STATUS AND IDENTIFICATION OF HYDROCHARIS MORSUS-RANAE AND LIMNOBIUM SPONGIA (HYDROCHARITACEAE) IN NORTHEASTERN NORTH AMERICA

P. M. CATLING AND W. G. DORE

Abstract. Since 1939, when it escaped into the Rideau canal at Ottawa, Hydrocharis morsus-ranae has spread throughout much of southeastern Ontario, southern Quebec, and northern New York State. Over the past fourteen years it has increased its area of occurrence in North America by three times and is now known throughout the Rideau canal system, the lower Ottawa River, the entire St. Lawrence, eastern Lake Ontario, and also at Rondeau Park on the north shore of Lake Erie. It has also become much more frequent in areas from which it has been known for 10-20 years. Occurrence in isolated pools suggests effective dispersal and colonization which may involve both seeds and turions. Although H. morsus-ranae differs from most other North American aquatics in having very rounded leaves with five prominent and converging primary veins, these characters do not distinguish it from floating-leaved forms of Limnobium spongia. The recent spread of H. morsus-ranae has resulted in it closely approaching the range of L. spongia, although the present distribution of the latter does not extend north of Illinois in the Mississippi drainage or north of New Jersey on the Atlantic coastal plain. Hydrocharis morsus-ranae differs from L. spongia in having relatively less well developed aerenchyma on the undersurface of the leaf, relatively longer leaf lobes, leaf veins on either side of the midvein less ascending, free stipules in pairs, roots usually unbranched and stolon buds developing one instead of numerous roots initially. Other characters differing between the two taxa are described including flowers, seeds, petiole lengths, and leaf venation. These latter characters are less significant in identification either due to their frequent absence on collected material or qualitative and overlapping nature.

The European Frog-bit, *Hydrocharis morsus-ranae* L., was planted in ponds beside Dow's Lake in the Central Experimental farm arboretum at Ottawa in 1932. By 1939 it had spread to the adjacent Rideau Canal (Minshall, 1940). By 1953 masses were noticed free-floating in the Rideau Canal and it was discovered on the Ottawa River near Cumberland, 21 km to the east (Dore, 1954). Also in 1953 it was found floating on Riviere des Mille-Iles near the confluence of the Ottawa and the St. Lawrence Rivers. These plants may have come from stock established at Ottawa or may have escaped from the Montreal Botanical Garden where it was also cultivated. By 1967 *H. morsus-ranae* had been found along the Ottawa River between Ottawa and Montreal and on the St. Lawrence River from Montreal as far as Lake St. Peter (Louis-Marie, 1958, 1960,

1961, 1962; Dore, 1968a,b). The distribution of *H. morsus-ranae* in Quebec was shown by Joyal (1970). In addition it had been found at numerous localities from Merrickville on the Rideau River to the confluence of the Rideau and Ottawa Rivers (Dore, 1968a,b). The total extent of its North American occurrence at this time was a stretch of major waterways approximately 340km in length. It occurred primarily in marshy bays but was often seen free-floating downstream.

Since 1967 it has been found at several localities substantially outside this area, suggesting a rapid spread (Reddoch, 1976; Roberts et al., 1981). The status of *H. morsus-ranae* up to 1967 was outlined in detail by Dore (1968a,b).

The recent spread of *H. morsus-ranae* has resulted in increased opportunities for confusion with native species, especially with the North American Frog-bit, *Limnobium spongia* (Bosc.) Steud. Since *H. morsus-ranae* is a relatively recent European introduction and did not occur near to the neartic *L. spongia*, very few authors have compared the two taxa and there are no detailed comparisons. The only readily available key including both species is that of Scoggan (1978) which is difficult to use and often fails to separate them correctly. The purpose of this article therefore is to update information on the status and distribution of these two taxa in northeastern North America and also to present the results of a comparative morphological study indicating salient differences.

METHODS

Specimens of *Hydrocharis morsus-ranae* and *Limnobium spon-gia* from several northeastern herbaria (CAN, DAO, GH, NYS OAC, SFS, TRT) were examined. These specimens provided the basis for mapping of distribution and for morphological comparison. In addition to specimen records, an indication of status and distribution was obtained through communication with herbarium curators and field botanists.

Herbarium specimens of *Limnobium spongia* from the southeastern United States, *Hydrocharis morsus-ranae* from Canada and *H. morsus-ranae* from Europe were selected for recording of character states and measurement. They were selected to cover a broad geographical area within each of the above regions and also so as to avoid measuring more than two plants from a single locality. Three measurements were made and character states recorded on one or

two separate rosettes per sheet. In this way 49 sets of measurements were taken from 26 sheets of *L. spongia*, with no more than two sets of measurements being made per sheet. Similarly 31 sheets of *H. morsus-ranae* from Europe resulted in 55 sets of measurements and 24 sheets of *H. morsus-ranae* from Canada gave 46 sets of measurements. Label data were recorded for each sheet and the three characters (including maximum aerenchyma space diameter, leaf length, and leaf lobe length) were measured using a scale marked in tenths of a mm. The states of various other characters were noted (*i.e.* approximate angle of primary lateral vein divergence, presence of branching roots, number and attachment of stipules, number of stolon bud roots, and presence or absence of flowers and fruit).

