differences previously attributed to hybridization.

INTRODUCTION

Aquatic angiosperms represent a polyphyletic assemblage of diverse evolutionary lineages unified as a 'biological group' by their common invasion of the aquatic environment. Water plants have long been a fascination to naturalists, horticulturists, and aquarists; issues of their complex transition from terrestrial to aquatic life, however, have scarcely been addressed by evolutionary biologists.

Some of the best examples of convergent adaptation to similar environmental conditions are found among aquatics, e.g. reduction in vascular tissue and highly polymorphic vegetative form. A striking convergent pattern per-

Correspondence to: D.H. Les, Department of Ecology and Evolutionary Biology, Box U-42, The University of Connecticut, Storrs, CT 06269-3042, USA.

tains to clonal reproduction (see Grace, 1993). Extensive vegetative apomixis, attendant with rare or sporadic sexual reproduction, characterizes this biological group better than any other single feature. It is reasonable to predict that clonal reproduction is a fundamental factor influencing the patterns and processes of evolution in aquatic angiosperms.

However, clonal growth per se is not solely responsible for the unique identity of this biological group, but their high vagility also contributes. Unlike terrestrial plants where vegetative reproductive structures are typically deeply embedded in the soil, similar structures in aquatics are often liberated in the water column. Indeed, many aquatics possess modified vegetative structures that serve as exceptionally efficient propagules of dispersal, e.g. turions, winter buds, and even simple stem fragments. The role of sexual propagules (seeds, fruits) appears to be of secondary importance for the dispersal of most clonal aquatic plants. High vagility linked to vegetative propagules represents a life-history trait unique to clonal aquatic plants, and predictably is of profound evolutionary importance.

The significance of interactions involving clonal growth, high vagility, and other evolutionary factors in aquatic plants is poorly understood. Moreover, the information needed to adequately address these issues is dispersed throughout botanical, genetic, ecological, and evolutionary literature. We have two main goals in this contribution. The first is to provide a review of the pertinent literature. Secondly, we will develop a conceptual framework for assessing the evolutionary significance of interactions between clonal growth in aquatics and two factors that have played major roles in the evolution of terrestrial angiosperms, namely hybridization and chromosome number change (polyploidy and aneuploidy). We suggest that the high vagility and rarity of sexual reproduction in aquatics has dramatically influenced the evolutionary consequences of both hybridization and chromosome number change. Specifically we present our current understanding of the roles that hybridization and chromosome number change have played in the evolution of aquatic groups by reviewing and discussing the evidence for, and implications of, each process.

This survey is based on literature studies published on 177 aquatic plant genera. We have restricted our study to genera that we regard as representative more of truly aquatic rather than helophytic species. Although space limitations do not allow us to include the total list of citations in the present study, a more comprehensive listing of titles and genera surveyed can be requested from the authors.

We have used 'selected' groups to serve as the focus of our discussion. These groups are typically those that have been studied in some detail. Details for lesser studied groups are essentially provided by tabulations although additional information is generally available from references cited.

Owing to the extensive literature, the Cyperaceae were not surveyed thor-

oughly in the present review. This family has prolific inter- and intraspecific chromosome number variation, due in large part to the occurrence of agmatoploidy (Grant, 1981). The genus *Carex* alone contains species with every successive gametic chromosome number from $n=12$ to $n=43$ (Grant, 1981). *Eleocharis palustris*, with 24 cytotypes (see Table 3), clearly exemplifies the degree of intraspecific chromosome number variation encountered. For the sake of further brevity, our discussion of the Poaceae is restricted to a few genera that are principally aquatic.

Note that some intraspecific examples indicate that a species has no reported euploid variation although the species itself may be a polyploid.

THE EXTENT OF HYBRIDIZATION IN AQUATIC ANGIOSPERMS

In our sample of 177 hydrophyte genera, 35 genera (20% of the total) have references containing discussions of natural or experimental hybridization. If we recalculate this number to exclude monotypic genera (wherein interspecific hybridization is impossible), the percentage approaches 26%. Dicots account for only 37% (monocots 63%) of the genera with reports of hybridization. The largest concentration of genera with hybridization reports (40% of total; more than reports for all dicot genera combined) occurs within the monocot subclass Alismatidae. High percentages reflect the extent of study in a group and do not necessarily indicate a propensity for natural hybridization. Within the aquatic subclass Alismatidae, for example, natural hybrids probably occur in only six genera (Table 1). Surely these percentages are underestimates due to our inability to satisfactorily compensate for poorly studied groups.

Several factors contribute to the difficulty of studying hybridization in water plants. In many cases, the rarity of flower production precludes attempts to conduct experimental hybridizations and to investigate the regularity of meiosis in synthetic or putative natural hybrids. Hydrophiles (water-pollinated plants) provide even greater challenges because controlled pollinations cannot be readily made. Furthermore, sterility, a commonly used indicator of hybridization, is difficult to document with certainty in hydrophytes, owing to their often predominant asexual rather than sexual mode of reproduction.

Asexuality can also limit sources of material for cytological study to somatic tissue. Furthermore, several hydrophytes (e.g. *Ceratophyllum*, *Utricularia*) lack roots, a favored source of material for somatic chromosome counts. Aquatic genera such as *Ceratophyllum* (which is highly asexual, hydrophilous, and lacks roots) provide formidable obstacles to biosystematic research.

Table 1 summarizes a listing of aquatic plants with references reporting the occurrence of hybridization or experimental studies of hybridization. The following section provides more specific details of hybridization in selected groups for which adequate information was available for reasonable discussion.

TABLE 1

Summary of reported natural hybrids and experimental studies of hybridization in aquatic angiosperms (arranged alphabetically by family)

Taxon	Experimental crosses performed	Natural hybrid occurrence	References
Dicots			
(1) Brassicaceae			
(a) <i>Nasturtium</i>	+	+	Manton, 1935; Howard and Lyon, 1950, 1951, 1952; Shaw, 1951; Green, 1962; Stace, 1975a
(2) Callitrichaceae			
(a) <i>Callitriche</i>	-	+	Savidge, 1959; Stace, 1975e
(3) Ceratophyllaceae			
(a) <i>Ceratophyllum</i>	+	-	Les, 1985
(4) Haloragaceae			
(a) <i>Myriophyllum</i>	+	?	Patten, 1954; Löve, 1961; Aiken et al., 1979;
(b) <i>Proserpinaca</i>	-	?	Fassett, 1957; Ogden (1957) in Fassett, 1957
(5) Lentibulariaceae			
(a) <i>Utricularia</i>	+	?	Stace, 1975f; Taylor, 1975, 1989; Thor, 1988
(6) Nelumbonaceae			
(a) <i>Nelumbo</i>	+	-	Perry, 1961; Sculthorpe, 1967
(7) Nymphaeaceae			
(a) <i>Nuphar</i>	+	+	See text
(b) <i>Nymphaea</i>	+	+	See text
(8) Ranunculaceae			
(a) <i>Ranunculus</i>	+	+	See text
(9) Scrophulariaceae			
(a) <i>Bacopa</i>	+	+	Barrett and Strother, 1978
(b) <i>Limosella</i>	-	+	Vachell and Blackburn, 1939; Stace, 1975b
(c) <i>Veronica</i>	+	+	See text
Monocots			
(1) Alismataceae			
(a) <i>Alisma</i>	+	+	See text
(b) <i>Baldellia</i>	-	?	Glück, 1913; Björkqvist, 1968; Stace, 1975c
(c) <i>Echinodorus</i>	-	?	Rataj and Horeman, 1977
(d) <i>Sagittaria</i>	+	?	Bogin, 1955; Lohammer, 1973; Beal et al., 1982
(2) Aponogetonaceae			
(a) <i>Aponogeton</i>	+	+	See text

Taxon	Experimental crosses performed	Natural hybrid occurrence	References
(3) Araceae (a) <i>Cryptocoryne</i>	+	+	Sculthorpe, 1967; Jacobsen, 1976, 1977, 1981, 1982, 1985; De Graaf and Arends, 1986
(4) Cyperaceae (a) <i>Eleocharis</i>	+	+	See text
(b) <i>Scirpus</i>	-	+	See text
(5) Hydrocharitaceae (a) <i>Egeria</i>	+	-	Ernst-Schwarzenbach, 1945, 1953; Cook and Urmi-König, 1985
(b) <i>Elodea</i>	+	+	Ernst-Schwarzenbach, 1945, 1953; Cook and Urmi-König, 1985
(c) <i>Hydrilla</i>	+	-	Ernst-Schwarzenbach, 1945, 1953; Cook and Urmi-König, 1985
(d) <i>Lagarosiphon</i>	+	-	Ernst-Schwarzenbach, 1945, 1953; Cook and Urmi-König, 1985
(e) <i>Ottelia</i>	+	?	Kaul, 1969
(6) Najadaceae (a) <i>Najas</i>	-	+	See text ¹
(7) Poaceae (a) <i>Glyceria</i>	+	+	Borrill, 1956, 1975; Lambert, 1947
(b) <i>Oryza</i>	+	+	Morinaga and Fukushima, 1956; Ranganadhacharyulu and Raj, 1974 ²
(c) <i>Zizania</i>	+	?	De Wet and Oelke, 1978; Warwick and Aiken, 1986
(8) Potamogetonaceae (a) <i>Potamogeton</i>	-	+	See text
(9) Sparganiaceae (a) <i>Sparganium</i>	-	?	Beal, 1960; Cook, 1961, 1962, 1975a; Cook and Nicholls, 1986, 1987
(10) Typhaceae (a) <i>Typha</i>	+	+	See text
(11) Zannichelliaceae (a) <i>Zannichellia</i>	-	+	Van Vierssen, 1982
(12) Zosteraceae (a) <i>Zostera</i>	-	?	Druce, 1920; Tutin, 1938, 1975

¹Intraspecific hybrids only.²The literature for *Oryza* is voluminous; these references are offered only as a sample.

HYBRIDIZATION IN HYDROPHILES

Hybridization studies in hydrophiles are virtually unknown, with reports existing for only four genera: *Ceratophyllum* (Ceratophyllaceae), *Elodea*

(Hydrocharitaceae), *Najas* (Najadaceae), and *Zostera* (Zosteraceae) (Table 1). A discussion of *Elodea* follows under Hydrocharitaceae.

Some controlled crosses have been conducted in *Ceratophyllum* (Les, 1980) although natural hybrids have never been reported for this genus. Numerous reciprocal crosses were made between the two diploid species *Ceratophyllum demersum* and *Ceratophyllum echinatum*, but only a few (using the latter as the female parent) yielded fruit. Only one fruit germinated, producing a seedling that was short lived, but which revealed tenable intermediacy in plumule leaf features (Les, 1985). The production of even one fertile seed from this cross is perhaps surprising given that the genetic identity between the parental species (determined electrophoretically) is only 0.17 (Les, 1991). Habitat divergence may play a part in maintaining isolating barriers in *Ceratophyllum* (Les, 1986). In rare instances where two species coexist within a pond, vegetative growth and the lack of flowering further reduce opportunities for hybridization.

Najas marina subsp. *marina* and *Najas marina* subsp. *intermedia* possess different karyotypes and were successfully crossed by Viinikka (1976) although few fertile offspring were produced. Triest et al. (1986) demonstrated that sufficient electrophoretic variability existed between *Najas marina* subsp. *marina* and *Najas marina* subsp. *intermedia* for examining questions of hybridization. Subsequently, Triest (1989) reported isozymic evidence of hybridization between these subspecies within a Swiss population in which they co-occurred. In this population, floral phenology apparently resulted in uni-directional hybridization from subsp. *intermedia* to subsp. *marina*, with hybrid plants all resembling subsp. *marina* (Triest, 1989). The occurrence of interspecific hybridization in *Najas* is still questionable. *Najas muenscheri* is reputed to be of hybrid origin (Chase, 1947), but documentation is lacking. Haynes (1979) regards this taxon to be a variety of *Najas guadalupensis*.

Hybrids involving *Zostera marina* and *Zostera noltii* have been reported by Druce (1920), but probably represent specimens of *Zostera angustifolia* which is intermediate morphologically to the suspected parents (Tutin, 1938, 1975).

