On the Biology of *Orontium aquaticum* L. (Araceae), Golden Club or Floating Arum

Larry H. Klotz
Department of Biology
Shippensburg University
Shippensburg, PA 17257, USA

On May 16, 1982, I visited a group of the small, natural ponds that are abundant near my home in the Appalachian Mountains of southcentral Pennsylvania. As I entered the first pond, I was surprised by a spectacular display: a large population of golden club in full bloom (Figs. 1 and 6). The time was late afternoon, when the low angle of the sun made the inflorescences seem like glowing white candles in a lake of black water. I could then visualize a description published 72 years earlier by Witmer Stone (1910): "The Golden Club is one of the attractions of the [New Jersey] Pine Barrens in springtime, when the surface of the pools bristle with its brilliant, slender, orange-yellow spikes bordered below with white where they join the green stalks. . . ."

Orontium aquaticum, the sole species of the genus, is a highly distinctive aroid. Its closest relatives are probably the skunk cabbages, *Symplocarpus* and *Lysichiton* (Barabé & Forget, 1987; Grayum, 1990), which also inhabit North Temperate freshwater wetlands (Krause, 1908; Huttleston, 1953). *Orontium* is endemic to the eastern deciduous forest biome in the United States, primarily on the Coastal Plain and less frequently in the Appalachians, where it reaches an elevation of 850 meters (Huttleston, 1953). The range of the species extends from Massachusetts and central New York to Kentucky, Florida, and Louisiana (Grear, 1966; Godfrey & Wooten, 1979). It is generally rare or local in the northern and western parts of its range (Beal & Thieret, 1986; Hellquist & Crow, 1982; Hough, 1983; Huttleston, 1953; Ogden, 1974; Weatherbee & Crow, 1990). In Pennsylvania it is considered rare and seems to be declining. The population depicted here is one of the largest in the state.

Orontium inhabits sandy, muddy, or peaty soil (Ogden, 1974) in many types of shallow freshwater wetlands or their moist banks and shores: cold mountain spring runs (Strausbaugh & Core, 1977), freshwater tidal wetlands, seeps (Tiner, 1988), pools (Godfrey & Wooten, 1979), sloughs (Harshberger, 1970), marshes (Beal, 1977), bogs (Radford et al., 1968), rivers (Hellquist & Crow, 1982), streams, ponds, lakes, and swamps (Beal & Thieret, 1986). It has been observed to grow in depths as great as 12 to 15 dm (J. C. French, pers. comm.). The water in which it occurs is typically acidic and "organic" (tanniniferous). The measurements of pH from the habitats of *Orontium* in North Carolina have a median value of 6 (somewhat acidic) and range from slightly less than 5 to slightly above 7 (just above neutral) (Beal, 1977).

The population depicted from southcentral Pennsylvania dominates a shallow, seasonal pond that commonly lacks standing water (but remains moist or muddy) from midsummer through midautumn. In the Appalachian Mountains of central Virginia, a large population of *Orontium* occurs in a *Sphagnum*-lined, spring-fed pond (Rawlinson & Carr, 1937) that maintains relatively constant water levels (Virginia Natural Heritage, unpubl. data). In the Okefenokee Swamp in Georgia, *Orontium* prevails under inundated conditions in a marsh that undergoes drawdown only during drought years, which are infrequent and unpredictable (Greening & Gerritsen, 1987).

Orontium is a perennial herb with a stout, firm rhizome (Figs. 2 and 3). The rhizome is often deeply sunken because it produces contractile roots, which pull it into the soil (Hotta, 1971; French, unpubl. data). The

Fig. 1. Natural population of *Orontium aquaticum* in a seasonal pond along the base of South Mountain, Franklin County, Pennsylvania.

shoot has a definite organization: each segment bears three foliage leaves (Ray, 1987). Above these is one inconspicuous bractlike leaf, often designated as the spathe (e.g. Wilson, 1960). It sheaths the base of the inflorescences but is sometimes deciduous by the time of anthesis (Brown & Brown, 1984). Each segment of the shoot terminates in a pair of inflorescences, one arising from a bud on the base of the other. One or both of them often abort at an early stage of development (Ray, 1988). The stem is continued by a branch from the axil of the uppermost foliage leaf (Ray, 1987). There are no resting bud scales even though the species is temperate (Ray, 1988).

The leaves are either emersed or floating, depending on the depth of the water. Their buoyancy results from large intercellular air spaces, which impart a spongy texture. (Such "aerenchyma" tissue occurs in most emergent aquatic plants. Besides providing buoyancy and mechanical strength, it enhances the diffusion of gases in the interior of the organs [Sculthorpe, 1967].) The upper surface of the blade is dark, velvety, matte bluish green. It strongly repels water and contains the stomates, which are overarched by the surrounding epidermal cells (Grear, 1973; French, unpubl. data). The lower surface is pale, glossy, and silvery-green with numerous, fine, dark green parallel veins and a broad, whitish, protruding midrib, which extends from the petiole to the leaf tip. The leaves do not noticeably emit a musky odor when crushed or bruised as do some Araceae, such as *Symplocarpus*. The leaves are not evergreen but instead wither when the plants enter dormancy in autumn.