The leaves chosen for measurement were generally selected to include the apparent range of variation (on the sheet) in the characters measured. Frequently this criterion could not be applied due to backmounting, folded leaves or damage, with the result that only one or two leaves were measurable.

The maximum aerenchyma space diameter is defined as the maximum diameter of an aerenchyma space (*i.e.* a space in the lacunate mesophyll) in the basal portion of the leaf between the midvein and the first primary lateral vein (Figure 1). In an attempt to standardize this measurement, it was determined that the space selected for measurement had to be at least 2 mm above the point where the veins diverge and 1 mm from the midvein. The measurement of leaf length and leaf lobe length is illustrated in Figure 1.

The ranges, means, standard errors, and standard deviations were recorded for characters measured. In addition, leaf lobe length was expressed as a ratio of leaf length to determine the extent to which *H. morsus-ranae* has proportionately longer basal lobes. Other distinctive features were recorded in tracings, camera lucida drawings, or photographs.

RECENT SPREAD OF HYDROCHARIS MORSUS-RANAE

(a) St. Lawrence River region

In 1970, botanists at Queen's University found *Hydrocharis* morsus-ranae at two locations in the St. Lawrence River below Rockport in Leeds County (A. E. Garwood, pers. comm., Table 1). In 1972 it was observed to be locally abundant in the cattail (*Typha* spp.) marsh surrounding the bays around Squaw, Adelaide, and

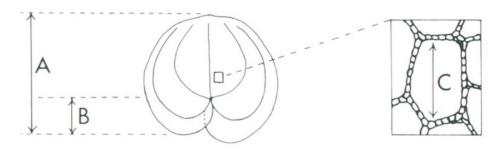


Figure 1. Method of measurement of leaf length (A), leaf lobe length (B) and maximum aerenchyma space diameter (C).

Grenadier Islands and it was recorded from this area in a subsequent floristic survey (Cody, 1975). In 1974 *Hydrocharis morsus-ranae* was discovered in the Lake St. Francis area lower down the St. Lawrence, at South Lancaster, Glengarry Co., Ontario and at Ogdensburg in St. Lawrence Co., New York (Table 1). Subsequently it was discovered at other nearby localities in New York State (Table 1, Roberts et. al., 1981).

In addition *H. morsus-ranae* has extended down the St. Lawrence River to Quebec City (Table 1), about 124 km beyond its 1967 limit shown by Dore (1968a,b) and its 1970 limit shown by Joyal (1970).

(b) Rideau Canal and Ottawa systems

Confined to sections of the Ottawa River downstream from Ottawa in 1967, *H. morsus-ranae* has extended upstream to Shirleys Bay (D.F. Brunton, 1981, Ecological inventory of the Shirleys Bay study area, Ottawa-Carleton, Ontario, National Capital Commission), to the Constance Bay area (P.M. Catling, pers. obs.), and further upstream to Lavergne Bay, Morris Island, near Arnprior, ca. 50 km upstream fro Ottawa (A. H. Reddoch, pers. comm., Table 1) and to Fort Coulonge, ca. 100 km upstream (Table 1). In 1975 it was collected at Lake Opinicon along the Rideau Canal (Table 1) ca. 55 km to the southwest of the limit established by Dore in 1968.

(c) Lake Ontario

In 1972 *H. morsus-ranae* was found in the Bay of Quinte near Rossmore, Prince Edward County. It was discovered at another location ca. 40 km to the west near Deseronto, also in the Bay of Quinte in 1974. In 1977 it was found in Presqu'Ile Bay, an embayment of Lake Ontario near Brighton in Northumberland County (Table 1).

Table 1.

Specimen citations for *Hydrocharis morsus-ranae* collected in North America beyond the range indicated by Dore (1968).

CANADA

Ontario

FRONTENAC CO.: creek running under Lake Opinicon Rd., 3 miles from Perth Rd. (east of Cambells farm (44°37′ N.L., 76°18′ W.L.), 6 Aug. 1975. A. Kitces (OAC).

stormont, dundas and Glengarry co.: Forming dense floating mats on water less than 3 feet deep, in a small marshy boatchannel along the northwest side of the "Lake St. Francis" section of the St. Lawrence River, South Lancaster, Ontario, 12 September 1974, F. M. Uhler (NYS).

HASTINGS CO.: Bay of Quinte, Deseronto, 1974, G. Miller (OAC).