HYBRIDIZATION IN AQUATIC DICOTS

Nymphaeaceae

The water lily genus *Nuphar* reportedly undergoes natural hybridization (Beal, 1956). In North America, *Nuphar* \times *ruberdisca* is considered to be a

fertile hybrid between *Nuphar variegata* and *Nuphar pumila* (Hellquist and Crow, 1984). Miller and Standley (1912) argued that *Nuphar rubrodisca* may be a distinct species with low fertility compensated for by asexual vegetative reproduction, noting that no convincing evidence for a hybrid origin of this taxon had been presented. Other reports of natural North American hybrids are between *Nuphar advena* and *Nuphar sagittifolia* and between *Nuphar variegata* and *Nuphar advena* (Wood, 1959).

Perhaps the best known European *Nuphar* hybrid is *Nuphar* × *spennerana* ('*Spennerianum*'), a 'natural cross' involving *Nuphar lutea* and *Nuphar pumila* (Heslop-Harrison, 1953, 1975a; Perry, 1961). Here, reciprocal synthetic F₁ hybrids have been produced experimentally, and possess highly reduced pollen fertility compared with the parental species. These hybrids apparently can survive for long periods as evidenced by their persistence in regions where the parents no longer exist. Introgression reportedly occurs (Heslop-Harrison, 1975a), but is not substantiated.

Hybridization in the genus *Nymphaea* has been well studied, owing much to the pursuit of artificial hybrids in the horticultural trade. Water lilies are better subjects for manipulative crossing than many aquatics (they are easily raised, flower frequently, are large-flowered, etc.), a factor that has undoubtedly encouraged their study. Furthermore, the apparent weak genetic isolating mechanisms between *Nymphaea* species promote interspecific hybridization (Gupta, 1980). Swindells' (1983) list of nearly 400 hardy and tropical water lily hybrids attests to the potential for hybridization in this genus, but offers little insight into the frequency of natural hybrids.

The most famous artificial hybridizer of hardy water lilies was Latour-Marliac, who unfortunately, divulged neither the parentages nor methods involved in producing his array of about 70 horticultural hybrids (Perry, 1961, 1981; Masters, 1974; Swindells, 1983). Attempts to reproduce his hybrids and/or deduce their parentages have met with nearly total failure (Perry, 1961). Many of Latour-Marliac's hybrids putatively involved *Nymphaea alba*, *Nymphaea alba* var. *rubra*, *Nymphaea odorata* var. *rosea*, and *Nymphaea mexicana* (Perry, 1989).

George Pring, an authority on tropical water lily hybrids, was the antithesis of Latour-Marliac. Pring (1934a,b) published comprehensive data revealing fertility information obtained from 283 different hybridizations involving taxa in subgenera *Brachyceras* and *Lotos*. He also provided full details on the pedigrees of many hybrids, including selection and inbreeding programs used in perfecting them. In addition, the accounts of Pring (1934a,b) provide valuable information on the genetic basis of floral and vegetative traits, including dominance, and progeny ratios. In water lilies, results of breeding studies have revealed that vegetative traits are inherited mainly from the female parent, and floral traits from the male parent (Pring, 1934a,b; Masters, 1974).

Wiersema (1987) obtained seed in 20 of 28 experimental interspecific

crosses among species of *Nymphaea* subgenus *Hydrocallis*, but none in seven crosses made between species of subgenus *Hydrocallis* and those of subgenera *Lotos* and *Nymphaea*. These results support conclusions that hybridization in *Nymphaea* is restricted to species within taxonomically recognized subgenera (Conard, 1905; Wood, 1959; Wiersema, 1987).

Little information exists for natural hybrids in *Nymphaea*. Gupta (1978) observed that many *Nymphaea* taxa (ten of 19 taxa sampled) are characterized by irregular meiosis which suggests their hybrid origin. In seven of the eight native taxa studied by Gupta, meiosis was regular. A diploid variety of native Indian *Nymphaea stellata* (var. *cyannea*), however, exhibited irregular meiotic behavior, whereas, tetraploid and hexaploid varieties exhibited regular meiosis (Gupta, 1978). Wiersema (1987) described natural triploid hybrids of *Nymphaea prolifera* and *Nymphaea amazonum* from Argentina, and identified a putative Brazilian hybrid population involving *Nymphaea amazonum* and *Nymphaea lasiophylla* where pollen fertility was less than 5%. Reports of natural hybrids between *Nymphaea alba* and *Nymphaea occidentalis* in Europe (Godwin, 1956) are possibly erroneous, and may represent clinal variants of *Nymphaea alba* (Heslop-Harrison, 1975b). Williams (1970) believed that hybridization was evolutionarily unimportant in the *Nymphaea odorata*/*Nymphaea tuberosa* complex because of low levels of reproduction by seed.

Hybridization in *Nymphaea* has undoubtedly provided significant levels of heterozygosity in derivative hybrid species. High levels of heterozygosity are also reported in *Nymphaea sturtevantii*, a cultivar arising from seed of *Nymphaea devoniensis* (Gupta, 1980; Conard, 1905). In this instance, structural chromosomal changes are believed responsible, and are thought to be preserved in many *Nymphaea* species by vegetative reproduction (Gupta, 1980).

Ranunculaceae

Ranunculus subgenus *Batrachium* reportedly contains a wide array of hybrids involving many possible combinations of interspecific crosses. Much of the experimental work has been cytological or has involved artificial hybrid synthesis.

Cook (1975b) reviewed hybrid reports for *Ranunculus* subgenus *Batrachium* in Britain and a brief synopsis is presented here. Suspected natural hybrids ($2n=40$) between *Ranunculus omiophyllus* ($2n=32$) and *Ranunculus tripartitus* ($2n=48$) resemble the latter species but are variable morphologically. Synthetic F₁ hybrids with low fertility and back-crossed progeny have been produced artificially, but fertility was restored by selection in further generations (Cook, 1966). A trihybrid cross involving this hybrid and *Ranunculus peltatus* has also been synthesized (Cook, 1975b).

The natural hybrid *Ranunculus* × *hiltonii* (*Ranunculus omiophyllus* × *Ran-*

unculus peltatus) was reported in one British locality (Groves and Groves, 1901; Williams, 1926), but may now be extinct (Cook, 1975b). Attempts to synthesize the hybrid have failed. The putative hybrid between *Ranunculus aquatilis* and *Ranunculus tripartitus* is sterile, weak, and intermediate morphologically between the suspected parents (Cook, 1975b). Presumed hybrids involving *Ranunculus circinatus* \times *Ranunculus fluitans* are intermediate morphologically but have not been studied in detail (Vollrath and Kohler, 1972; Cook, 1975b). Hybrids of *Ranunculus fluitans* and either *Ranunculus trichophyllus* or *Ranunculus aquatilis* are similar morphologically to *Ranunculus penicillatus* and are sterile (Cook, 1966, 1975b). Both hybrids exhibit vegetative vigor and spread easily, displacing *Ranunculus fluitans* in some localities. It has not been possible to create either of these hybrids artificially (Cook, 1975b).

Haplodids have been obtained experimentally from sterile triploid *Ranunculus fluitans* \times *Ranunculus trichophyllus* hybrids. The sterile natural hybrid ($2n=40$) between *Ranunculus fluitans* ($2n=16,32$) and *Ranunculus peltatus* ($2n=16,32,48$) is intermediate morphologically and is vigorous (Cook, 1966, 1975b). A sterile, putative hybrid of *Ranunculus circinatus* and *Ranunculus trichophyllus* is reported from disturbed (artificial) sites in Britain, but corroborative experimental studies are lacking (Cook, 1966, 1975b). Sporadic, non-persisting hybrids (*Ranunculus* \times *lutzii*, $2n=32,40$) between *Ranunculus aquatilis* ($2n=48$) and *Ranunculus trichophyllus* ($2n=16,32,48$) are reported from Europe (Cook, 1966, 1975b; Turala and Wolek, 1971). Hybrids between *Ranunculus peltatus* and *Ranunculus trichophyllus* (Groves and Groves, 1901; White et al., 1916; Cook, 1975b) are intermediate morphologically, but have not been studied experimentally.

A sporadic, non-persistent sterile hybrid (*Ranunculus* \times *segretii*) occurs from crossing of *Ranunculus baudotii* and *Ranunculus trichophyllus* (Félix, 1927; Cook, 1966, 1975b). Synthetic hybrids resemble the natural ones and are sterile tetraploids (Cook, 1975b). The sterile natural hybrid *Ranunculus* \times *lambertii* ($2n=40$) occurs only with the putative parents *Ranunculus aquatilis* and *Ranunculus baudotii* (Erikson, 1905; Sørensen, 1955; Cook, 1975b). The putative hybrid *Ranunculus* \times *virzionensis* is rare and believed to be derived from *Ranunculus aquatilis* and *Ranunculus peltatus* (Cook, 1975b). *Ranunculus longipes* ($2n=48$) is hexaploid and a putative amphiploid of diploid *Ranunculus ophioglossifolius* and tetraploid *Ranunculus nodiflorus* (Barros-Neves, 1945).

Brassicaceae

Sterile triploid hybrids (*Nasturtium* \times *sterilis*, $2n=48$) involving the diploid *Nasturtium officinale* ($2n=32$) and tetraploid *Nasturtium microphyllum* ($2n=64$) are well studied and display intermediate fruit, seed, and stomatal

characters (Manton, 1935; Howard and Lyon, 1950, 1951, 1952; Shaw, 1951; Stace, 1975a). Hybrids are partly fertile, but undergo vigorous vegetative reproduction enabling them to persist at sites where one or both parents are absent.

Triploid hybrids have been synthesized experimentally using tetraploid *Nasturtium microphyllum* as the maternal parent although the reciprocal cross has been unsuccessful (Stace, 1975a). Artificial autotetraploids of *Nasturtium officinale* resemble the diploids, have lower fertility, and produce tetraploids with low fertility when crossed with *Nasturtium microphyllum* (Howard and Manton, 1946). Green (1962) observed that a high degree of vegetative plasticity in the parental species renders morphological comparisons of leaf shape and size of little use in distinguishing hybrids from parents. Naturally occurring populations of hybrid watercress (*Nasturtium* \times *sterilis*) are reported from several North American localities (Green, 1962).

Scrophulariaceae

A putative hybrid of *Limosella* is apparently a sterile triploid ($2n=30$) resulting from a cross between the tetraploid ($2n=40$) *Limosella aquatica* and the diploid ($2n=20$) *Limosella australis* (Vachell and Blackburn, 1939; Stace, 1975b). Hybrids are described as more vigorous vegetatively with a better tolerance to winter conditions than their parental species (Stace, 1975b). We have found no experimental data to confirm this report.

Natural interspecific hybrids in *Veronica* sect. *Beccabunga* subsect. *Anagallides* create notorious taxonomic difficulties (Fischer, 1981; Öztürk and Fischer, 1982). The naturally occurring *Veronica* \times *lackshewitzii* is reportedly a hybrid between *Veronica anagallis-aquatica* and *Veronica catenata* (Williams, 1929; Keller, 1942; Walters, 1975). Although sterility is the most diagnostic feature of these F_1 hybrids, the pollen fertility can vary from as much as 3–99% (Marchant, 1970). Marchant (1970) artificially produced F_1 hybrids of these species which were (incompletely) sterile and resembled the natural hybrids morphologically. It is interesting that fertility was increased markedly in F_2 and subsequent generations. *Veronica* \times *lackshewitzii* reportedly has greater vegetative vigor, allowing it to optimally colonize shallow, flowing streams (Marchant, 1970).

A natural hybrid involving *Veronica poljensis* and *Veronica anagalloides* has been reported by Öztürk and Fischer (1982) on the basis of morphological intermediacy. Natural hybrids are also reported to involve *Veronica anagallis-aquatica* and *Veronica anagalloides* (Fischer, 1981). Marchant (1970) reported successful artificial crosses between *Veronica scardica* and *Veronica beccabunga*, although seeds were inviable. Supposed naturally occurring hybrids of this cross are believed to represent instead hybrids of *Veronica scardica* and *Veronica anagallis-aquatica* (Fischer et al., 1985), although their

precise parentage is debatable. Several intraspecific hybrids (among subspecies) have also been reported in *Veronica* sect. *Beccabungae* subsect. *Anagallides*, but interspecific hybrids involving subsect. *Anagallides* and subsect. *Beccabunga* are not known to occur (Fischer, 1981; Öztürk and Fischer, 1982).

HYBRIDIZATION IN AQUATIC MONOCOTS

Alismataceae

Intergeneric hybrids between *Alisma plantago-aquatica* and *Baldellia ranunculoides* were described by Glück (1913) from Britain and Ireland. The putative hybrids exhibited different morphologies (greater resemblance to one or the other parent) representing reciprocal crosses (Stace, 1975c). Björkqvist (1968), however, could not produce the hybrid experimentally. Upon re-examining specimens cited by Glück, Björkqvist concluded that 'hybrids' resembling *Baldellia* were simply variants of that species, and those resembling *Alisma* were actually *Alisma lanceolatum*, not *Alisma plantago-aquatica*.