The season of flowering and leaf expansion ranges from March and April in the southern part of the range to May and June in the northern part (e.g. Hough, 1983). In southcentral Pennsylvania, flowering occurs from early April to mid-June and peaks

Fig. 2. Basal portion of excavated plant; the white leaf bases indicate the depth of submergence in the soil.

Fig. 3. Rhizome with adventitious roots.

about mid-May. Inflorescences at various stages of flowering and immature fruit can occur simultaneously on a single plant.

The spadix is concealed by the flowers, which adjoin each other in a hexagonal or rhombic pattern (Fig. 7). The flowers are all bisexual (Huttleston, 1953; Krause, 1908), or they are bisexual at the base of the spadix and intergrade to staminate toward the tip (Bogner, pers. comm.; Schaffner, 1937). Meiosis apparently occurs in the flower buds sometime during the summer—more than eight months in advance of anthesis the following spring (Grear, 1966). Anthesis occurs in ascending sequence on the spadix.

Orontium is stated to be entomophilous (Cook, 1990), but published data on pollination are lacking (Grayum, 1990). Various insects (e.g. dragonflies) perch on the spadices but may be using them simply as landing sites (P. B. Tomlinson, pers. comm.). I have not detected any odor from a single spadix, but numerous flowering spadices placed in a jar produce a perceptible foul, fungal odor (J. C. French, pers. comm.), which may serve as an attractant for flies or beetles (Grayum, 1990). It would be interesting to determine whether the spadix generates heat during flowering, as it does in some other Araceae, such as *Symplocarpus* (Grayum, 1990).

The pollen grains of *Orontium* lack starch and are relatively large (mean of longest diameter: 64 μm). In the Araceae, starchless pollen is associated with pollination by bees or flies (Grayum, 1985) while large pollen is correlated with pollination by bees or beetles (Grayum, 1986). The type of pollen sculpturing in *Orontium* (foveolate-reticulate—Grayum, 1985) is considered to be unspecialized for particular pollinators but is associated with pollination by bees, flies, and beetles in this family (Grayum, 1986).

The perianth is green when the flowers are very young, turns yellow before and during anthesis, and becomes green again during fruit development. The yellowing is

Fig. 4. Infructescence with mature fruits.

Fig. 5. Bisected fruits, showing pericarp and embryo; the embryo characteristically contains a small cavity.

due to a decrease in chlorophyll concentration rather than an increase in carotenoids (Casadoro et al., 1982). In flower and immature fruit, the tips of the tepals are sharply folded over the ovary. Growth of the fruit straightens the tepals and hides the stamens, which persist beyond fruit abscission.

The spadix is borne on an elongated scape, which is white distally and erect or ascending during flowering (Fig. 7). After anthesis is completed, the scape becomes green and grows downward so that fruit maturation occurs in the water. The scape and the spadix disintegrate after the ripe fruits abscise.

The ovary contains a single, basal ovule. Hairs on and around the ovule probably produce the mucilage that often fills the entire locule and is conspicuous as a clear, slimy, jellylike covering on the mature seed. After pollination, the mucilage may provide a medium for pollen tube growth between the style and the ovule (French, 1987). The ripe pericarp is fleshy but relatively thin (Figs. 4 and 5). Its outer surface is green and often partly brown or dark maroon, especially distally. The inner surface is whitish. The seed is globose, 6–10 mm in diameter. Its surface is dark green and has no obvious seed coat except for the slimy covering described above. No endosperm is present in the mature seed (Grayum, 1990). The mature embryo is firm-textured and pale green (or sometimes yellow) internally, except toward the distal end, where it is creamy white and contains a small, smooth cavity.

I have observed ripening of the fruits during June and July in southcentral Pennsylvania, but it is reported to occur during July and August in New Jersey (Hough, 1983). The fruits are "probably mostly animal dispersed" (Cook, 1990). They detach from the spadix when ripe and are able to float. Their buoyancy results from air spaces in the pericarp: the seed sinks immediately if the pericarp is removed. Ridley (1930) observed that after the fruits have floated for about a week, they sink as the pericarp becomes water-logged and that after anoth-

Fig. 6. Natural population of *Orontium aquaticum* in a seasonal pond along the base of South Mountain, Franklin County, Pennsylvania.

er week, the pericarp splits at the apex and releases the seed.