KENT CO.: Rare, drainage channel, Rondeau Provincial Park, 23 June 1976, H. Dale and J. Gerrath (OAC); abundant North channels, Rondeau Park, 1978, E. Woodley (herb. H. M. Dale, n.s.); very abundant, dominant, Rondeau Park, 1980, H. Dale and V. Posluszny (herb H. M. Dale, n.s.).

LEEDS AND GRENVILLE CO.: Squaw Island in St. Lawrence about 4 miles below Rockport, tangled among Typha plants in still water and lagoon; (plant first detected here in 1970 by A.E. Garwood and M. Good, specimen 0K96127 1971, W. G. Dore et al 24845 (DAO); water and reeds, Squaw Island, Front of Yonge Township, 28 July 1972, J. G. Woods 43 (DAO); Adelaide Island, F. of L. & L. Twp., reeds, still water, much duckweed, 28 July 1972, J. G. Woods 44 (DAO). Squaw Island (about 4 miles below Rockport) in St. Lawrence River, 11 July 1973, W. G. Dore et al 25118 (DAO); Squaw Island, 44° 25′ N., 75° 52'33". W., drying up depression in marsh, 17 June 1975, W. J. Cody & D. Munro 21871 (DAO); Squaw Island 44°25'N. 75°52'3"W., in Typha marsh, 17 June 1975, W. J. Cody and D. Munro 21885 (DAO); Grenadier Island East, 44°26′ N., 75°51′ W., wet ditches, 19 June 1975, W. J. Cody and D. Munro 21996 (DAO); Adelaide Island in Thousand Islands archipelago of St. Lawrence River among cattails and shallow water vegetation, 10 August 1976, W. G. Dore, A. Crowder, S. Vander Kloet and A. Garwood 24848 (DAO); shal-

- low, marshy water of middle Kemptville Creek, 4 miles sw of Bishops Mills, 27 July 1979, W. G. Dore (DAO).
- OTTAWA-CARLETON, REG. MUNIC.: Lavergne Bay on Ottawa River ca. 5 miles east of Arnprior on Morris Island, 11 Aug. 1969, A. H. Reddoch and J. M. Reddoch (DAO).
- NORTHUMBERLAND CO.: Shallow water in bay, Presqu'ile Bay, a few miles south of Brighton, just outside Presqu'ile Provincial Park, Brighton Tp, 44°00′ N., 77°43.5′ W., 23 July 1977, P. M. Catling, et al. (DAO, TRT).
- PRINCE EDWARD CO.: growing at edge of *Typha* marsh, Ameliasburg, 23 July 1972, *S. Vander Kloet* (QK); Hennesey Point (Rossmore) along creek channel 60-120 cm deep, substrate—sedge peat, 23 July 1972, *S. Vander Kloet and M. R. King* (QK, OAC); growing in a few cm of water in thick stands among bases of *Typha*, around Deseronto, 29 July 1974, *G. Miller* (OAC).

Quebec

- PONTIAC Co.: dans un étange, Fort-Coulonge, 27 juillet 1979, *N. Lesage 1391* (SFS).
- QUEBEC CO.: marécage du camp Maizerets, 4 août 1974, 3 août 1978, *J. St.-Pierre 76 and 120* (SFS).

UNITED STATES

New York

- JEFFERSON CO.: Kring Point, Kring Point State Park, shore of the St. Lawrence River in a small bay ca. 10 miles east of Alexandria Bay. Abundant in bay in 2-3 feet of water on mucky bottom, 20 September 1979, M. L. Roberts 5133 (NYS; duplicates at OS, DH n.v.)
- ST. LAWRENCE CO.: small bay along the west side of the Oswegatchie River, just south of Ogdensburg, 13 September 1974, F. M. Uhler (NYS); 1.2 miles north of highway 11 on the road to Rensselear Falls, 15 June 1977, R. S. Mitchell and J. K. Dean 6032 (NYS): open marsh on highway 68, 5.8 k north of Canton, 9 May 1981, P. M. Catling 3120 (DAO, MICH, NYS, OS).

(d) Lake Erie

Hydrocharis morsus-ranae was found in Rondeau Park on the north shore of Lake Erie, Kent County, in 1976 (Table 1). It was noted as "rare' in 1976 at the site, but "abundant" in 1978, and "very abundant, dominant" in 1980 (H.M. Dale, pers. comm., Table 1).

The new discoveries of *H. morsus-ranae* described above suggest that it has increased its area of occurrence in North America by about three times over the past 14 years (Figure 2.).

Local increases

In addition to spreading outside the area from which it was known in 1967, *H. morsus-ranae* has become much more abundant and frequent within this area of 1967 occurrence, the lower Rideau and lower Ottawa watersheds. It is now present in numerous locations where it was unknown previously according to the carefully compiled field records of absence. Some of these locations are road-side ditches, ponds, and marshy pools created by beaver dams along small creeks, all largely isolated from the major rivers (Ottawa, St. Lawrence, Rideau) to which *Hydrocharis* was initially confined. Similarly it has been found at additional locations in the St. Lawrence system downstream from Montreal, suggesting that it has increased in this area as well (S.G. Hay, pers. comm.).