Suspected interspecific hybrids between *Alisma lanceolatum* and *Alisma plantago-aquatica* (*Alisma* × *rhicnocarpum*) were confirmed by progeny from artificial hybridizations with intermediate morphology, low fertility, and additive chromosome numbers (Schotsman, 1949; Björkqvist, 1968). *Alisma plantago-aquatica* ($2n=14$) is apparently diploid and *Alisma lanceolatum* ($2n=26, 28$) is tetraploid. Wild hybrids are $2n=20$ or 21 depending on the cytotype of *Alisma lanceolatum* involved (Pogan, 1965; Stace, 1975d). Pogan (1971) obtained F_2 progeny from wild hybrids and found diploid chromosome numbers ranging from $2n=21-25$. Pogan (1961) believed that *Alisma lanceolatum* was an allotetraploid derivative of *Alisma plantago-aquatica*. Hybrid fertility is generally low; however, higher fertility has been reported in some instances (Allen, 1964; Pogan, 1971). Natural hybrids may be rare because of phenological isolation, with *Alisma lanceolatum* flowering earlier in the day than *Alisma plantago-aquatica* (Stace, 1975d).

Triest et al. (1988) conducted experimental studies of hybridization between *Alisma lanceolatum* and *Alisma plantago-aquatica* using numerical and isozyme analyses. They examined plants from 17 *Alisma plantago-aquatica* populations, two *Alisma lanceolatum* populations, and seven populations where both species coexisted. The lack of additivity for one enzyme (ADH) was used as evidence that none of the mixed populations represented hybrids, although the morphological results indicated some degree of intermediacy in the sympatric populations. Overlooked, however, was the possibility that hybrids resembling *Alisma lanceolatum* would show no apparent additivity for ADH (a fixed heterozygote in this species). Because of apparent fixed hetero-

zygosity of ADH in *Alisma lanceolatum* but not in *Alisma plantago-aquatica*, they concluded that the former species is an allotetraploid (a single ADH gene has also been observed in *Alisma gramineum* by Roelandt, 1986).

Although this conclusion supports cytological observations of tetraploidy in *Alisma lanceolatum* (Pogan, 1961, 1965), it does not exclude the possibility that the ADH duplication arose by means other than polyploidy. The authors did not state whether fixed heterozygosity was observed at loci other than ADH. If these species are usually isolated phenologically (described above), then it is predictable that hybrids should be quite rare. Consequently, it would be more informative to carry out a similar study in a region of known hybridization. To effectively look at hybridization in these taxa, however, it may be necessary to screen populations for enzyme phenotypes which are fixed for different alleles in both parents, rather than for ADH which simply has or lacks a duplication.

Rataj and Horeman (1977) speculated that natural hybridization may occur between *Echinodorus cordifolius* and *Echinodorus berteroii* (and perhaps other *Echinodorus* spp.), although sufficient corroborative evidence is not available. They also acknowledge that artificial hybrids of *Echinodorus* have not yet been made.

Bogin's (1955) claims of hybridization in *Sagittaria* were investigated by Beal et al. (1982) who conducted experimental crosses of six taxa. Interspecific crosses involving *Sagittaria engelmanniana*, *Sagittaria australis*, *Sagittaria brevirostra*, *Sagittaria latifolia*, and *Sagittaria cuneata* were infertile; crosses between varieties *latifolia* and *pubescens* of *Sagittaria latifolia* were, however, fertile (Beal et al., 1982). This evidence suggests that natural interspecific hybridization does not occur in the *Sagittaria engelmanniana* complex. Adams and Godfrey (1961) emphasized the need for crossing studies in the *Sagittaria subulata* complex. Hybrids between *Sagittaria natans* and *Sagittaria sagittifolia* were reported by Lohammer (1973), but have not been verified experimentally.

Hydrocharitaceae

Extensive crosses among the genera *Egeria*, *Elodea*, *Hydrilla*, and *Lagarosiphon* (Hydrocharitaceae) were carried out by Ernst-Schwarzenbach (1945, 1953). Failed crosses of *Elodea* with *Egeria*, *Hydrilla*, and *Lagarosiphon* were later reported by Cook and Urm-König (1985), verifying Ernst-Schwarzenbach's earlier results. Experimental crosses between *Elodea callitrichoides* and *Elodea canadensis* were unsuccessful (Ernst-Schwarzenbach, 1945); however those made between *Elodea nuttallii* and *Elodea canadensis* produced viable offspring (Ernst-Schwarzenbach, 1953; Cook and Urm-König, 1985) and are believed to occur naturally (Cook and Urm-König, 1985). Interestingly, plants of these interfertile species occur sympatrically (Cook and Urm-König, 1985), yet there have been no reports of widespread natural hybridization

between them. The widespread incidence of vegetative growth in both species may limit their opportunities for hybridization. The hybrid origin of *Elodea schweinitzii* has also been suggested; it is not believed, however, to represent an F₁ of *Elodea canadensis* × *Elodea nuttalli* (Cook and Urmi-König, 1985).

Kaul (1969) studied the morphology and floral development in synthetic hybrids between *Ottelia cordata* and *Ottelia alismoides*. This is an unusual cross because it involved hybridization between a dioecious species and a hermaphroditic one. The interspecific F₁ hybrids (*Ottelia alismoides* as the pollen donor) are hermaphroditic, and are self-fertile and interfertile with *Ottelia cordata*. Kaul provided a comprehensive summary of comparative morphological and anatomical features of the hybrids that indicate intermediacy with the parents. In hermaphroditic *Ottelia* species, natural hybrids may be uncommon because of breeding system isolation. *Ottelia alismoides* and *Ottelia ovalifolia* are self-compatible and highly autogamous, even producing cleistogamous flowers (Ernst-Schwarzenbach, 1956; Cook, 1982).

Aponogetonaceae

Hybridization has been described as 'common' in the genus *Aponogeton* which (except for *Aponogeton ulvaceus*) includes mainly self-compatible species, several of which are also interfertile (Rataj and Horeman, 1977; Mühlberg, 1980). Artificial and natural crosses involving *Aponogeton crispus*, *Aponogeton echinatus*, *Aponogeton natans*, *Aponogeton elongatus*, and *Aponogeton ulvaceus* have generated a number of hybrids (most designated horticulturally as '*Aponogeton hybridus*') which reportedly have led to selected aquarium-hardy plants that are sterile or fully fertile (Stodola, 1967; Rataj and Horeman, 1977). Hybrids involving *Aponogeton crispus* × *Aponogeton undulatus* and *Aponogeton natans* × *Aponogeton undulatus* are reported by Brünner (1973). Putative natural hybrids involving *Aponogeton crispus* have created difficulty with identification of wild stock collected by aquarium plant breeders (Mühlberg, 1980). Given that species of *Aponogeton* are known to produce fertile hybrids, this genus offers exceptional potential for experimental studies on the consequences of hybridization in aquatic angiosperms. Empirical data are greatly needed to supplement the essentially narrative information that currently describes hybridization in the genus. Furthermore, the fact that *Aponogeton* species flower regularly and are mostly propagated by seed (Mühlberg, 1980) circumvents the impediment of sterility that often hinders biosystematic studies of other aquatic species.

Potamogetonaceae

A 'classic' example of hybridization in aquatic plants has been the genus *Potamogeton*. Ascherson and Graebner (1907) reported nearly 50 hybrids in

the genus, and Hagström (1916) recognized over 200 *Potamogeton* hybrids worldwide. Hagström (1916) detailed several criteria for the proper recognition of hybrids including sterility (deformed or abortive pistils, stamens and pollen), morphological intermediacy, and occurrence in the zone of overlap with both putative parents. St. John (1925), however, provided lengthy criticism of Hagström's inadequate application of these criteria, and enumerated many examples of flawed logic in his recognition of putative North American *Potamogeton* hybrids. As Wehrmeister (1978) also pointed out, Hagström insisted on the use of stem anatomical features to identify hybrids of *Potamogeton crispus*, yet did not hesitate to annotate numerous herbarium sheets as hybrids although he made no anatomical study of them. Although at least seven different hybrid reports implicate *Potamogeton crispus* as one parent, Ogden (1943) and Wehrmeister (1978) indicate that none have been verified.

Ogden (1943) believed that hybridization was common in broad-leaved *Potamogeton* species, and recognized more than 20 hybrids supposedly based on observations of morphological intermediacy and features of stem anatomy. Others, such as Fernald (1932), believed that hybridization is actually uncommon in *Potamogeton*.

It is remarkable that hybridization in *Potamogeton* has become a dogmatic attribute of the genus despite the lack of supporting empirical evidence. A great extent of morphological variability is widely recognized in most hydrophytes, and in *Potamogeton* is further complicated by seasonal dimorphisms (Hunt, 1962; Haynes, 1974; Wehrmeister, 1978). The extent of genetically versus environmentally induced variability is scarcely known for any water plant species. Particularly in a group as variable as *Potamogeton*, it is exceedingly difficult to discriminate between specimens that are 'intermediate' between species, from those that are simply variable. Moreover, such conclusions of intermediacy have been made mostly by inspection, generally without any tabulation or analysis of comparative data (e.g. Dandy, 1975; Wiegleb, 1988). Haynes (1974) noted that the criterion of morphological intermediacy is of little value in the linear-leaved *Pusilli* group, because of the vegetative similarity among species. It is surprising that many taxonomists identify hybrids in *Potamogeton* from single specimens, without consideration of the range of variation in suspected hybrid populations. Making such judgements on single specimens is precarious at best.

Another complicating factor of assessing hybridization is the widespread occurrence of polyploidy and aneuploidy in *Potamogeton* (see below). Textbook examples such as studies of trisomy in Jimson Weed (Blakeslee and Belling, 1924) and many other examples from plants (Khush, 1973) have shown the profound influence of aneuploidy on the morphology of diploid species. Aneuploidy is also commonly associated with reduced fertility in plants (Urbanska-Worytkiewicz, 1980; Kimber and Sears, 1980). With these

considerations in mind, we question how sterile, morphologically aberrant, pondweed specimens can be unequivocally substantiated as hybrids (rather than aneuploid variants) without extensive experimental study. Reports of intraspecific chromosome number variation (from references cited in Les, 1983) in suspected hybrids (based on listing of Wiegleb, 1988) such as *Potamogeton biwaensis* ($2n=52,98$), *Potamogeton fauriei* ($2n=27,28,29$), and *Potamogeton kamogawaensis* ($2n=27,28,42$) raise further suspicion. Have such aneuploid numbers truly arisen through hybridization, or have they been derived through other processes? The causes and effects of chromosome number variation deserve further investigation in *Potamogeton* and other aquatic plants.

A large number of *Potamogeton* hybrids are reported from localities where either one or both suspected parents do not occur. Hutchinson (1975) referred to an "extraordinary ... case" proposed by Hagström (1916) of five coexisting hybrids involving seven species in a single stretch of the Jutland River, some comprising *Potamogeton nodosus* which does not occur there. We do not disallow such possibilities when convincing evidence of hybridization is presented (e.g. see discussion of *Nasturtium* above); in *Potamogeton*, however, these instances warrant further investigation.

Denny and Lye (1973) indicate that the putative hybrid *Potamogeton* × *bunyonyiensis* exists in shallow waters of Lake Bunyonyi, whereas one presumed parent, *Potamogeton schweinfurthii*, occurs in deep water and the other, *Potamogeton thunbergii*, occurs only in marginal pools. In such instances, experimental evidence would lend credibility and offer a means of determining whether the 'hybrids' have occupied a zone of intermediate depth, or if they are actually variants of one or the other species showing depth-related plasticity.

Raunkiaer (1903) provided anatomical evidence to support arguments that sterile plants identified previously along with *Potamogeton fluitans* were actually of hybrid origin (*Potamogeton lucens* × *natans*). Stern (1961) reported a suspected octoploid hybrid population of *Potamogeton richardsonii* from Minnesota in which the karyotype appears to consist of two size classes of chromosomes (of which he, unfortunately, makes no mention). Bance (1946) rendered anatomical and morphological data to propose the hybrid origin of *Potamogeton* × *suecicus*, a suspected cross between *Potamogeton pectinatus* and *Potamogeton filiformis* (Dandy and Taylor, 1946). This putative hybrid occurs outside of the present range of the latter parental species (Sculthorpe, 1967).

