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The Adventive Status of Salvinia minima and S. molesta in the Southern United States and the Related Distribution of the Weevil Cyrtobagous salviniae

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ABSTRACT

The recent introduction of Salvinia molesta constitutes a serious threat to aquatic systems in the warm temperate regions of the United States. Salvinia minima, the only other member of Salviniaceae present in North America, is considered native by current floras. Evidence is presented which suggests that Salvinia minima was also introduced to North America, probably during the late 1920s and early 1930s. Likely sites of introduction and subsequent range expansions are identified. The accidentally introduced salvinia weevil, putatively Cyrtobagous salviniae, was found to occur widely on S. minima in Florida but is not established in other states. The disparate distribution of this Salvinia herbivore may account for the reduced aggressiveness of S. minima in Florida as compared to its troublesome growth in Texas and Louisiana, where the weevil is not yet known.

INTRODUCTION

The aquatic fern family Salviniaceae consists of a single genus, Salvinia. They are small floating rootless plants best represented in tropical and warm temperate regions. Horizontal branching rhizomes bear leaves in whorls of three. Two are floating, green and entire; the third is submersed and highly divided. Submersed leaves resemble but are not known to function as roots. Floating leaves are generally ovate to cordate with distinct midribs, water repellant hairs on the upper surface, and castaneous hairs on the undersurface. Submersed leaves support heterosporous sporangia. Megasporangia and microsporangia occur on the same plant but in separate sporocarps. The genus represents, mainly polyploid species with a base chromosome number n = 9 (Schneller 1981, Madhusoodanan 1988). Salvinia molesta is pentaploid, demonstrates irregularities during meiosis that prevent normal spore formation, and is functionally sterile (Loyal and Grewal 1966). The chromosome number for S. minima has not been reported, however like S. molesta, it is postulated to be a hybrid (Schneller 1980). All Salvinia species reproduce vegetatively.

Ten species of Salvinia occur worldwide (Herzog 1935; de la Sota 1962, 1963, 1964, 1982; Mitchell 1972). Seven originate in the tropical Americas, where S. minima Baker and S. auriculata Aublet are most common (de la Sota 1976). Salvinia auriculata represents a complex of four species, S. auriculata, S. molesta Mitchell, S. biloba Raddi and S. herzogii de la Sota. All bear divided hairs on the upper surface that are joined apically, a feature commonly described as an "egg-beater like" structure (de la Sota 1962, Mitchell and Thomas 1972, Forno 1983). All members of the S. auriculata complex are predicted to grow aggressively if introduced to the United States and are therefore prohibited as Federal noxious weeds.

Through the agency of humans, *Salvinia molesta* is now widely distributed in tropical and subtropical regions, where it is notorious for dominating water bodies with slow moving fresh water (Forno and Harley 1979, Mitchell et al. 1980). Prodigious vegetative proliferation (Mitchell and Tur 1975, Room and Thomas 1986, Lemon and Posluszny 1997) and tolerance to

environmental stress such as low temperatures (Whiteman and Room 1991) enable it to be an extremely competitive species. However, the density and extent of S. molesta populations is much less in its native distribution of southeastern Brazil. There it occurs to altitudes of 500 m between latitudes $24^{\circ}05'S$ and $32^{\circ}05'S$ extending 200 km inland (Forno and Harley 1979). Salvinia molesta was recently reported as naturalized in North America, in Texas and Louisiana (Jacono 1999). It has since been found in Alabama [Bryant s.n. (UNA)] and Mississippi [Henderson s.n. (IBE)]. Sterile plants collected in Florida [Smith s.n. (FLAS)] and Georgia [Ellis s.n. (GA, VSC)] and from the lower Colorado River, bordering Arizona and California [Velasco s.n. (FLAS)], are also attributed to this species.