Hydrocharis morsus-ranae usually occurs in water of pH 6.5–7.8 with cattails (Typha spp.) and duckweed (Lemna minor) in areas that are apparently nutrient-rich. These conditions are widespread, except in parts of the Canadian Shield region, and habitat requirements seem unlikely to limit its further spread in North America.

DISPERSAL OF HYDROCHARIS MORSUS-RANAE

Hydrocharis morsus-ranae may be rooted in mud or lodged in shoreline debris or it may be free-floating. Any free-floating aquatic may be effectively spread by the natural flow and circulation of water. The initial spread of H. morsus-ranae was essentially downstream (with the exception of a canal; Dore, 1968a) and it seems likely that dispersal by water played a significant role.

Hydrocharis morsus-ranae reproduces vegetatively and overwinters through the development of turions (modified stolon buds around which the scales remain tightly clasped). These turions separate from the parent plant by abscission in late fall, sink to the bottom where they overwinter, and rise to the surface in the following spring to start new plants (pers. obs.: Ridley, 1930, p. 184; Sculthorpe, 1967, p. 350; Dore, 1968a). The characteristic occurrence of stolon buds and turions, which represent relatively small vegetative reproductive parts (ca. 1 cm long) on almost all plants

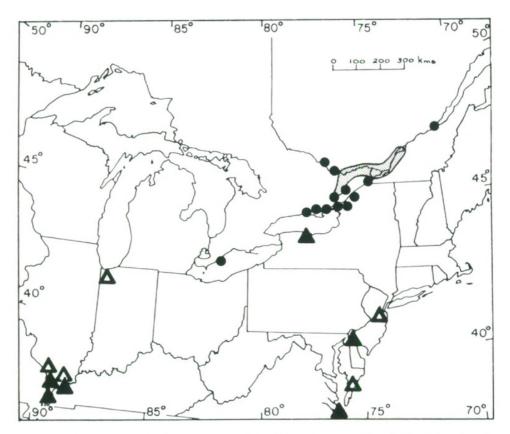


Figure 2. Map of a southwestern portion of northeastern North America showing the distribution of H. morsus-ranae (shaded area = to 1967, dots = from 1968 – 1981) and L. spongia (solid triangles = specimens seen, open triangles = literature reports (specimens not seen)).

encountered, greatly increases the likelihood of dispersal and establishment. Parts of plants, including stolon buds or turions, may be carried by boats on anchors and ropes. Plant parts may also be carried by waterfowl over considerable distances by lodging in the feet or bill. Several gullets from Black Ducks (*Anas rubripes*) collected during the autumn of 1971 on the Ottawa River near Thurso, Quebec and Wendover, Ontario, were found to contain the turions of *H. morsus-ranae* (F.H. Uhler, pers. comm.). Whether or not these turions would come out of the ducks alive and capable of growth is unknown.

Turions are very important in the establishment and persistence of *Hydrocharis morsus-ranae*. Flowering is irregular and the plants are dioecious and some colonies are of one sex so that seed production is limited. Weber (1972) has indicated the importance of turions in the propagation of *Myriophyllum exalbescens*. In his Douglas Lake (Michigan) study area most of the plants present had devel-

oped from turions and most produced turions with an average of more than one turion per plant. Similarly, it appears that most North American colonies of *H. morsus-ranae* develop from overwintering turions and that most populations also produce turions abundantly. At three stations near Ottawa and one near Ogdensburg in New York State, each having hundreds of plants, the entire colonies in 1981 developed from overwintering turions, there being no evidence of germinating seed.

There is a possibility that some colonies of *Hydrocharis morsus*renae have been started either intentionally or accidentally by humans. Some duck hunting clubs introduce aquatic plants intentionally from other regions in order to provide food and cover for waterfowl. People frequently take aquatic plants into an aquarium with fish, salamanders, and turtles, and later release the entire contents (including aquatic plants) into an environment removed some distance from the point of origin.

Although *Hydrocharis morsus-ranae* is dioecious, plants of different sexes sometimes occur abundantly together (Dore, 1968a) and capsules ripen with seed (e.g.: Ste. Anne de Bellevue, 28 Aug. 1961, D. E. Swales (DAO). Ridley (1930, pp. 538, 621) discusses the possibility of dispersal of H. morsus-ranae by adhesion of the seeds to waterfowl (due to the viscid exudation with which they are surrounded). McAtee (1939; see also Ridley, 1930, p. 491) reports that the seeds of Limnobium spongia (a species closely related to H. morsus-ranae and with very similar seeds) may represent an important duck food. They have been identified in the stomachs of several species of ducks, with 32,000 being found in a single bird. The extent to which the seed of H. morsus-ranae and L. spongia are capable of passing through the digestive tracts of waterfowl without damage is unknown.