With refined methods available for the study of hybridization including advanced numerical, electrophoretic, and molecular techniques, it is ironic that hybridization in *Potamogeton* has not been studied more intensively. To our knowledge, only two studies have provided any truly empirical evidence for hybridization in *Potamogeton*. These studies involved similar approaches

incorporating numerical hybrid indices and evidence of additive biochemical profiles to suggest the hybrid origin of *Potamogeton* \times *longiligulatus* (Haynes and Williams, 1975) and *Potamogeton ogdenii* (Hellquist and Hilton, 1983). Moreover, Les and Sheridan (D.H. Les and D.J. Sheridan, unpublished data, 1988) studied a Wisconsin population of putative hybrids between *Potamogeton natans* and *Potamogeton illinoensis*. In this instance, electrophoretic evidence provided no indication of hybridization despite the convincing morphological intermediacy of several plants.

We offer no estimation of the actual frequency of hybridization in *Potamogeton*, but simply point out that convincing evidence is lacking for most hybrid reports. We encourage the redirection of research in this area to focus on the use of empirical methodologies. With widespread polyploidy in pondweeds (reviewed below), hybridization would certainly be expected. In any case, it will be critical for researchers to distinguish between hybridization and aneuploidy/polyploidy as alternate possible causes of observed morphological variation and sterility in aberrant pondweeds.

Araceae

In the genus *Cryptocoryne*, artificial hybrids have been produced successfully between several $2n=28$ species (*Cryptocoryne beckettii* \times *Cryptocoryne lutea*, *Cryptocoryne beckettii* \times *Cryptocoryne nevillii*, *Cryptocoryne lutea* \times *Cryptocoryne wendtii*), as well as among species of different ploidy levels: *Cryptocoryne lutea* ($2n=28$) \times *Cryptocoryne* sp. ($2n=42$); *Cryptocoryne willisii* ($2n=28$) \times *Cryptocoryne petchii* ($2n=42$) (Sculthorpe, 1967). Jacobsen (1981) demonstrated that *Cryptocoryne* \times *willisii* is a hybrid of *Cryptocoryne parva* and *Cryptocoryne walkeri* and occurs naturally in several localities in Sri Lanka (Jacobsen, 1976, 1977, 1982; De Graaf and Arends, 1986). Sterile triploids ($2n=33$) of *Cryptocoryne ciliata* ($2n=22$) occur naturally in Borneo, but their origin is uncertain (Jacobsen, 1985). The triploids generally display a correlated morphology of short runners and broad leaves (Rataj, 1975; Jacobsen, 1985).

Cyperaceae

In *Eleocharis*, natural hybrids have been reported between *Eleocharis palustris* and *Eleocharis uniglumis*, as well as between subspecies of *Eleocharis palustris* (Walters, 1975). Putative intermediate hybrids ($2n=38-46$) between *Eleocharis palustris* (subsp. *palustris* (cited as subsp. *vulgaris*), $2n=38$) and *Eleocharis uniglumis* ($2n=46$) are often found where the suspected parents coexist (Walters, 1975). Artificial hybrids of this cross were synthesized by Strandhede (1965, 1966) and showed high seed set. Lewis and John (1961) studied sterile, chromosomally intermediate hybrids ($2n=22-36$) in a mixed

population of *Eleocharis palustris* subsp. *microcarpa* ($2n=16$) and *Eleocharis palustris* subsp. *palustris* ($2n=38$). The added presence of *Eleocharis uniglumis* at the site provided some uncertainty regarding the true parentages of the hybrids. Nevertheless, the chromosome numbers of suspected hybrids ($2n=27$) matched expectations for the intraspecific cross (Lewis and John, 1961). Strandhede (1965, 1966) successfully synthesized hybrids of the two subspecies of *Eleocharis palustris*, and obtained high seed set by using subsp. *microcarpa* (which is self-incompatible) as the maternal parent. Natural hybrids reportedly occur in a grazed meadow (where flowering spikes are eaten systematically), a situation where vegetative reproduction may overcome their sexual sterility (Lewis and John, 1961). In parts of the meadow, the hybrids occur in exclusion of the parental species.

Many reports of hybridization exist for species in the *Scirpus lacustris* 'complex' (Smith, 1969). There have been no experimental investigations of European hybrids reported to involve *Scirpus lacustris* \times *Scirpus triqueter* (Jackson and Domin, 1908; Lousley, 1931, 1975; Otzen, 1962), *Scirpus tabernaemontani* \times *Scirpus triqueter* (Brügger, 1882; Junge, 1905; Koyama, 1962; Otzen, 1962; Bakker, 1968; Lousley, 1975), *Scirpus americanus* \times *Scirpus lacustris*, or *Scirpus lacustris* \times *Scirpus tabernaemontani* (Lousley, 1975).

In North America, hybrids (*Scirpus* \times *oblongus*) between *Scirpus acutus* and *Scirpus heterochaetus* have been reported by Koyama (1962). Smith (1969) conducted an intensive investigation of hybridization in the North American *Scirpus lacustris* complex, developing hybrid indices from natural populations, and gathering information on cytology and reproductive biology. *Scirpus acutus* is $n=19$ and karyotypically similar to Japanese *Scirpus lacustris* (Smith, 1969). In a suspected hybrid swarm involving *Scirpus acutus* \times *Scirpus validus*, putative hybrids revealed cytological evidence ($n=19-22$) of irregular meiosis (Smith, 1969). All monospecific stands and five of the mixed stands of *Scirpus acutus* and *Scirpus validus* studied by Smith (1969) showed no evidence of hybridization. Seventeen mixed populations of these species, however, displayed some evidence of hybridization (Smith, 1969). At some sites, intermediate plants also possessed poor seed set (10-15%) and reduced pollen viability (1-25%), further suggestive of their hybrid nature (Smith, 1969). At still other locations, many apparently fertile hybrids existed, and patterns of morphological variation were typical of hybrid swarms (Smith, 1969). Smith provided less convincing morphological evidence for hybridization involving *Scirpus acutus* and *Scirpus heterochaetus*. One population from Iowa, USA, however, showed evidence of hybridization involving all three species (*Scirpus acutus*, *Scirpus validus*, *Scirpus heterochaetus*). Smith also showed an intriguing correlation between specific conductivity of the water and morphological variability of the suspected hybrids and their parents. It would be interesting to conduct controlled experi-

ments to investigate the effects of such habitat differences on the morphology of clones representing both putative parents. Smith (1969) proposed that phenological, ecological, and sterility factors serve as isolating mechanisms that reduce instances of hybridization of these *Scirpus* species.

Schuyler (1961) provided morphological, ecological, and sterility evidence to suggest *Scirpus atrovirens* and either *Scirpus atrocinctus* or *Scirpus pedicellatus* as parents involved in the hybrid origin of *Scirpus peckii*. Schuyler (1961) relied on observations of univalent formation and the lack of mature seed to supplement observations of morphological intermediacy in *Scirpus peckii*. Sterile, intermediate hybrids between *Scirpus atrovirens* and *Scirpus ancistrochaetus* have also been described (Schuyler, 1962). Further reports of hybridization in the *Scirpus cyperinus* complex are mentioned in Schuyler (1964). Undoubtedly, many other studies of hybridization exist in this large genus.

Poaceae

Borrill (1975) summarized British hybrids of *Glyceria*. Hybrid sweet-grass (*Glyceria* \times *pedicillata*) is an intermediate hybrid with inviable pollen suspected to originate from natural crossing between *Glyceria fluitans* and *Glyceria plicata* (Borrill, 1956, 1958, 1975). Artificial synthesis of the hybrid, however, has not yet been possible. Putative hybrids between *Glyceria declinata* ($2n=20$) and *Glyceria fluitans* ($2n=40$) have been described, but are suspect (Borrill, 1975) due to the lack of experimental verification or cytologically supportive evidence. No naturally occurring triploids have been found. The authenticity of *Glyceria* \times *digenea*, a putative hybrid between *Glyceria fluitans* and *Glyceria maxima*, has also been questioned (Lambert, 1947; Borrill, 1975). Obviously these and other reports of hybridization in *Glyceria* would benefit from more intensive experimental study.

The report by De Wet and Oelke (1978) that natural hybrids between *Zizania aquatica* and *Zizania palustris* occur frequently in sympatric populations, was based exclusively on their analysis of herbarium material. Some successful experimental crosses of these species have been made, but the species are seldom sympatric and there has been no evidence of hybrids in the field (Warwick and Aiken, 1986). An extensive electrophoretic investigation by Warwick and Aiken (1986) provided no evidence of naturally occurring hybridization between these species. Ample electrophoretic variability exists among both *Zizania* species as well as the varieties of *Zizania aquatica* to provide sufficient genetic markers for use in anticipated breeding programs (Warwick and Aiken, 1986). Crossing studies by Duvall and Biesboer (1988) indicate that hybridization between *Zizania aquatica* and *Zizania palustris* is at least possible, and may occur naturally at low frequencies.

There has been a vast amount of study on hybridization in the genus *Oryza*

(rice), and information concerning cultivars is voluminous. Suffice it to say that interspecific hybrids are common in *Oryza* sect. *Sativa* (some are also reported in sect. *Officinalis*) and *Oryza sativa* has been crossed experimentally with many species (e.g. *Oryza minuta*, *Oryza latifolia*) (Morinaga and Fukushima, 1956; Ranganadhacharyulu and Raj, 1974). With much of this information summarized elsewhere and in monographs, we consider it to be of little utility to further review it here.

Sparganiaceae

Cook (1961, 1975a) reported hybrids of *Sparganium angustifolium* and *Sparganium emersum* although there has been no supporting experimental evidence. Reports of hybrids involving *Sparganium erectum* and *Sparganium neglectum* are questionable as these taxa are now regarded as subspecies of *Sparganium erectum* (Cook, 1975a). Reported hybrids between *Sparganium emersum* and *Sparganium erectum* are probably erroneous; 'hybrid' specimens have been assigned to other taxa, and attempts to obtain viable F₁ progeny from this cross have been unsuccessful (Cook, 1962, 1975a). Beal (1960) hypothesized possible past hybridization between *Sparganium androcladum* and *Sparganium americanum*; natural hybrids of these species have not been found, however. He strongly encouraged the use of experimental studies to investigate this possibility.

Typhaceae

The cattail genus *Typha* is perhaps the best-studied example of hybridization in water plants from an experimental perspective. As early as the 1880s, hybridization involving *Typha latifolia* and *Typha angustifolia* was recognized in Europe (Roscoe, 1927; Lee, 1975; Smith, 1987). Kronfeld (1889) experimentally synthesized F₁ hybrids between the two species that were similar to *Typha glauca*. Experimental cytological observations documented the diploid nature of the suspected parents and revealed both regular meiosis and bivalent formation, as well as univalent formation in 'Typha angustifolia hybrids' (Roscoe, 1927). Fassett and Calhoun (1952) first suggested that *Typha glauca* was an introgressive hybrid between *Typha latifolia* and *Typha angustifolia* based upon intermediate recombinations of six morphological characteristics. Smith (1962, 1967) substantiated the proposed hybrid origin of *Typha* × *glauca* in more detail using cytological and morphological approaches. Lee and Fairbrothers (1969) used electrophoretic, morphological, and serological approaches to further investigate the occurrence of hybrids among *Typha angustifolia*, *Typha latifolia*, and *Typha domingensis* reported by Smith (1967). Their study confirmed the hybrid origin of *Typha* × *glauca*, and the distinctness of *Typha domingensis* from the other taxa (but see below).

Additional evidence of interspecific hybridization between *Typha angustifolia* and *Typha latifolia* was provided by further morphological and electrophoretic studies (Lee and Fairbrothers, 1973). Introgressive aspects of hybridization between *Typha angustifolia* and *Typha latifolia* were later studied by Bayly and O'Neill (1971) and Lee (1975). Lee (1975) provided electrophoretic and morphological evidence to document the occurrence of introgression, principally in the direction of *Typha angustifolia*. Tompkins and Taylor (1983) doubted the occurrence of introgressive hybridization in Michigan populations of *Typha angustifolia* and *Typha latifolia*. Sharitz et al. (1980) summarized the available evidence, concluding that no approach has provided unequivocal evidence that *Typha glauca* is an F₁ hybrid, represents introgressive hybrids, or is a genetically distinct species.