Salvinia minima ranges from south central Mexico to northern Argentina (Mickel and Beitel 1988, Stolze 1983). In North America, it is listed for Florida, Georgia, Alabama and Louisiana (Nauman 1993), where it pre-dates *S. molesta*. Recent works consider *S. minima* native to North America (Nauman 1993, Wunderlin 1998). However, Fernald (1950) considered the species to be introduced to the United States. *Salvinia minima* is regarded as introduced to Bermuda (Weatherby 1937), Puerto Rico (Proctor 1989) and Spain (Lawalree 1964). Although smaller, it is best distinguished from species in the *S. auriculata* complex by the presence of divided hairs on the upper leaf surface that are spreading and free at the tips. Nauman (1993) noted that this character could sometimes be difficult to interpret in herbarium specimens. We found that intact hairs could often be found in undeveloped or folded leaves of dried specimens and were always distinguishable on fresh plants.

The salvinia weevil, Cyrtobagous salviniae Calder and Sands, has been used to effectively control Salvinia molesta in many tropical and subtropical countries (Thomas and Room 1986, Cilliers 1991). This highly specialized insect tunnels through rhizomes and feeds on buds. This has the effect of greatly reducing large infestations of S. molesta and maintaining low population levels (Sands et al. 1983, Sands and Schotz 1985, Room et al. 1981). Cyrtobagous salviniae feeds only on Salvinia species (Forno et al. 1983). This weevil ranges naturally in south-eastern Brazil, Bolivia, Paraguay and northern Argentina (Wibmer and O'Brien 1986, Calder and Sands 1985). The genus Cyrtobagous is adventive to North America. Cyrtobagous salviniae was accidentally introduced to Miami, Florida sometime before 1960, the date of the first specimen collected in the United States (C.W. O'Brien, private collection), which was initially reported as C. singularis Hustache (Kissinger 1966). To date, the North American distribution of C. salviniae and its impact on S. minima has not been determined.

This study was undertaken to investigate the status and occurrence of Salvinia in the southern United States. Objectives were 1) to determine the geographic distribution of S. minima, 2) to develop a chronology for early records on S. minima in order to evaluate native status and 3) to determine the distribution of Cyrtobagous salviniae associated with S. minima.

METHODS

The distribution of Salvinia minima was determined from a number of sources: from location data on specimens deposited at A, CLEMS, FLAS, FSU, GA, GH, HGCLR, IBE, NLU, NY, NYBG, PH, PIHG, UNA, USCH, USF, USM, VSC (acronyms from Holmgren et al. 1990), from published location data (Landry 1981, Hatch 1995, Montz 1989, Nauman 1978, Faircloth 1975), from aquatic vegetation surveys (Florida Department of Environmental Protection Aquatic Plant Survey Database 1999; Helton and Hartmann 1996, 1997; Zolcynski and Eubanks 1990; Zolcynski and Shearer 1997), from observations communicated to the principal author by regional biologists, and from collection by the authors. All locality data were geographically referenced by aligning location within the United States Geological Survey (USGS) 8-digit Hydrologic Unit Code in order to illustrate the occurrence of aquatic species according to natural drainage basins. Maps were made with Arc/Info® version 7.2.1 computer software (Environmental Systems Research Institute, Inc., Redlands, California). A total of 1486 records from over 640 locations in seven states were geographically referenced to determine the distribution of S. minima in 69 drainage basins.

Surveying was conducted to determine the presence and distribution of *Cyrtobagous sal*viniae on Salvinia in the southern United States. In Florida, 46 populations of *S. minima* were

sampled within 30 of the 38 drainage basins known to support that species. Outside of Florida, S. minima was sampled at one site in South Carolina, five in Georgia, one in Alabama, 16 in Louisiana and one in Texas. Salvinia molesta was sampled at one site each in Florida and in Alabama and at five sites in Texas.

Plant material selected for collection covered at least one-tenth of a square meter. Plants were stored in plastic bags that were perforated with small holes to allow water drainage through the bottom. Material was kept cool with ice chests and refrigeration and processed within three days. Representative herbarium vouchers prepared from each site are stored at the Florida Caribbean Science Center (USGS, Gainesville, Florida). Samples were analyzed for the presence of *Cyrtobagous salviniae* first by visual examination, followed by extraction with Berlese funnels (Boland and Room 1983). The Berlese funnels used were very similar to those described by Boland and Room with the exception of the light placement and the funnel dimensions. A single 75-w light bulb was used which was positioned 23 cm from the plant material. The funnel diameter was 31 cm. Weevils were identified to species level using characters described by Calder and Sands (1985). Initial identifications were verified by C.W. O'Brien [Florida A&M University (FAMU), Tallahassee, Florida], an acknowledged expert on weevil taxonomy.