DISTRIBUTION AND STATUS OF LIMNOBIUM SPONGIA IN NORTHEASTERN NORTH AMERICA

The distribution of *Limnobium spongia* in northeastern North America is shown in Figure 2. It occurs on the Atlantic coastal plain from New Jersey southward and in the Mississippi drainage from southern Illinois southward, with disjunct stations reported in Monroe Co., New York and Lake Co., Indiana.

References to the occurrence of Limnobium spongia in Ontario

(Taylor, 1915; Small, 1933) are erroneous and apparently based on previously recorded occurrences in "Lake Ontario" (e.g.: Britton, 1901; Britton and Brown, 1913; Robinson and Fernald, 1908). All references to "Lake Ontario" refer to the station at Braddock's Bay, Greece, in Monroe County, New York (Paine, 1865; House, 1924). There are correctly identified specimens to document this occurrence (Table 2) collected in 1828. By 1895 it was noted that *L. spongia* had "not been seen for several years" at Braddock Bay (House, 1924). Clausen (1940) surveyed Braddock Bay but did not find *L. spongia*. More recently it has been reported to be "probably extinct" in Monroe Co. (e.g. Fernald, 1950). There are apparently no recent observations of *L. spongia* in the Braddock Bay area (H.S. Forest, pers. comm.).

The literature report from Lake County, Indiana (Deam, 1940) is apparently not supported by material evidence (F.A. Swink, pers. comm.).

IDENTIFICATION OF HYDROCHARIS MORSUS-RANAE AND LIMNOBIUM SPONGIA

A number of North American aquatic genera may have wide floating leaves with cordate bases (i.e. Alisma, Caltha, Echinodorus, Heteranthera, Nuphar, Nymphaea, Nymphoides, Ottellia, Polygonum, Potamogeton, and Sagittaria), but only two genera have leaves that combine: more or less circular shape, rounded lobes, more or less rounded apex and five pronounced and converging primary veins. These latter features are shared by the genera Hydrocharis and Limnobium.

Louis-Marie (1959) noted that *Hydrocharis morsus-ranae* and *Limnobium spongia* may resemble one another very closely, but that the floral structures are quite different. Cook, et al. (1974), in their work on aquatic plant genera, also concentrated on flowers, indicating that *Limnobium* spp. are either without petals or with petals less than 1½ times as long as the sepals, whereas *Hydrocharis* spp. have petals more than 1½ times as long as the sepals. This latter distinction is a very useful one (Figure 3).

The staminate flowers of *Hydrocharis morsus-ranae* have 9–12 stamens with relatively long free filaments not obviously connate at the base, and with the free portion as long as the anthers. In contrast, *Limnobium spongia* has 3–12 stamens with filaments largely

Table 2. Specimen citations for *Limnobium spongia* in northeastern North America.

UNITED STATES

Delaware

NEW CASTLE CO.: In ditches along canal, Delaware City, 11 September 1871, A. Commons (2 sheets, NY); in stagnant ditches near Delaware City, September 1, 1880, A. Commons (GH, NY); margin of lagoon, ¾ mile southwest of Delaware City along road to St. Georges, 13 July 1937, R. R. Tatnall 3439 (GH).

Kentucky

BALLARD CO.: Floating with *Lemna* in Bald Cypress swamp, Peal Wildlife Management area, 3 km west of Barlow, 23 April 1981, *P. M. Catling 3907 and K. L. Catling* (DAO).

Illinois

UNION CO.: Jonesboro, August 1862, G. Vasey (GH); Jonesboro, G. Vasey (NY); southern Illinois, G. Vasey (GH).

Missouri

MISSISSIPPI CO.: Margin of muddy shallow bank of Big Lake ditch No. 1 along road N, just north of junctionwith road K, T27N, R16E, sect. 30 2½ miles (by air) north of Charleston, 21 August 1955, J. A. Steyermark 79593 (GH).

New York

MONROE CO.: growing in stagnant water, surrounded with *Azolla*, on the shore of Lake Ontario in the town of Greece, 21 April 1828, *Bradley* (NY - Torrey herbarium and label in Torrey's hand; photo DAO); Braddocks Bay, Lake Ontario, *H.P. Sartwell* (GH); north shore of Braddock's Bay, Greece, Herbarium *Wm. Boott* (GH).

Virginia

NORFOLK CO.: Sandy and peaty margin of Lake Drummond, near Jericho ditch, Great Dismal Swamp west of Wallaceton, 6 September 1941, M. L. Fernald and Bayard Long 13519 (NYS, GH); wooded river-swamp along Northwest River, northeast of Northwest, 17 October 1941, M. L. Fernald and B. Long 13861 (GH).