An electrophoretic study conducted by Mashburn et al. (1978) found no evidence of hybridization between *Typha domingensis* and *Typha latifolia*, although this cross has been made experimentally (Smith, 1987). Interspecific hybridization involving *Typha angustifolia* × *Typha shuttleworthii* and *Typha latifolia* × *Typha shuttleworthii* have also been studied biochemically (Krattinger, 1978; Krattinger et al., 1979). Other reports of *Typha* hybrids have remained essentially unconfirmed by biochemical data (Smith, 1987).

It is interesting that conclusions about hybridization have not been reached with certainty, even in a genus that has been studied extensively by experimental approaches. With this in mind, we emphasize that one should not place much confidence in the majority of hybrid reports offering only morphologically supportive evidence.

HYBRIDIZATION SUMMARY

Although it is impossible to adequately substantiate every claim of natural hybridization reported in aquatic angiosperms, several generalizations can be drawn from the studies discussed above. Vegetative reproduction has undoubtedly promoted the perpetuation of hybrid individuals in aquatic angiosperms because it allows for the survival and reproduction (asexual) of hybrids with low sexual fertility (e.g. *Cryptocoryne*, *Eleocharis*, *Limosella*, *Nasturtium*, *Potamogeton*, *Ranunculus*, *Scirpus*, *Veronica*). On the other hand, asexuality may also be a strong deterrent to hybridization in hydrophytes because widespread vegetative reproduction (e.g. *Ceratophyllum*, *Elodea*, *Nymphaea*, *Scirpus*) functions as an effective isolating mechanism. Because vegetative reproduction functions both to promote the perpetuation of hybrids once they are produced and to restrict hybridization via the production of large, clonal populations, the net result may be that the frequency of hybridization in aquatic plants is essentially similar to that found in terrestrial plant groups. Overall, the evolutionary role of hybridization in aquatic plants does not appear to differ in any fundamental way from that in terrestrial plants.

The propensity for vegetative growth may result in a higher incidence of 'apomictic speciation' (Grant, 1981) in hydrophytes. Vegetative apomixis circumvents the common sterility and incapacity for true breeding associated with *F₁* hybrids that may be adaptively superior (Grant, 1981).

Several hydrophyte hybrids demonstrate extreme vegetative vigor, allowing them to compete with or even displace parental species (e.g. *Eleocharis*, *Limosella*, *Nasturtium*, *Potamogeton*, *Ranunculus*, *Veronica*). In the unusual case of *Eleocharis palustris*, vegetative reproduction enables survival in a habitat where there is strong selection (i.e. grazing) against sexual reproduction.

Although selective advantages associated with hybridization are more difficult to ascertain, several possibilities exist. Certainly, hybridization contributes to increased heterozygosity, allowing for higher vigor where heterozygous advantage exists (e.g. *Nymphaea*). Several hybrids are reported to persist in areas where the parental species have disappeared (e.g. *Nasturtium*, *Nuphar*, *Potamogeton*), a conceivable indication of their greater competitive advantage. Hybrids may display greater vegetative vigor than the parental species (see above), or possess higher tolerances to extreme environmental conditions (e.g. *Limosella*). Hybrids have the potential to occupy zones of intermediate habitat conditions along environmental gradients such as water depth (*Potamogeton*) or specific conductivity (*Scirpus*). Some hybrids (e.g. *Eleocharis*) apparently survive in zones of disturbance better than parental species. Vegetative reproduction also functions to preserve structural chromosomal changes (e.g. *Nymphaea*) which may result in increased heterozygosity.

Currently, hybridization remains unstudied in many aquatic plant groups. Where studies are reported, only a small number have incorporated biochemical, isozyme, molecular, or even sophisticated numerical analyses. The wider application of empirical techniques to the study of hybridization in aquatic plants would benefit nearly every group that we have discussed. We also see the elucidation of effects of cytotypic variation on morphology and fertility as essential to the better understanding of aquatic plant hybrids.

POLYPLOIDY AND ANEUPLOIDY IN AQUATIC PLANTS

Polyplody is proclaimed as the most widespread cytogenetic speciation process in angiosperms (Dobzhansky et al., 1977). Owing to heterozygous advantage, allopolyploidy has been implicated in the stabilization of newly adapted species that result from hybridization of differently adapted genomes. This process results in the genetic isolation of diploid progenitors and polyploid derivatives, providing opportunity for rapid sympatric speciation (Briggs and Walters, 1984).

Polyplody mainly results from non-reduction in meiosis or by somatic mitotic doubling (Grant, 1981). Indeed, the fusion of non-reduced gametes is

TABLE 2

Reports of intrageneric (+/-) and intraspecific (species and counts listed) chromosome number variation in aquatic angiosperms (*, monotypic genus). References are excluded for genera where polyploidy and aneuploidy are documented by listed intraspecific examples. List is alphabetical by genus

Taxon	Euploid counts (2n)	Aneuploid counts (2n)	References
<i>Acorus</i>	+	+	
<i>Acorus calamus</i> L.	18, 36, 54	—	Packer and Ringius, 1984; Petersen, 1989
<i>Acorus gramineus</i> Soland.	—	22, 24	Petersen, 1989
<i>Acorus triquetus</i> Turc. & Schott	—	42, 44, 45, 46, 47, 48	Petersen, 1989
<i>Anubias</i>	+	—	Petersen, 1989
<i>Anubias barteri</i> Schott	48, 72	—	Petersen, 1989
<i>Alisma</i>	+	+	
<i>Alisma canaliculatum</i> A. Br. & Bouche	28, 42	34	Ornduff, 1967; Bolhovskikh et al., 1969
<i>Alisma lanceolatum</i> Withering	—	26, 28	Pogan, 1965
<i>Alisma plantago-aquatica</i> L.	14, 28	10, 12, 16	Bolkhovskikh et al., 1969
<i>Aponogeton</i>	+	+	
<i>Aponogeton distachyos</i> L.f.	16, 24, 32, 40, 48, 56, 80	—	Sharma and Chatterjee, 1967; Ornduff, 1968; Moore, 1977; Van Bruggen, 1985
<i>Aponogeton natans</i> (L.) Engl. & Krause	—	76, 78, 92	Sharma and Chatterjee, 1967; Ornduff, 1968; Moore, 1977
<i>Bacopa</i>	+	—	Barrett and Strother, 1978
<i>Baldellia</i>	—	+	Casper and Krausch, 1980
<i>Baldellia ranunculoides</i> (L.) Parlatore	—	14, 16, 18, 22	Casper and Krausch, 1980
<i>Barclaya</i>	—	+	Bolkhovskikh et al., 1969
<i>Bergia</i>	+	—	Bolkhovskikh et al., 1969

<i>Berula</i>	-	+	Bolkhovskikh et al., 1969; Casper and Krausch, 1981
<i>Berula erecta</i> (Hudson) Coville	-	12, 18, 20	Bolkhovskikh et al., 1969; Casper and Krausch, 1981
<i>Blyxa</i>	+	+	
<i>Blyxa octandra</i> (Roxb.)	16, 32	18	Sharma and Chatterjee, 1967; Ornduff, 1968; Bolkhovskikh et al., 1969
Planchon ex Thwaites			
<i>Buonomus umbellatus</i> L.*	20, 40	16, 22, 24, 26, 28, 39, 42	Sharma and Chatterjee, 1967; Bolkhovskikh et al., 1969; Casper and Krausch, 1981
<i>Cabomba</i>	+	+	
<i>Cabomba caroliniana</i> A. Gray	24, 96	104	Les, 1988b
<i>Calla</i>	+	-	Goldblatt, 1988
<i>Calla palustris</i> L.	36, 60, 72	-	
<i>Callitrichie</i>	+	+	
<i>Callitrichie cophocarpa</i> Sandtn.	-	10, 12	Bolkhovskikh et al., 1969
<i>Callitrichie hamulata</i> Kutz.	-	38, 40	Bolkhovskikh et al., 1969
<i>Callitrichie pedunculata</i> D.C.	-	20, 28	Bolkhovskikh et al., 1969
<i>Callitrichie petrei</i> R. Mason	20, 30	-	Bolkhovskikh et al., 1969
<i>Callitrichie polymorpha</i> Lönnr.	-	10, 12	Bolkhovskikh et al., 1969
<i>Callitrichie stagnalis</i> Scop.	10, 20	18	Bolkhovskikh et al., 1969; Hedberg and Hedberg, 1977
<i>Callitrichie verma</i> (L.) Lönnr.	-	16, 20	Bolkhovskikh et al., 1969
<i>Ceratophyllum</i>	+	+	
<i>Ceratophyllum demersum</i> L.	24, 48	38, 40	Goldblatt, 1988; Les, 1988b
<i>Ceratophyllum submersum</i> L.	24, 72	-	Les, 1988b
<i>Cotula</i>	+	+	Bolkhovskikh et al., 1969
<i>Cotula coronopifolia</i> L.	20, 40	-	Moore, 1977
<i>Cryptocoryne</i>	+	+	
<i>Cryptocoryne beckettii</i> Trimen	28, 42	-	Petersen, 1989
<i>Cryptocoryne ciliata</i> Schott	22, 33	-	Petersen, 1989
<i>Cryptocoryne cordata</i> Griff.	34, 68, 85, 102	-	Petersen, 1989
<i>Cryptocoryne crispatula</i> Eng.	36, 54	-	Petersen, 1989
<i>Cryptocoryne retrospiralis</i> (Roxb.) Kunth	36, 72, 90	-	Petersen, 1989
<i>Cryptocoryne spiralis</i> Wyd.	33, 66, 88, 132	-	Petersen, 1989

TABLE 2 (continued)

Taxon	Euploid counts (2n)	Aneuploid counts (2n)	References
<i>Cryptocoryne undulata</i> Wendt	28, 42	—	Petersen, 1989
<i>Cryptocoryne walkeri</i> Schott	28, 42	—	Petersen, 1989
<i>Cryptocoryne wendetii</i> De Wit	28, 42	—	Petersen, 1989
<i>Cymodocea</i>	+	—	
<i>Cymodocea nodosa</i> (Ucria) Aschers.	14, 28	—	Den Hartog et al., 1987
<i>Damasonium</i>	+	—	Bolkhovskikh et al., 1969; Moore, 1977; Goldblatt, 1985
<i>Downingia</i>	—	+	Bolkhovskikh et al., 1969
<i>Downingia concolor</i> Greene	—	16, 18	Bolkhovskikh et al., 1969
<i>Egeria</i>	+	—	Cook and Urmi-König, 1984b
<i>Egeria densa</i> Planch.	24, 48	—	Cook and Urmi-König, 1984b
<i>Eichhornia</i>	+	+	Banerjee, 1974; Eckenwalder and Barrett, 1986
<i>Eichhornia crassipes</i> (Mart.) Solms-Laubach	—	30, 32, 58	Banerjee, 1974; Eckenwalder and Barrett, 1986
<i>Elatine</i>	+	+	Bolkhovskikh et al., 1969; Löve and Löve, 1982
<i>Eleocharis</i>	+	+	
<i>Eleocharis palustris</i> (L.) Roemer & Schultes	16, 32, 40, 48	10, 14, 15, 17, 18, 33–39, 41, 42, 44, 46, 47, 49–51	Ornduff, 1967; Bolkhovskikh et al., 1969; Moore, 1977
<i>Elodea</i>	+	+	
<i>Elodea callitrichoides</i> (L.C. Richard) Caspary	16, 48	—	Cook and Urmi-König, 1985
<i>Elodea canadensis</i> Michx.	24, 48	—	Cook and Urmi-König, 1985
<i>Elodea nuttallii</i> (Planch.) St. John	24, 48, 56	32, 42–56	Cook and Urmi-König, 1985
<i>Eriocaulon</i>	+	+	
<i>Eriocaulon septangulare</i> With.	32, 64	60	Bolkhovskikh et al., 1969; Casper and Krausch, 1980
<i>Glossostigma</i>	+	—	Goldblatt, 1985