Locality data for *Cyrtobagous salviniae* collected during this survey were supplemented with label data from specimens housed at FAMU, the C.W. O'Brien private collection (Tallahassee, Florida), the Florida State Collection of Arthropods (Florida Department Agriculture and Consumer Services, Gainesville, Florida), and the USDA-ARS Invasive Plant Research Laboratory. Voucher specimens of *C. salviniae* were deposited at the National Museum of Natural History (Washington, D.C.) and the Florida State Collection of Arthropods.

RESULTS AND DISCUSSION

Nomenclature problems with Salvinia minima

Understanding the nomenclatural history of Salvinia is imperative for deciphering the early literature concerning S. minima. Most herbarium specimens consulted in this study were labeled S. rotundifolia Willdenow and later annotated S. minima. Early collections, those made before 1949, were initially labeled S. auriculata Aublet or misidentified as the European species S. natans (L.) Allioni. Robert Herzog (1935) prepared a revision of the genus that recognized eight species. He separated the two common tropical American species according to the stalked hairs on the upper leaf surface. Specimens with divided hairs that were joined apically were grouped as S. auriculata, while plants with hairs spreading and free at the tip were named S. rotundifolia. Following Herzog's work, Weatherby (1937) reviewed specimens in the United States and placed all but one in S. rotundifolia. Later, upon reviewing the holotype, Morton (1967) found that the type specimen for S. rotundifolia actually had hairs joined at the tips. He concluded (as had Baker in 1886) that the name S. rotundifolia should "disappear into synonymy." Accordingly, he revived the name S. minima for plants with spreading hairs. While most taxonomists now use the name S. minima (Kartesz 1994, Wunderlin 1998), many biologists and horticulturists continue to employ S. rotundifolia. This nomenclatural misunderstanding has resulted in confusion with noxious weed regulation in some states (Aquatic Weed Control Act 1991, Howells 1992, Coile 1995).

Geographic distribution of Salvinia minima and chronology for early records

The genus Salvinia was not included in early floras of the southern United States. Likewise, it is not represented in the Stephen Elliott herbarium at the Charleston Museum, a collection of specimens from South Carolina and Georgia that span the years 1808 to approximately 1825 (A.E. Sanders, Charleston Museum, pers. comm.; see Sanders and Anderson 1999). The flora of the entire Southeast was first detailed in Chapman (1860) with D.C. Eaton contributing the section on ferns. While Chapman (1860) included the floating plants Azolla and Lemna, both now common associates of S. minima, the genus Salvinia was not noted. Likewise, Salvinia was absent from Baerecke's (1914) Guide to Plants in the Atlantic Section

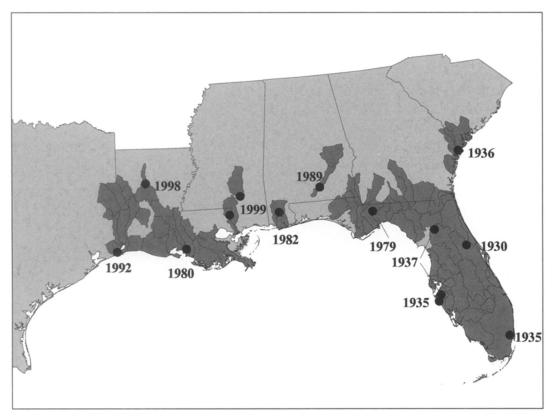


Figure 1. Geographic distribution of *Salvinia minima* in drainages of the southern United States; dated dots indicate significant introduction sites.

of Mid-Florida, which described plants from the same county in which S. minima was subsequently first documented.