PRINCESS ANNE CO.: In water of cove, southern end of Lake Joyce, 12 September 1935, M. L. Fernald et al 4744 (GH, NY); on water margin of Lake Joyce, 4 May 1935, M. L. Fernald and L. Griscom 4296 (GH): inlet into Rainy Pond, back of Sand Bridge, 15 July 1940, M. L. Fernald and B. Long 12238 (GH, NY).

connate forming a pyramidal structure (Figure 3), and with a relatively short free portion much exceeded in length by the anthers. The anthers of *H. morsus-ranae* are oval, approximately as long as wide and ca. 1.0 mm long, while the anthers of *L. spongia* are elongate, much longer than wide and ca. 3.5 mm in length (Figure 3.).

The styles of *H. morsus-ranae* are usually 6 in number, bifid for one half of their length, ca. 4.0 mm long, and much shorter than the petals. The styles of *L. spongia* on the other hand, are 6–9 in number, bifid nearly to the base, 10–15 mm long, and exceeding the petals in length.

Although these floral features are conclusive in separating the two species, their usefulness is limited by the fact that flowering material is often not available. This is especially true of the floating-leaved form of *L. spongia* which is without flowers more than 90% of the time based on herbarium specimens examined.

Hotchkiss (1972) noted that the leaves of *Hydrocharis morşus-ranae* resemble the floating form of *Limnobium spongia* but the former have almost no central sponginess. This sponginess is due to aerenchyma (lacunate mesophyll) which is readily observed on the underside of the leaf. Aerenchyma is more extensive in *L. spongia* and the aerenchyma spaces are generally larger (Figures 4, 5, & 6, Table 3). The emergent leaves of *L. spongia* are usually without aerenchyma, but are not likely to be confused with leaves of *H. morsus-ranae* because of their truncate bases (Figure 7).

In addition to the difference in the size of aerenchyma spaces, the leaves of *H. morsus-ranae* tend to have relatively longer basal lobes (Figure 7). This is readily apparent when leaf lobe length is expressed as a ratio of leaf length (Figure 4, Table 3).

There are also differences in leaf venation between these two species. Limnobium spongia tends to have the primary veins on either side of the midvein more ascending while in Hydrocharis morsus-ranae these veins tend to be more widely curving, often forming an angle of 80° or 90° with the midvein at the leaf base

LIMNOBIUM SPONGIA **HYDROCHARIS** MORSUS-RANAE 10 mm

Figure 3. Flowers and leaf petiole bases (with stipules) of *Hydrocharis morsus-ranae* (left) and *Limnobium spongia* (right). From top to bottom (and left to right in brackets), male flowers (Ontario, *Dore 21280*, DAO and Florida, *Chapman*, GH), female flowers (Ontario, *Dore 21717*, DAO and Texas, *Mitchell 4057*, NY) and petiole bases (Ontario, *Catling 3279*, DAO and Kentucky, *Catling 3097*, DAO).

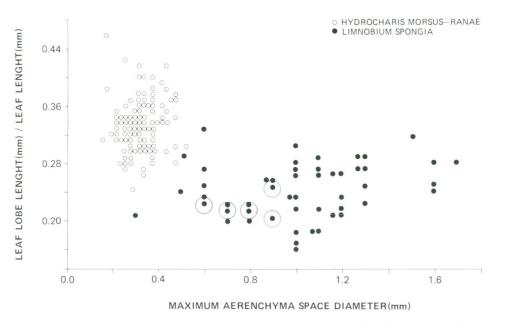


Figure 4. Aerenchyma space diameter plotted against the ratio of leaf lobe length/leaf length for H. morsus-ranae (including 55 specimens from Europe and 46 from Canada) and L. spongia (including 49 specimens from the eastern United States). More than half of the H. morsus-ranae had flowers but the only L. spongia specimens with flowers are represented by the five encircled dots.

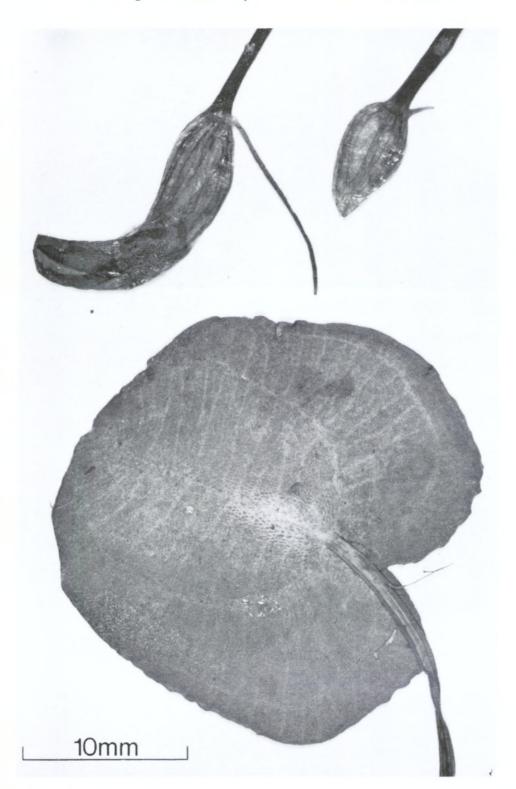


Figure 5. *Hydrocharis morsus-ranae*. Leaf viewed from below (left) and stolon buds (right). Rideau River, Merrickville, Lanark Co., Ontario, 24 Aug. 1965, *W. G. Dore 21790* and *C. Crompton* (DAO).