<i>Glyceria</i>	+	+	-	Bolkhovskikh et al., 1969
<i>Glyceria acutiflora</i> Torr.	20, 40	28, 56	-	Bolkhovskikh et al., 1969
<i>Glyceria aquatica</i> (L.) Wahlenb.	28, 56	-	20, 28	Bolkhovskikh et al., 1969
<i>Glyceria elata</i> (Nash) Hitchc.	-	-	28	Bolkhovskikh et al., 1969
<i>Glyceria fluitans</i> (L.) R. Br.	20, 40	-	28	Bolkhovskikh et al., 1969
<i>Glyceria grandis</i> S. Wats.	-	-	20, 28	Bolkhovskikh et al., 1969
<i>Glyceria maxima</i> (Hartm.) Holmb.	28, 56	60	-	Bolkhovskikh et al., 1969
<i>Glyceria plicata</i> Fries	-	-	28, 40	Bolkhovskikh et al., 1969
<i>Glyceria striata</i> (Lam.) Hitchc.	-	-	20, 28	Bolkhovskikh et al., 1969
<i>Gratiola</i>	+	+	+	Bolkhovskikh et al., 1969
<i>Haloragis</i>	+	+	+	Bolkhovskikh et al., 1969
<i>Heteranthera</i>	+	+	+	Eckenwalder and Barrett, 1986
<i>Heteranthera reniformis</i>	16, 32	-	-	Eckenwalder and Barrett, 1986
<i>Ruiz & Pavon</i>	-	-	-	
<i>Hippuris</i>	+	+	+	Bolkhovskikh et al., 1969; Casper and Krausch, 1981; Goldblatt, 1988
<i>Hippuris vulgaris</i> L.	32, 48	30	-	Bolkhovskikh et al., 1969
<i>Hottonia</i>	-	+	-	Chaudhuri and Sharma, 1978; Davenport, 1980; Verkleij et al., 1983; Goldblatt, 1988
<i>Hydrilla verticillata</i> (L.f.) Royle*	16, 24, 32	-	-	
<i>Hydrocharis</i>	+	+	+	Sharma and Chatterjee, 1967; Ornduff, 1968
<i>Hydrocharis asiatica</i> Miquel	-	-	14, 16	Goldblatt, 1988
<i>Hydrocharis dubia</i> (Blume)	-	-	14, 16	
<i>Backer</i>	-	-	-	
<i>Hydrocharis morsus-ranae</i> L.	14, 28	-	-	Bolkhovskikh et al., 1969
<i>Hydrocleys</i>	+	-	-	Bolkhovskikh et al., 1969
<i>Hydrocleys nymphoides</i> (Humb. & Bonpl. ex Willd.) Buchenau	16, 24	-	-	Bolkhovskikh et al., 1969
<i>Hygrophila</i>	+	-	-	Bolkhovskikh et al., 1969
<i>Hygrophila spinosa</i> T. Andres.	24, 32	-	-	Bolkhovskikh et al., 1969
<i>Lagarosiphon</i>	+	+	+	Bolkhovskikh et al., 1969

TABLE 2 (continued)

Taxon	Euploid counts (2n)	Aneuploid counts (2n)	References
<i>Lagenandra</i>	+	-	Petersen, 1989
<i>Lemna</i>	+	+	
<i>Lemna aequinoctialis</i> Welwitsch	20, 40, 50, 60, 70, 80	66, 72, 78, 81, 84	Urbanska-Worytkiewicz, 1980
<i>Lemna gibba</i> L.	40, 50, 70, 80	45, 64	Urbanska-Worytkiewicz, 1980
<i>Lemna japonica</i> Landolt	40, 50	-	Urbanska-Worytkiewicz, 1980
<i>Lemna minor</i> L.	20, 30, 40, 50	36, 38, 41, 42, 43	Urbanska-Worytkiewicz, 1980
<i>Lemna minuscula</i> Herter	-	36, 40	Urbanska-Worytkiewicz, 1980
<i>Lemna obscura</i> (Austin) Daubs	40, 50	42	Urbanska-Worytkiewicz, 1980
<i>Lemna trisulca</i> L.	20, 40, 60, 80	42, 44	Urbanska-Worytkiewicz, 1980
<i>Lemna turionifera</i> Landolt	40, 50, 80	36, 38, 42	Urbanska-Worytkiewicz, 1980
<i>Lemna valdiviana</i> Phil.	-	40, 55	Urbanska-Worytkiewicz, 1980
<i>Lilaeopsis</i>	+	-	Bolkhovskikh et al., 1969; Moore, 1977
<i>Limnobium</i>	-	+	Cook and Urmi-König, 1983
<i>Limnobium laevidatum</i> (Humb. & Bonpl. ex Willd.) Heine	-	26, 27, 28, 29, 30	Cook and Urmi-König, 1983
<i>Limnophila</i>	+	+	Bolkhovskikh et al., 1969
<i>Limnophyton</i>	-	+	Bolkhovskikh et al., 1969
<i>Limnophyton obtusifolium</i> (L.) Miq.	-	22, 24	Sharma and Chatterjee, 1967
<i>Limosella</i>	+	+	Bolkhovskikh et al., 1969
<i>Limosella aquatica</i> L.	-	36, 40	Bolkhovskikh et al., 1969
<i>Limosella australis</i> R. Br.	-	20, 48	Goldblatt, 1985
<i>Limosella macrantha</i> R.E. Fries	-	58, 59, 60	Bolkhovskikh et al., 1969
<i>Lobelia</i>	+	+	Bolkhovskikh et al., 1969
<i>Lobelia dortmanna</i> L.	-	14, 16	Bolkhovskikh et al., 1969
<i>Ludwigia</i>	+	-	Bolkhovskikh et al., 1969; Casper and Krausch, 1981
<i>Luronium natans</i> (L.) Raf.*	-	38, 42	Bolkhovskikh et al., 1969; Moore, 1977

<i>Luziola</i>	+	-	Moore, 1977
<i>Menyanthes trifoliata</i> L.*	54, 108	-	Bolkhovskikh et al., 1969
<i>Monochoria</i>	+	+	
<i>Monochoria vaginalis</i> Presl	26, 52	24, 28, 58, 60, 72, 74, 80, 87	Goldblatt, 1985; Eckenvelder and Barrett, 1986
<i>Monochoria hastaefolia</i> Presl	-	28, 34, 70, 76, 80, 82, 84	Banerjee, 1974; Moore, 1977; Goldblatt, 1985
<i>Montia</i>	+	+	
<i>Montia fontana</i> L.	20, 40	18	Taylor and Brockman, 1966; Casper and Krausch, 1981; Ward and Spellenberg, 1982
<i>Myriophyllum</i>	+	+	
<i>Myriophyllum spicatum</i> L.	-	36, 42	Moore, 1977; Aiken, 1979; Casper and Krausch, 1981; Ceska et al., 1986
<i>Myriophyllum ussurense</i> (Regel)	14, 21, 28	-	Aiken, 1979; Casper and Krausch, 1981; Ceska et al., 1986
<i>Najas</i>	+	+	
<i>Najas ancistrocarpa</i> A. Br.	12, 24	-	Bolkhovskikh et al., 1969
<i>Najas flexilis</i> (Willd.) Rostk. & Schmidt	12, 24	16	Bolkhovskikh et al., 1969
<i>Najas foveolata</i> A. Br.	12, 24	34	Bolkhovskikh et al., 1969
<i>Najas gracillima</i> (A. Br.) Magnus	12, 24, 36	-	Bolkhovskikh et al., 1969
<i>Najas guadalupensis</i> (Sprengel) Magnus	12, 36, 42, 48, 54, 60	-	Bolkhovskikh et al., 1969
<i>Najas marina</i> L.	12, 24	13, 14	Bolkhovskikh et al., 1969; Viinikka et al., 1987; Triest, 1989
<i>Najas minor</i> All.	12, 24, 36	-	Bolkhovskikh et al., 1969
<i>Najas tenuicaulis</i> Miki	-	12, 13, 14	Bolkhovskikh et al., 1969
<i>Nasturtium</i>	+	+	
<i>Nasturtium officinale</i> R. Br.	32, 48, 64	14	Bolkhovskikh et al., 1969
<i>Nelumbo</i>	+	-	Goldblatt, 1988
<i>Nephrophyllidium</i>	<i>cristi-galli</i>	-	
<i>Nephrophyllidium</i> (Menz.) Gilg.*		62, 68, 102	Bolkhovskikh et al., 1969

TABLE 2 (continued)

Taxon	Euploid counts (2n)	Aneuploid counts (2n)	References
<i>Nymphaea</i>	+	+	
<i>Nymphaea alba</i> L.	56, 84, 112	48, 52, 64, 96, 105, 160	Bolkhovskikh et al., 1969
<i>Nymphaea caerulea</i> Savigny	28, 56	48, 50	Gupta, 1980
<i>Nymphaea candida</i> Presl	—	112, 160	Bolkhovskikh et al., 1969
<i>Nymphaea daubeniana</i> Hort.	42, 84	56, 70	Gupta, 1980
<i>Nymphaea lotus</i> L.	56, 84	—	Bolkhovskikh et al., 1969
<i>Nymphaea odorata</i> Ait.	56, 84	—	Bolkhovskikh et al., 1969
<i>Nymphaea tetragona</i> Georgi	84, 112	120	Bolkhovskikh et al., 1969
<i>Nymphoides</i>	+	+	Bolkhovskikh et al., 1969
<i>Oenanthe</i>	+	+	Bolkhovskikh et al., 1969
<i>Ottelia</i>	+	+	
<i>Ottelia alismoides</i> (L.) Pers.	22, 44, 55, 66, 110, 132	28, 38, 40, 42, 48, 50, 52, 56, 60, 64, 68, 72	Sharma and Chatterjee, 1967; Chaudhuri and Sharma, 1978; Cook and Urmi-König, 1984a
<i>Oryza</i>	+	+	
<i>Oryza sativa</i> L.	12, 24, 36, 48	18, 22, 23	Moore, 1973; Ornduff, 1968; Bolkhovskikh et al., 1969; Goldblatt, 1985
<i>Phyllospadix</i>	—	+	
<i>Phyllospadix</i> sp.	—	16, 17, 18, 20	Harada, 1956
<i>Pistia stratiotes</i> L.*	14, 28	—	Petersen, 1989
<i>Pontederia</i>	+	—	Eckenwalder and Barrett, 1986
<i>Potamogeton</i>	+	+	
<i>Potamogeton crispus</i> L.	26, 52, 78	36, 42, 50, 72	Moore, 1973, 1977; Goldblatt, 1988
<i>Potamogeton filiformis</i> Pers.	—	66, 78	Bolkhovskikh et al., 1969
<i>Potamogeton foliosus</i> Raf.	14, 28	—	Bolkhovskikh et al., 1969
<i>Potamogeton natans</i> L.	—	42, 52	Bolkhovskikh et al., 1969
<i>Potamogeton pectinatus</i> L.	—	42, 70, 71, 73–87	Misra, 1972; Kalkman and Van Wijk, 1984
<i>Potamogeton perfoliatus</i> L.	26, 52	14, 48	Bolkhovskikh et al., 1969; Moore, 1973
<i>Potamogeton richardsonii</i> (A. Benn.) Rydb.	26, 52, 104	—	Stern, 1961; Bolkhovskikh et al., 1969

<i>Potamogeton trichoides</i> Cham. & Schlecht.	—	26, 28, 38-41	Bolkhovskikh et al., 1969
<i>Potamogeton vaginatus</i> Turcz.	—	78, 88	Bolkhovskikh et al., 1969
<i>Ranunculus</i>	+	+	Bolkhovskikh et al., 1969
<i>aquatilis</i> L.	32, 48	—	Cook, 1975b; Casper and Krausch, 1981
<i>fluitans</i> Lam.	16, 24, 32	—	Cook, 1975b; Casper and Krausch, 1981
<i>omniophyllus</i> Tenore	16, 32	—	Cook, 1975b; Casper and Krausch, 1981
<i>peltatus</i> Schrank	16, 24, 32, 48	—	Cook, 1975b; Casper and Krausch, 1981
<i>penicillatus</i> (Dumort.) Babington	16, 24, 32, 40, 48	—	Cook, 1966
<i>trichophyllum</i> Chaix	16, 24, 48	—	Cook, 1975a; Casper and Krausch, 1981
<i>Ruppia</i>	+	+	Darlington and Wylie, 1956; Cave, 1958-1965; Gamarro, 1968
<i>cirrhosa</i> (Petagna)	40, 60	39	
Grande			
<i>maritima</i> L.	20, 30, 40	14, 16, 24, 28	Darlington and Wylie, 1956; Cave, 1958-1965; Gamarro, 1968;
<i>Ruppia polycarpa</i> R. Mason	20	18	Bolkhovskikh et al., 1969; Richardson, 1983
<i>Ruppia tuberosa</i> J.S. Davis & Tomlinson	20, 30	—	Jacobs and Brock, 1982
			Snoeijs and Van der Ster, 1983
<i>Sagittaria</i>	+	+	Jiajkuau, 1989; Sharma and Chatterjee, 1967
<i>sagittifolia</i> L.	—	16, 20, 21, 22	Jiajkuau, 1989
<i>subulata</i> (L.) Buchenau	22, 44	—	Jiajkuau, 1989
<i>trifolia</i> L.	—	20, 22	Jiajkuau, 1989
<i>Sparganium</i>	+	—	Bolkhovskikh et al., 1969
<i>stenocephalum</i>	30, 45	—	Bolkhovskikh et al., 1969
<i>Maximovich ex Meinshausen</i>			
<i>Spirodela</i>			
<i>hiperforata</i> W. Koch	20, 30	+	Urbanska-Worytkiewicz, 1980
<i>intermedia</i> W. Koch	20, 30	32	Urbanska-Worytkiewicz, 1980
<i>polyrhiza</i> (L.) Schleid.	40, 50, 80	—	Urbanska-Worytkiewicz, 1980
<i>punctata</i> (G.F.W. Meyer)	40, 50	34, 38, 62	Urbanska-Worytkiewicz, 1980
Thompson		43, 44	