Small (1931) constitutes the first report of Salvinia in the southeastern United States, reporting it as introduced and naturalized in Florida. He referred to a 1928 discovery from the "Saint Johns River and some of its tributaries." Earlier collections during the late 1880s and early 1900s of *S. natans* (actually *S. auriculata* or *S. minima*) from Minnesota and New York, and of *S. natans* from Missouri, represented one-time collections from short-term, unsuccessful introductions (Butters 1921, Weatherby 1921). The earliest specimen from the Southeast is dated 1930 [Keeley s.n. (PH)] and was collected from the upper St. Johns River, east central Florida (Figures 1 and 2). It is on a sheet also including plants collected a few miles upstream in 1931. Accompanying the specimen is a letter written by the collector that refers to earlier correspondence with Small, suggesting that Keeley was involved with the 1928 discovery.

Beyond the St. Johns River drainage, Salvinia minima was subsequently documented from widely separated regions of Florida and Georgia. Plants were found in Miami, Florida [St. John 373 (FLAS and NYBG)] and in Sarasota, Florida [Perkins 228 (GH)] in 1935, near Savannah, Georgia [Correll 5422 (GA and GH)] in 1936, and in Gainesville, Florida [Murrill s.n. (FLAS)] and Bradenton, Florida [Weber s.n. (FLAS)] in 1937 (Figures 1 and 2). These earliest localities are in drainage basins independent from that of the St. Johns River and likely were the result of independent introductions (Figure 2).

All early *Salvinia* discoveries were near well-populated towns (Andriot 1993, Anonymous 1952) where the plant may have been grown in pools and ponds. *Salvinia minima* has been cultivated in greenhouses and gardens in the United States since the late 1880s (Weatherby 1921, 1937; Fernald 1950). We can speculate, therefore, that plants entered natural areas from

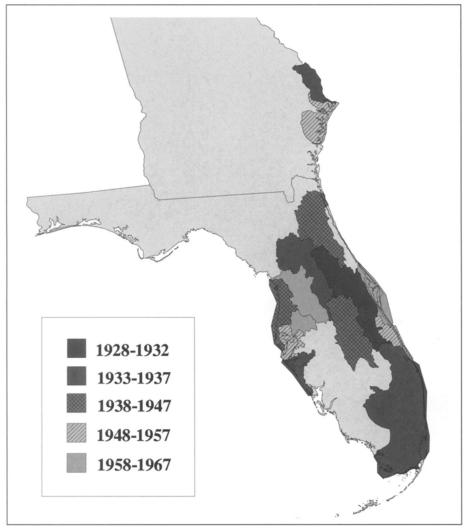


Figure 2. Chronological occurrence of Salvinia minima to 1967 (by drainage basin).

flooding of cultivated ponds or through intentional release. It has been suggested that *S. minima* entered the St. Johns River through the discharge of ship ballast contaminated with spores (Schmitz 1990, Schardt and Schmitz 1991). This route seems unlikely, however, as that would have required freshwater ballast; and *Salvinia* is intolerant of saline conditions (Divakaran et al. 1980). Further, as a hybrid, *S. minima* is unlikely to produce viable spores (Mickel 1979).

By 1967, Salvinia minima was known from 14 drainages in Florida and Georgia, 20% of the current coverage (Figure 2). It was unknown in the Florida Panhandle until 1979 [Godfrey 77112 (FLAS)], was not commonly collected there until the late 1980s, and is still not known from the far western portion of the state (Figure 1).

The earliest collection of Salvinia minima from Alabama was made in 1982 [Reicke s.n. (UNA)] (Figure 1). Populations are common in creeks and bays of the Mobile Delta, however, Alabama also hosts the most northern location of S. minima at latitude 32°36'N [Bayne s.n. (UNA)]. Salvinia minima is new to Mississippi where it was collected in 1999 from a tributary of the upper Leaf River [Schweizer s.n. (IBE)]. The suspected source of infestation is a recently