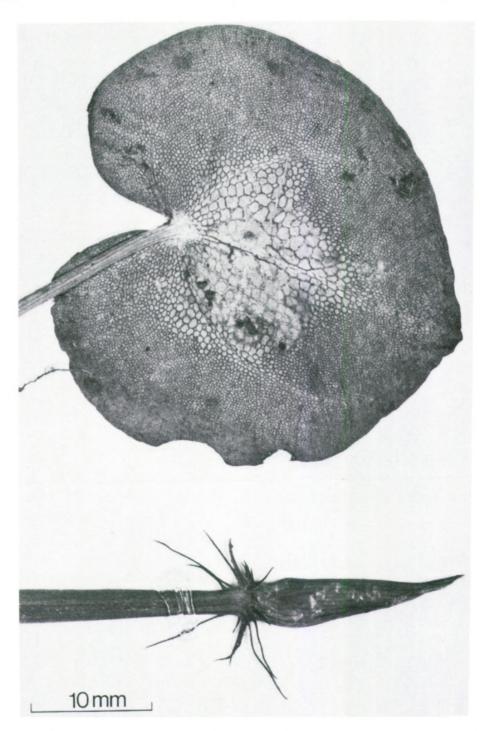


Figure 6. Limnobium spongia. Leaf viewed from below (left) and stolon bud (right). Sumter Wildlife Management area, Sumter Co., Florida, 13 Aug. 1958, R. Kral 7869 (GH).

Table 3.

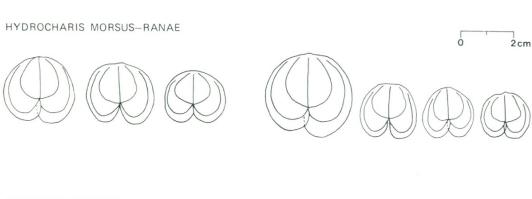
Leaf character data.

Minimum, maximum, mean, standard error (SE) and standard deviation (SD) for four leaf characters in *Hydrocharis morsus-ranae* from Europe (HME, n = 55), *H. morsus-ranae* from Canada (HMC, n = 46) and *Limnobium spongia* from eastern United States (LS, n = 49)

	MIN./MAX.	MEAN	SE	SD
1. Arenchyma	a space diameter (mm)			
HME	0.160/0.480	0.319	0.011	0.081
HMC	0.220/0.540	0.353	0.010	0.065
LS	0.300/1.700	1.016	0.045	0.315
2. Leaf length	(mm)			
HME	12.000/45.000	28.725	0.886	6.573
HMC	15.500/42.800	26.922	0.879	5.962
LS	13.000 / 57.000	28.598	1.480	10.360
3. Leaf lobe le	ength (mm)			
HME	3.300/15.000	9.675	0.334	2.477
HMC	5.000/17.000	9.359	0.369	2.502
LS	2.400/16.000	7.202	0.452	3.164
4. Lef lobe les	ngth/leaf length			
HME	0.275/0.462	0.336	0.005	0.038
НМС	0.272/0.423	0.346	0.005	0.034
LS	0.167/0.339	0.247	0.006	0.039

(Figure 7). The secondary venation also frequently differs. In *L. spongia* there is usually much more secondary venation parallel to the primary venation and this secondary venation is essentially oriented either parallel or perpendicular to the primary venation. In *H. morsus-ranae* there is less secondary venation parallel to the primary venation and much of it is neither parallel nor perpendicular, but rather diagonal and/or circular or wavy (Figure 8). The very young and earliest-produced floating leaves of *L. spongia*, however, may be very similar to mature leaves of *H. morsus-ranae* in their secondary venation.

Although *Hydrocharis morsus-ranae* does not have a mud form with truncate based leaves like *Limnobium spongia* (see Figure 7,) it does occasionally produce leaves which rise out of the vegetation mat, especially in dense colonies of mature plants. Thus both species can be said to have either floating or emergent leaves. Although



LIMNOBIUM SPONGIA

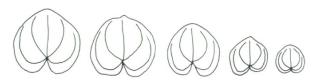




Figure 7. Variation in the leaves of H. morsus-ranae (Canada) and L. spongia (United States) made from direct tracings.