TABLE 2 (continued)

Taxon	Euploid counts (2n)	Aneuploid counts (2n)	References
<i>Stratiotes aloides</i> L.*	24, 48	40	Sharma and Chatterjee, 1967; Bolkhovskikh et al., 1969; Moore, 1977
<i>Subularia</i>	+	+	
<i>Subularia aquatica</i> L.	-	28, 36	Bolkhovskikh et al., 1969
<i>Trapa natans</i> L.*	36, 48	40	Bolkhovskikh et al., 1969
<i>Triglochin</i>	+	-	Löve and Löve, 1958
<i>Triglochin maritimum</i> L.	12, 48	-	Darlington and Wylie, 1956
<i>Typha</i>	+	-	Bolkhovskikh et al., 1969
<i>Utricularia</i>	+	+	
<i>Utricularia dichotoma</i> Labill.	28, 56	-	Moore, 1974; Goldblatt, 1985
<i>Utricularia inflata</i> Walt.	18, 36	-	Bolkhovskikh et al., 1969
<i>Utricularia minor</i> L.	-	34-40, 44	Bolkhovskikh et al., 1969; Goldblatt, 1985
<i>Utricularia neglecta</i> Lehmann	-	36-40	Bolkhovskikh et al., 1969
<i>Utricularia vulgaris</i> L.	-	36-40, 44	Bolkhovskikh et al., 1969; Goldblatt, 1985
<i>Vallisneria</i>	+	+	
<i>Vallisneria asiatica</i> Miki	-	20, 24	Chaudhuri and Sharma, 1978
<i>Vallisneria spiralis</i> L.	20, 30, 40	16, 18, 24	Sharma and Chatterjee, 1967; Chaudhuri and Sharma, 1978
<i>Veronica</i>	+	+	
<i>Veronica anagallis-aquatica</i> L.	18, 36	-	Bolkhovskikh et al., 1969
<i>Veronica anagalloides</i> Guss.	18, 36	-	Öztürk and Fischer, 1982
<i>Veronica beccabunga</i> L.	18, 36	-	Öztürk and Fischer, 1982
<i>Victoria</i>	-	+	Bolkhovskikh et al., 1969
<i>Villarsia</i>	+	-	Ornduff, 1974
<i>Villarsia reniformis</i> R. Br.	18, 36, 54	-	Ornduff, 1974
<i>Wolffia</i>	+	+	
<i>Wolffia arrhiza</i> L.	30, 40, 50, 60, 70, 80	44-46, 62, 74, 76	Urbanska-Worytkiewicz, 1980
<i>Wolffia australiana</i> (Benth.) Den Hartog & Plas	20, 40	-	Urbanska-Worytkiewicz, 1980
<i>Wolffia borealis</i> (Engelm.) Landolt	20, 30, 40	23, 38	Urbanska-Worytkiewicz, 1980
<i>Wolffia brasiliensis</i> Weddell	20, 40, 50, 60, 80	42, 44	Urbanska-Worytkiewicz, 1980

<i>Wolfia columbiana</i> Karsten	30, 40, 50, 70	42	Urbanska-Worytkiewicz, 1980
<i>Wolfia globosa</i> (Roxb.) Den Hartog & Plas	30, 40, 50, 60, 70, 80	46	Urbanska-Worytkiewicz, 1980
<i>Wolfia microscopica</i> (Griff.) Kurz	40, 70, 80	—	Urbanska-Worytkiewicz, 1980
<i>Wolfiella</i>	+	—	Urbanska-Worytkiewicz, 1980
<i>Wolfiella denticulata</i> (Hegelm.) Hegelm.	20, 40	—	Urbanska-Worytkiewicz, 1980
<i>Wolfiella lingulata</i> (Hegelm.) Hegelm.	20, 40, 50	—	Urbanska-Worytkiewicz, 1980
<i>Wolfiella oblonga</i> (Phil.) Hegelm.	40, 50, 70	—	Urbanska-Worytkiewicz, 1980
<i>Zannichellia</i>	+	+	Talavera et al., 1986
<i>Zannichellia palustris</i> L.	24, 36	28, 34	Talavera et al., 1986
<i>Zannichellia pedunculata</i> Reichenb.	24, 36	—	Talavera et al., 1986
<i>Zannichellia peltata</i> Bertol.	12, 36	—	Van Vierssen and Van Wijk, 1982
<i>Zizania</i>	—	+	Bolkhovskikh et al., 1969
<i>Zizania latifolia</i> (Griseb.) Stapf	—	30, 34	Bolkhovskikh et al., 1969

assumed to be the most common mechanism of polyploid formation in plants (De Wet, 1980). However, because of the highly attenuated sexual reproduction in hydrophytes (Sculthorpe, 1967; Hutchinson, 1975; Bartley and Spence, 1987; Les, 1988a) we predict that somatic doubling may be a common, if not predominant, mode of polyploidy in aquatic plants. Certainly the predominance of clonal growth and the vagility of asexual propagules in aquatics would serve to perpetuate and disperse polyploid genotypes regardless of their mode of origin.

Interestingly, the experimental study of polyploidy extends back to Winkler (1916) who discovered that diploid *Solanum* shoots regenerated tetraploid shoots vegetatively (somatic doubling) from stem callus. The documentation of allopolyploidy in *Primula kewensis* also revealed that somatic doubling could result in the production of fertile tetraploid branches from sterile diploid shoots (Briggs and Walters, 1984). The association between vegetative reproduction and polyploidy has been emphasized repeatedly. Vegetative reproduction prolongs the opportunity for somatic doubling to occur (Stebbins, 1938; Grant, 1956, 1981).

Aneuploidy provides the potential for novel genetic variation and abrupt modes of speciation (Briggs and Walters, 1984). Here too, as in polyploidy, asexuality furnishes a mode of replicating favorable new variants arising from aneuploidy (Grant, 1981). Because hydrophytes represent some of the most effective vegetatively reproducing plants, they are ideal models for the evolutionary study of aneuploidy and polyploidy.

Aneuploidy and polyploidy are common in angiosperms. It is clear that hybridization, which is necessary for the production of either allo- or segmental allopolyploids, is intimately tied to the process of polyploidy. In aquatic plants, sexual reproduction and high vagility may provide opportunities for 'raw' polyploid genotypes to persist for extended periods and to be dispersed regardless of their fertility. The same is true for somatically derived aneuploid derivatives. This idea has received little attention in the evolutionary or taxonomic literature, yet the implications on each may be significant. Dispersal of vegetatively vigorous but sexually sterile genotypes could affect our general understanding of the importance of hybridization in aquatic plants (see above). Cytological polymorphisms could also play a role in the evolutionary 'success' of aquatics, and also relate to why aquatic groups are typically poor in species. Herein we focus on cytological variation at the intrageneric and intraspecific levels.

INTRAGENERIC AND INTRASPECIFIC POLYPLOIDY AND ANEUPLOIDY IN AQUATIC ANGIOSPERMS

We found reports of intrageneric chromosome number variation in 80% of the aquatic genera for which chromosome number reports are available

(Table 2). Chromosome numbers are unreported for roughly 40% of the aquatic angiosperm genera. Of this sample, 85% contained polyploid derivatives and 76% contained aneuploid derivatives. Approximately 61% of these genera contained both aneuploid and polyploid derivatives. Of the cytologically 'uniform' genera (where chromosome number reports indicate no variation), 65% are monotypic and 90% have fewer than five species (Table 3). In context, about 30% of aquatic angiosperm genera are monotypic, with 59% of these in the dicots. Monotypic genera are common in some families (e.g. 44% of genera in Podostemaceae).

Intraspecific chromosome number variation is reported in 155 aquatic species from 63 genera (Table 2). The number of cytotypes ranges from 2 to 24 with 71% of these species possessing euploid cytotypes and 58% possessing aneuploid cytotypes. About 30% of these species have both euploid and aneuploid cytotypes.

DISCUSSION OF POLYPLOIDY AND ANEUPLOIDY IN SELECTED GROUPS OF AQUATIC ANGIOSPERMS

Nymphaeaceae (*Nymphaea*)

Polyploidy is estimated to occur in more than 85% of the species of *Nymphaea*, with most showing multivalent formation indicating segmental allo-

TABLE 3

Cytologically 'uniform' aquatic genera (no reported chromosome number variation)

Taxon	Diversity
<i>Aldrovanda</i>	(Monotypic)
<i>Amphianthus</i>	(Monotypic)
<i>Brasenia</i>	(Monotypic)
<i>Butomopsis</i>	(Monotypic)
<i>Caldesia</i>	(Four species)
<i>Cymodocea</i>	(Four species)
<i>Enhalus</i>	(Monotypic)
<i>Euryale</i>	(Monotypic)
<i>Groenlandia</i>	(Monotypic)
<i>Halophila</i>	(Ten species)
<i>Hygroriza</i>	(Monotypic)
<i>Lepilaena</i>	(Five species)
<i>Lilaea</i>	(Monotypic)
<i>Limnocharis</i>	(Two species)
<i>Littorella</i>	(Three species)
<i>Megalodonta</i>	(Monotypic)
<i>Neopaxia</i>	(Monotypic)
<i>Nuphar</i>	(Seven to 20 species)
<i>Orontium</i>	(Monotypic)
<i>Scheuchzeria</i>	(Monotypic)

polyploidy (Gupta, 1978, 1980), or perhaps, autoployploidy. The lack of multivalents in three polyploid taxa indicated allopolyploidy (Gupta, 1980). Most species of *Nymphaea* are hexaploid, arising from hybridization between diploids and tetraploids (followed by chromosome doubling), or from hybridization between tetraploids and octoploids (Gupta, 1980). These proposed modes of origin provided convenient explanation for varying levels of fertility observed among hexaploid nymphaeas (Gupta, 1980). Similarly, tetraploid origins are either from diploids or by hybridizations involving diploid and hexaploid species (Gupta, 1980). Structural chromosomal changes are believed to play a large role in speciation at all ploidy levels (Gupta, 1980).

Ranunculaceae (*Ranunculus*)

Species in the *Ranunculus penicillatus* group with $2n=32,48$ are putative amphiploids resulting from the hybrids *Ranunculus fluitans* \times *Ranunculus aquatilis* and *Ranunculus fluitans* \times *Ranunculus trichophyllus* (Cook, 1966, 1975b). Cook (1975b) suggested that *Ranunculus aquatilis* subsp. *pseudofluitans* may be an amphiploid derivative of the hybrid *Ranunculus fluitans* \times *Ranunculus peltatus*. Synthetic hybrids of *Ranunculus omiophyllus* and *Ranunculus tripartitus* exhibit aneuploidy ($2n=36-42$) in the normally $x=8$ group (Cook, 1975b).

Brassicaceae

Meiotic configurations of triploid hybrids between diploid *Nasturtium officinale* and tetraploid *Nasturtium microphyllum* (see above) display 16 bivalents and 16 univalents, evidence that *Nasturtium microphyllum* is an allopolyploid containing the genome of *Nasturtium officinale* and one unknown parent (Stace, 1975a). Synthetic autotetraploids of *Nasturtium officinale* have low fertility and resemble diploids; they cross successfully with *Nasturtium microphyllum* (tetraploid), although these hybrids also have low fertility (Stace, 1975a).