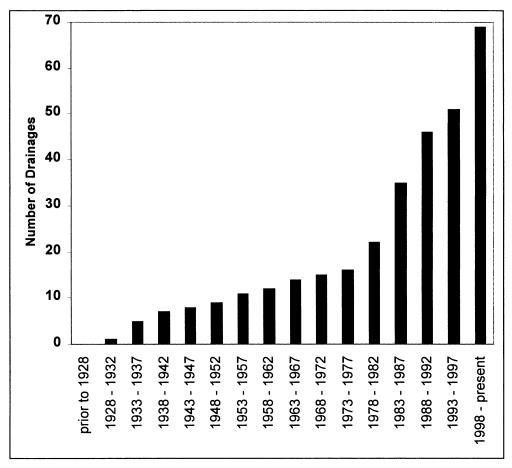


Figure 3. Number of drainage basins occupied by Salvinia minima (1928-99).

created and landscaped lake (Peter Schweizer, University of Southern Mississippi, pers. comm.).

Landry (1981) documented the introduction of *Salvinia minima* west of the Mississippi River, in southern Louisiana. There, the species quickly spread through waterways, marshes and swamps of coastal regions. New drainages in Louisiana continue to be affected as the species spreads north and eastward (Figure 1). *Salvinia minima* was introduced to Texas in 1992, suspected as having been carried there from western Louisiana, on a "marsh buggy," during geologic exploration (Hatch 1995; Rhandy Helton, Texas Parks and Wildlife Department, pers. comm.). Initial spread was confined to the freshwater drainages of coastal regions, however recent expansion has extended inland. Along the Atlantic coast, *Salvinia minima* extends north to the Broad River drainage of South Carolina at latitude 32°28'N [*Jacono 118* (USCH, CHARL) (Figure 1).

The dramatic geographic expansion of *Salvinia minima* over the last 70 years is demonstrated by its present occurrence in 69 drainage basins of the southern United States (Figure 3). Expansion in geographic distribution alone, however, does not necessarily reflect the aggressiveness of a non-native plant. In Texas and Louisiana, *S. minima* typically occurs in abundant stands and is viewed as a very troublesome weed. Densely packed populations are common. At Lacassine Bayou, in west coastal Louisiana, plants extend over an area 19.3 km long and 110 m wide (Charles Dugas, Louisiana Department of Wildlife and Fisheries, pers. comm.) (Figure 4). In Louisiana the species has been noted to form mats 20–25 cm thick (Montz 1989),



Figure 4. Densely packed Salvinia minima at Lacassine Bayou, Jefferson Davis and Cameron Parish, Louisiana. Area shown is approximately 37 cm \times 24 cm.

and plants are often found with leaves growing upright in a compacted habit (Charles Dugas, Louisiana Department of Wildlife and Fisheries, pers. comm.), a response to self-competition at high densities (Mitchell and Thomas 1972). In Texas, Hatch (1995) observed S. minima shading out some submersed plant species. Plants collected in South Carolina during this study were also larger than those normally found in Florida and produced excessive biomass requiring herbicide management.

In Florida, Salvinia minima is grouped with seven other species as a nuisance aquatic plant (Schardt 1993); under most situations, however, it is not identified as causing problems (Jeffrey Schardt, Florida Department of Environmental Protection, Bureau of Invasive Plant Management, pers. comm.). The Florida Bureau of Aquatic Plant Management once regarded S. minima as exotic, but it has since adopted the position of more recent literature and changed the status to native (Schardt 1993).

A competition study among Salvinia minima, Spirodela punctata (G.F.W. Mey.) C.H. Thompson, and Azolla caroliniana Willdenow in north Florida found that Salvinia minima dominated only during the summer (Dickinson and Miller 1998). Spirodela punctata was less influenced than Salvinia minima by spring floods and freezing and was the most abundant of these species over the entire course of the one-year study (Dickinson and Miller 1998). Where introduced in the United States, S. punctata extends to more temperate latitudes (Wohler et al. 1965, Landolt 1986) than does S. minima.