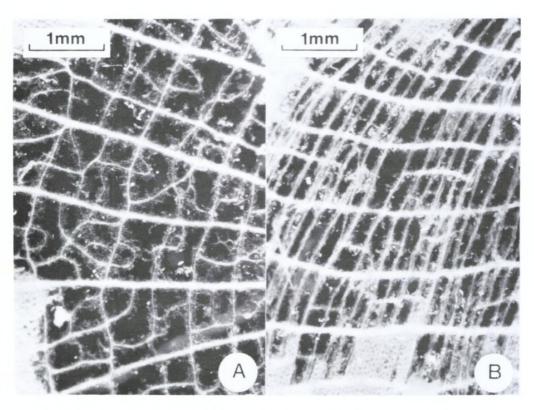


Figure 8. A, *Hydrocharis morsus-ranae* and B, *Limnobium spongia* showing leaf venation between first and second primary lateral veins (A, near Wressell, East Yorkshire, England, *J. Beanland* (T. W. Edmondson herb., NY); B, Delaware City, Delaware, 1 Sept. 1880, *C. Culbert* (A. Commons herb., NY)).

young floating plants of *L. spongia* tend to have relatively longer leaf petioles than *H. morsus-ranae*, there is much overlap in this character.

Hydrocharis morsus-ranae has two lateral stipules free from the leaf petiole base while Limnobium spongia has a single stipule adnate to the leaf petiole base (Figure 3). This is a very useful character in living material, but is much more difficult to assess in dried herbarium material.

Both Hydrocharis morsus-ranae and Limnobium spongia are stoloniferous, the short erect stems producing lateral stolons which travel for some distance below the surface of the water or soft mud and produce terminal buds which develop into new rosettes. The turions of H. morsus-ranae are modified overwintering stolon buds. Limnobium spongia also produces stolon buds. The stolon buds of H. morsus-ranae develop a single root initially and differ in this respect from stolon buds of L. spongia which produce numerous roots simultaneously from the base (Figures 5 and 6).

Another consistent and useful difference is observed in the roots. Those of *H. morsus-ranae* are usually unbranched (Sculthorpe, 1967, p. 190; Dore, 1968a), while roots of *L. spongia* usually have numerous simple branches.

Although Hydrocharis morsus-ranae often flowers, it rarely develops fruit in certain parts of its range (Sculthorpe, 1967, p. 319) and fruit production may be irregular. Fruit and seeds are developed in some Canadian populations (e.g.: St. Anne de Bellevue, 28 Aug. 1961, D. E. Swales (DAO)), but their apparent scarcity in the field and in herbarium specimens make them of limited value in identification. The floating-leaved form of Limnobium spongia, which is most likely to be confused with H. morsus-ranae, apparently possesses flowers and fruit rarely (less than 10%, based on examination of herbarium material). Although the fruiting structures are similar in many respects, the seeds of the two species appear to be quite different. Because of their limited value in identification (due to scarcity) and because of the relatively small sample available (preventing comparisons on a broad geographical basis), these differences have not yet been studied quantitatively. Seeds and illustrations of seeds of *H. morsus-ranae* that have been examined had a minutely tuberculate, rough, ridged and/or slightly winged surface while those of L. spongia are echinate with spines about 0.3mm long.

The salient differences between the two species in the characters discussed above have been summarized in Table 4.

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Table 4.
Selected comparisons between Hydrocharis morsus-ranae and Limnobium spongia.

	H. morsus-ranae	L. spongia
ROOTS	usually unbranched	branched
STOLON BUDS	developing a single root initially at base	with numerous roots de- veloping simultane- ously at base
LEAVES		
(a) acrenchyma (visible on lower leaf surface)	larger spaces confined to immediate region of mid-vein, those 1 mm from midvein 0.1-0.5 mm across	mm from midvein 0.4- 1.6 mm across
(b) Leaf lobe length (mm)/leaf length (mm)	0.26-0.41	0-0.32
(c) primary veins on either side of midvein	basally forming an angle of 75–90° with the midvein and broadly curving	basally forming an angle of about 30–80° with the midvein and ascending
(d) leaf stipules	two free stipules	single adnate stipule
FLOWERS		
(a) petals	more than 1½ times as long as sepals	less than 1½ times as long as sepals
(b) stamens	9–12, with long free filaments not obviously connate above base	3–12, with filaments lar- gely connate forming a pyramidal structure
(c) anthers	oval, approximately as long as wide, ca. 1.0 mm long	elongate, much longer than wide, <i>ca.</i> 3.5 mm long.
(d) styles	6, bifid for less than ½ of their length, ca. 4 mm long, much shorter than perianth	6–9, bifid nearly to the base, 10–15 mm long, exceeding perianth.
SEEDS	minutely tuberculate, or muricate or merely with a rough somewhat ridged or winged surface	echinate, the spines to 0.3 mm long.

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