Hydrocharitaceae

Verkleij et al. (1983) concluded that there was no correlation of chromosome numbers and morphology in the dioecious *Hydrilla verticillata*. Perhaps overlooked is the fact that none of the nine triploid ($2n=24$) populations they studied produced both male and female flowers under laboratory conditions, whereas ten diploid populations produced flowers of both sexes. In *Hydrilla*, the sex of individuals is not specifically a function of ploidy level as some believe. Diploid and tetraploid plants have been observed to produce both male and female flowers (Verkleij et al., 1983). Factors governing sex

expression in aneuploids and polyploids are virtually unknown in aquatic plants.

Potamogetonaceae (*Potamogeton*)

Studies of aneuploidy and polyploidy in *Potamogeton* were summarized by Les (1983) who verified two base numbers ($x=7$, $x=13$) with various euploid species in each group ($2n=26, 52, 78, 104; 14, 28, 42$). Later observations that derivatives of both base numbers occur in ten subsections of the genus and within six species seriously called into question a single origin of an $x=13$ series (Les and Sheridan, 1990). Chromosome numbers reported by Les (1983) were 'consensus' counts owing to a large number of studies reporting deviating numbers (more than a dozen taxa were reported with varying counts). Kalkman and Van Wijk (1984) subsequently revealed the existence of highly heterogeneous counts within and among 15 populations of *Potamogeton pectinatus*, yielding 17 cytotypes for the species. Some localities contained as many as ten different cytotypes.

Araceae (*Cryptocoryne*)

Cryptocoryne species display a wide range of aneuploidy and polyploidy with $2n=34$ species believed to have originated from $2n=35$ allopolyploids which resulted from crosses between $2n=28$ tetraploids and $2n=42$ hexaploids (Sculthorpe, 1967). The situation appears to be much more complex, however, with counts revealing a remarkable array of six aneuploid base numbers and 18 derived polyploid levels in the genus (Petersen, 1989). Petersen (1989) surmised that the series may have originated as $x=9$, and suggested that centric fission and fusion may have been the mechanism involved in producing the wide range of observed aneuploidy.

Lemnaceae

An excellent example of a highly vegetatively propagating group with wide cytological variability is the Lemnaceae (duckweeds). The Lemnaceae exhibit a wide range of both aneuploidy and polyploidy within individuals (clones), populations, and races, but levels of both intra-individual (3.3%) and intra-populational (1.3%) variability are low (Urbanska-Worytkiewicz, 1980).

VEGETATIVE REPRODUCTION AND CHROMOSOME NUMBER VARIATION IN AQUATIC ANGIOSPERMS

Somatically arising chromosome number variation (polysomy) has been observed in a number of aquatic species including *Nymphaea dentatamagnifica*, *Nymphaea bissetii*, *Nymphaea daubeniana*, *Sagittaria sagittifolia*, *Hydrocharis dubia*, and many Lemnaceae. Gupta (1978) observed that *Nymphaea dentatamagnifica* and the cultivar 'Sunrise' exhibit variation of somatic chromosome numbers in root-tip tissue. Later studies of this taxon (Gupta, 1980) revealed that only 64% of cells possessed the normal chromosome number of $2n=84$, with $2n=70$, 105, 126, and 168 also occurring. Sen and Bhaduri (1971) reported polysomy in other *Nymphaea* species, attributing the cause to non-disjunction. The presence of 'syncytes' containing up to 672 chromosomes (eight times the normal hexaploid number) were observed in root apices of *Nymphaea bissetii* (Gupta, 1980). Following division, chromosome complements fused and intermingled to produce highly polyploid nuclei. Meiotic counts of *Nymphaea daubeniana* ($2n=42$) have revealed anomalous numbers of 56, 70, and 84, and in *Nymphaea caerulea* ($2n=28$), counts of $2n=48$, 50, and 56 were similarly observed (Gupta, 1980). These anomalous meiotic counts are attributed to persistence of somatically originating abnormalities (Gupta, 1980).

Cells with $2n=20$ were detected in normally $2n=22$ tissue of *Sagittaria sagittifolia* (Sharma and Chatterjee, 1967). Because this species exhibits a high degree of vegetative reproduction, the perpetuation and perhaps, spread of the 'aberrant' cytotypes is predictable. In *Hydrocharis dubia* ($2n=22$), somatic cells also possess $2n=14,16,20$; pollen mother cells with $n=7,8,10$ and pollen grains with $n=10,11$ have been observed and meiosis was irregular (Sharma and Chatterjee, 1967). Both aneusomy and mixoploidy have been documented in individuals of Lemnaceae including species of *Lemna*, *Spirodela*, *Wolffia*, and *Wolfiella* (Urbanska-Worytkiewicz, 1980).

Studies of aquatic plant clones indicate that somatic changes in the chromosome number of individuals can occur rapidly. Of particular interest is the documented production of aneuploid ramets derived from the 'Wolf Lake strain' of *Elodea nuttallii* with four chromosomal complements ($2n=32,42,44,48$) arising after only 73 years in cultivation (Cook and Urm-König, 1985). In the Lemnaceae, a $2n=50$ clone of *Lemna aequinoctialis* produced $2n=78,81$ ramets in 10 years, one clone of *Lemna minor* was observed to exhibit fluctuating chromosome numbers during only a few years of study, a $2n=50$ clone of *Wolffia columbiana* produced $2n=40,42$ derivatives in 5 years, and $2n=70$ clones of *Wolfiella oblonga* changed to $2n=40$ in 3 years (Urbanska-Worytkiewicz, 1975, 1980). In *Monochoria vaginalis*, a clone changed from $2n=52$ to $2n=26$ in 2 years (Banerjee, 1974).

DISCUSSION OF CHROMOSOME NUMBER VARIATION

These studies establish that aquatic plants have a prodigious capacity for producing and vegetatively reproducing somatically induced chromosome number variation. This process efficiently allows for the perpetuation of novel cytotypes in future generations. Vegetative apomixis also helps to preserve and reproduce any structural chromosomal changes accompanying aneuploid changes.

The dispersal of genetically novel cytotypes to new environmental micro-habitats, and the survival and reproduction of sexually sterile (but potentially adaptive) cytotypes are likely to be critical factors influencing the evolutionary potential of aquatic plants. The suggestion that vegetative reproduction allows for unique evolutionary potential in plants has been made previously on several occasions (e.g. Sharma, 1956; Sharma and Sharma, 1959; Grant, 1981; Sutherland and Watkinson, 1986).

Grant (1981) attributed a greater evolutionary potential to agamic hybrids than to those reproducing vegetatively because of the higher vagility associated with seeds than vegetative propagules. Vegetative propagules produced by hydrophytes, however, were excluded in that account. In terrestrial plants, it may be true that ramets generally remain spatially close to the parental plant where they exist under similar environmental conditions. Unless environmental conditions change to favor genetically novel ramets, the new genotypes are unlikely to displace the parental genotypes. In hydrophytes, however, vegetative propagules commonly detach or are transported over considerable distances. Their vagility can be regarded at least as high as for seeds produced by agamic species. As a result, genetically novel ramets may eventually settle in habitats to which they are uniquely adapted, thus promoting adaptive evolution entirely in exclusion of sexual reproduction. It is irrelevant whether novel genetic variation has arisen through hybridization and/or by chromosome number change. If resulting individuals are sterile, the evolutionary potential of such changes will be greatly enhanced by vegetative reproduction and vagility.

Some possible examples of this process (relating to aneuploidy) have been suggested. The discovery that isolated populations of *Ottelia alismoides* possess different cytotypes suggests that particular genotypes are adapted to specific environmental conditions (Sharma and Chatterjee, 1967) although such correlations have not been firmly established (Cook and Urmi-König, 1984a). High pollen fertility suggests that their cytotypes are fairly stable meiotically (Chaudhuri and Sharma, 1978). Widespread unisexuality of *Hydrilla* populations has been hypothesized to indicate adaptive strains living in environments where seed production is unimportant (Verkleij et al., 1983). Urban-ska-Worytkiewicz (1980) suggested that the prolific vegetative reproduction of duckweeds overcomes deleterious effects associated with aneuploidy and

odd-ploidy, allowing for genetically distinct clones to respond differentially to environmental conditions, and to convey these genotypes to subsequent generations. Gupta (1978) concluded that endopolyploidy was an important factor in water lily speciation due to their predominantly vegetative means of reproduction.

A number of additional observations point to the evolutionary importance of chromosome number variation in aquatic angiosperms. Low species diversity correlates with genera (mainly monotypic) which lack reports of chromosome number variation (Table 3). This observation indicates a possible association between the extent of polyploidy and aneuploidy in a genus and the number of species. Certainly, polyploidy has been important evolutionarily in *Nymphaea* in which 85% of the species are estimated to be polyploids (see above). An interesting observation is that the higher polyploids of the perennial *Najas guadalupensis* are sterile, whereas tetraploids of the annual *Najas flexilis* are fertile (Chase, 1947). Ineffective sexual reproduction in the genus *Utricularia* (Yamamoto and Kadono, 1990) is correlated with a wide range of chromosome number variation (Table 2).

The effects of aneuploidy and polyploidy on the phenotypes and fertility of hydrophytes are uncertain. Too few detailed analyses have been conducted upon which a generalization can be based. Chromosome number change and/or hybridization can produce 'deviant' phenotypes, which may be intermediate between those of other species. Unless detailed studies are conducted, it is not possible to establish which of these two phenomena (or perhaps, a combination of the two) is responsible. Because aquatic plants are typically viewed as being phenotypically plastic, it is especially difficult to ascertain the degree of plasticity that is 'normal' rather than that which is induced by other factors.

DIRECTIONS FOR FUTURE RESEARCH

The current understanding of the extent and importance of hybridization and chromosome number change in aquatic plants varies considerably among taxonomic groups. Some species, genera or families are well known in one or both regards, whereas most others are poorly known. Considerable work in this area is needed before the systematic and evolutionary implications of these processes will be fully understood.

Future work should proceed in two directions: documentation and inference. Documentation should be viewed as only the first step leading to insight regarding the relationship of these processes to the distributions, life-history traits, vigor, fitness, and phylogenetic relationships of hydrophytes. It is evident that even in groups that have been fairly well studied, little more than initial documentation has yet been achieved.

The development of molecular techniques provides the opportunity for dramatic empirical and conceptual advances in this area. It is now possible to

proceed well beyond the largely anecdotal information currently available for questions of hybridization. There is no longer a need to rely on environmentally malleable markers to assess parental-hybrid relationships when molecular markers can now be applied with far greater accuracy. Molecular markers may also prove to be useful for quickly and precisely identifying chromosome number variants once they are initially identified cytologically. We also envision the use of molecular markers to trace the distribution of genotypes derived from hybridization and/or chromosome number change ('derived genotypes') both within and between populations, as well as throughout regional or broader geographical areas.

It will also be important to assess the influence of hybridization and chromosome number change on life history traits. Alterations in the reproductive system (both sexual and asexual) associated with such genetic changes deserve detailed analysis. It is worth questioning whether the rarity of flowering that characterizes aquatic plants is linked in some way to these processes. Other avenues of research should explore potential relationships between derived genotypes and the colonization of open and disturbed habitats. This issue may be particularly relevant to questions concerning aquatic weed invasions.

Aquatic angiosperms have received considerable attention from biologists during the past century. However, our understanding of their evolutionary patterns and processes lags well behind that of terrestrial plants. Yet, some of the most perplexing evolutionary questions in angiosperms pertain to aquatic groups. Aquatic plants provide a plethora of research opportunities for evolutionary biologists. We predict that the development of conceptual models which focus on hydrophytes, and their testing, will make the next decade an exciting period for the advancement of our understanding of this fascinating biological group.

NOTE ADDED IN PROOF

The reference: Goldblatt, P. and Johnson, D.E., 1991. Index to plant chromosome numbers 1988–1989. Monogr. Syst. Bot. Mo. Bot. Gard. Vol. 40, 238 pp. provides several additional counts and taxa for Table 2: *Alisma canaliculatum* ($2n=40$), *Egeria densa* ($2n=46$), *Elatine hexandra* ($2n=72, 108$), *Monochoria hastata* ($2n=82, 80$), *Monochoria korsakowii* ($2n=52-56$), *Montia hallii* ($2n=18, 20$), *Najas graminea* ($2n=12, 24, 36$), *Najas marina* ($2n=60$), *Najas minor* ($2n=46$), *Nasturtium officinale* ($2n=33, 34, 36, 60$), and *Triglochin maritimum* ($2n=120$). We encourage readers to provide us with other additions or corrections to this table.

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