Distribution of Cyrtobagous salviniae and possible effects on Salvinia minima

The present study found the accidentally introduced salvinia weevil, Cyrtobagous salviniae, occurring widely in Salvinia minima populations in Florida. It was not found on either S. minima or S. molesta in other southern states. Cyrtobagous salviniae was found by the

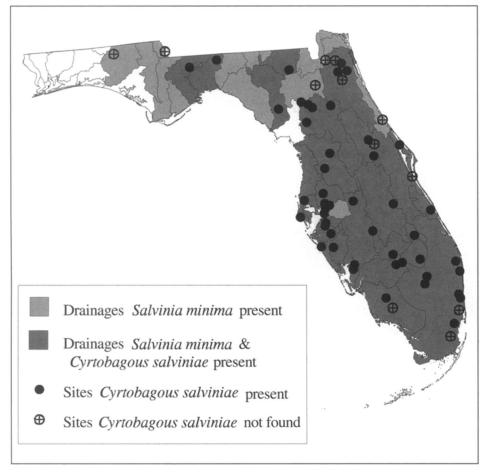


Figure 5. Distribution of Cyrtobagous salviniae on Salvinia minima in Florida drainage basins.

authors at 34 of the 46 Florida sample sites, corresponding to 23 drainages, or 77 percent of the drainage basins surveyed in that state. Earlier voucher collections from 12 sites contributed three additional drainages, resulting in a total distribution of 26 drainage basins where C. salviniae was recorded in association with S. minima (Figure 5). This is equivalent to 68 percent of all Florida drainages known to contain S. minima. The frequency of C. salviniae was greater in peninsular Florida and less in the northern and western regions of the state. The westward occurrence of C. salviniae was in the lower Ochlockonee drainage of the central Florida Panhandle (Figure 5), the same drainage as the Dickinson and Miller (1998) study site. In other southern states, C. salviniae was not found at any of the 28 sites surveyed [viz. within 80 percent of the known drainage basins having S. minima outside of Florida (Figure 6)].

While many factors such as light, temperature, nutrients and hydrologic conditions may contribute to the differences perceived in the growth of *Salvinia minima* among geographic regions of the South (Cary and Weerts 1981, 1983a, 1983b, 1984; Toerien et al. 1983), the possible influence of herbivory by *Cyrtobagous salviniae* must not be overlooked. The disparate distribution of this well-known biological control agent may account for the lesser aggressiveness of *S. minima* in Florida as compared to Louisiana and Texas.

Within its natural South American distribution, *Cyrtobagous salviniae* has been recorded on all four species in the *Salvinia auriculata* complex (Calder and Sands 1985, Forno 1983), but not on *S. minima*. Calder and Sands (1985) noted that *C. salviniae* specimens collected on *S. minima* in Florida were significantly smaller than those collected on *S. molesta* from Brazil.

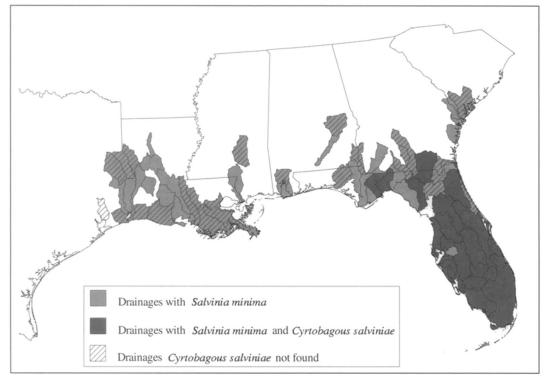


Figure 6. Distribution of *Cyrtobagous salviniae* on *Salvinia minima* in drainage basins of the southern United States.

Recent molecular evidence indicates that some Florida specimens are genetically distinct from C. salviniae released in Australia and could therefore ultimately be recognized as a third, as yet undescribed species (TDC, unpubl. data).

CONCLUSION

Although present in North America for 70 years, Salvinia minima continues to appear in new drainage basins within the southern states. Morphological features [such as hairs and serial lateral buds (Lemon and Posluszny 1997)] likely contribute tolerance to short-term desiccation so that boat trailers and gear contaminated with Salvinia may be expected to transport plants locally. Horticultural use in water-gardens and aquascaping can serve to introduce S. minima to new regions, including southern New Mexico and Arizona and coastal California. Outside of the range of the salvinia weevil, S. minima can be predicted to be a robust and abundant weed.

The recent introduction of Salvinia molesta also continues to involve new states, however, it is too early to assess its status in Mississippi, Alabama, Florida, and Georgia, where relatively small populations have been targeted for eradication. Salvinia molesta is well naturalized in Texas and Louisiana, and distribution there has increased greatly since 1998. Although few Texas sites have been vouchered with fertile specimens, Salvinia plants presumed to be this species have been observed at 22 localities within 14 drainage basins in that state. Many of the infested water bodies are private impoundments on tributaries that flow near federally protected wetlands in southeast Texas. In Louisiana, S. molesta now also occurs at a swamp east of Toledo Bend Reservoir (Jacono 1999) where plants escaped from an earthen pond [Rosen 887 (NO)] located near large bayous. If continued introduction and spread are not curtailed, S. molesta may at least become established in all drainages currently populated by S. minima.

If in fact the less aggressive nature of *Salvinia minima* in Florida is the result of suppression by *Cyrtobagous salviniae*, then areas in Florida with *C. salviniae* should prove less vulnerable to serious infestation by *S. molesta*. The introduction of *C. salviniae* outside of Florida would likely mediate adverse effects of both *Salvinia* species and facilitate integrated management efforts.

SPECIMENS CITED

Salvinia minima Baker—ALABAMA. Mobile Bay, 11 September 1982, Dennis Reicke s.n. (UNA). Lee County: Auburn University, in a stream and the small pond it drains, sporocarps present, 14 December 1998, Bayne s.n. (UNA). FLORIDA. Dade County: Small stream near Miami River, Miami, 17 March 1935, Edward and Robert St. John 373 with Charles Mosier and J.K. Small (FLAS, NYBG). Leon County: Lake Talquin, at Coe's Landing, 8 August 1979, R.K. Godfrey 77112 (FLAS). Manatee County: Bradenton, fishpond, 5 April 1937, G.F. Weber s.n. (FLAS). Sarasota County: T.C.T. campgrounds, 15 March 1935, Anne E. Perkins 228 (GH). Volusia County: Crow's Bluff, St. Johns River, 3 miles west of Deland, 22 April 1930, F.J. Keeley s.n. (PH); Blue Spring, 24 January 1931, F.J. Keeley s.n. (PH). GEORGIA. Chatham County: Growing in mud of open weedy marsh near Savannah, 19 June 1936, D.S. Correll 5422 (GA, GH). MISSISSIPPI. Forrest County: Mixons Creek, back eddy of lower creek, ca. 15 m upstream from spillway of artificial lake at Lake Terrace Convention Center, 30 October 1999, Peter E. Schweizer s.n. (IBE). SOUTH CAROLINA. Jasper County: Bass Lake, west of Great Swamp, off County Rd. S-27-22, west of Hwy 336, sporocarps present, 13 October 1999, C.C. Jacono 118 and L. Nico (USCH, CHARL).

Salvinia molesta Mitchell—ALABAMA. Lee County: Auburn, Indian Pines Country Club, abundant in pond, sporocarps present, 17 March 1999, W.D. Bryant s.n. (UNA). ARI-ZONA. Yuma County: Colorado River, at Imperial National Wildlife Refuge, 6 August 1999, Anthony L. Velasco s.n. (FLAS). FLORIDA. Collier County: North Naples, canal along east side Airport Rd., north of Pine Ridge Rd., 2 February 1999, Jacqueline Smith s.n. (FLAS). GEORGIA. Lamar County: Edie Creek, common in a 0.13 ha farm impoundment and along the margins of a 4 ha impoundment downstream, 03 December 1999, Frank Ellis s.n. (GA, VSC). LOUISIANA. Terrebonne Parish: Houma, residence, common mat-forming herbs on earthen pond and in mud along pond margin, sporocarps present, 07 September 1999, David Rosen 887 (NO). MISSISSIPPI. Jones County: Moselle, abundant in spring fed pond, sporocarps present, 01 April 1999, Milton Henderson s.n. (IBE). TEXAS. Orange County: Bridge City, Briggs' pond, nutria dug canal links private pond to Cow Bayou, sporocarps present, 29 June 1999, Tracy Davern s.n. (TAES).

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