In the population depicted, I have observed that the seeds can germinate within the fruits as they mature on the spadix in late June: the first three plumular leaves emerge near the base of the seed and curve around it, between the seed coat and the pericarp. I have noticed a few instances of complete vivipary: the pericarp had split and the plumular leaves had become exposed before the fruit abscised from the spadix. (Among the seed plants, vivipary is chiefly characteristic of mangroves [Tomlinson, 1986].) The plumular leaves are green, slender, tapering, and bladeless, with an adaxial groove in the basal part. The outermost leaf can attain a length of about four cm before the seed is released from the pericarp. The radicle has also emerged by this time but is short (1 mm) and whitish. At least some of the seedlings become rooted in this population: I have observed them to be abundant during the summer.

If dried, the seeds shrink greatly and die (Cook, 1987). They are relatively heavy compared to those of other aquatic plants: only 5,500 dried seeds per kg as compared to 331,000 per kg in *Calla palustris* or 386,000,000 per kg in *Utricularia cornuta* (Muenscher, 1944). I obtained a value of 17 percent dry mass from a sample of 100 seeds, and they lost an average of 42 percent of their diameter on drying.

Like other Araceae, *Orontium* has packets of needle-like crystals in almost all tissues. The crystals defend the plant against herbivory when it is eaten raw. When the crystal-containing cells are broken, they absorb water and discharge the crystals, which penetrate the tissues of the mouth and cause intense irritation (Wilson, 1960). (I have experienced such burning when touching my face while dissecting the fruits of *Orontium*.) Drying or prolonged cooking deactivate these cells and so remove the acrid pepperiness (Peterson, 1978; Wilson, 1960). The rhizomes and seeds are starchy and

Fig. 7. Inflorescences.

were a source of carbohydrate for the American Indians (Sculthorpe, 1967). After being thoroughly dried, these parts can be ground into a nutritious, mealy flour. Alternatively, the dried seeds can be boiled for 45 minutes in several changes of water and served like peas (Peterson, 1978). I have eaten a few fresh, mature seeds after microwaving them for five minutes in tap water. They had a firm texture and a pleasant, nutty flavor; they caused me no irritation.

Because *Orontium* requires only shallow water and forms a compact clump, it is suitable for small ornamental pools, where it can be grown with smaller, more delicate aquatics. The plant requires little attention and can flourish for many years in the same soil, but specimens grown in pots or tubs should be divided and replanted every two or three years (Everett, 1981). Because of its firm hold on the soil, *Orontium* may be planted in swifter water than most aquatics. Rhizomes should be planted in 3 to 5 dm of water in a sunny location and should be given a rooting medium enriched with fertilizer (Raffill, 1946). Propagation is chiefly by seed or by dividing the rootstocks at planting time in early spring. The plant may be difficult to eradicate once it is established where the rhizomes can grow freely (Bailey, 1929).

ACKNOWLEDGMENTS

This article was originally published in German, in a translation by Josef Bogner (Klotz, L. H. 1991. Ueber die Biologie von *Orontium aquaticum* L. (Araceae), der Goldkeule. *Aqua-Planta* 4-91:131–138.). I am grateful to Josef Bogner, P. Barry Tomlinson, and James C. French for their comments and suggestions. Shippensburg University provided support for interlibrary loans and a computerized bibliographic search (DIALOG). I especially thank the landowner and the neighbors of his property for protecting this population of *Orontium* and allowing me to study it.

LITERATURE CITED

Bailey, L. H. 1929. *The Standard Cyclopedia of Horticulture.* Vol. 2. Macmillan, New York.

Barabé, D. & S. Forget. 1987. Analyse phylogénetique des Calloideae (Araceae). Naturaliste can. *Rev. Ecol. Syst.* 114: 487–494.

Beal, E. O. 1977. A manual of marsh and aquatic vascular plants of North Carolina with habitat data. *Tech. Bul. 247, North Carolina Agricultural Experiment Station,* Raleigh.

Beal, E. O. & J. W. Thieret. 1986. Aquatic and wetland plants of Kentucky. *Kentucky Nature Preserves Commission Scientific and Technical Series No. 5,* Frankfort, KY.

Brown, M. L. & R. G. Brown. 1984. *Herbaceous Plants of Maryland.* Port City Press, Baltimore.

Casadoro, G., N. Rascio, M. Pagiusco, and N. Ravagnan. 1982. Flowers of *Orontium aquaticum* L.: membrane rearrangement in chloroplast-chromoplast interconversions. *J. Ultrastructure Research* 81:202–208.

Cook, C. D. K. 1987. Dispersion in aquatic and amphibious vascular plants. *In* R. M. M. Crawford (ed.), *Plant Life in Aquatic and Amphibious Habitats,* 179–190. Blackwell Scientific Publications, Boston.

———. 1990. *Aquatic Plant Book.* SPB Publishing, The Hague.

Everett, T. H. 1981. *The New York Botanical Garden Illustrated Encyclopedia of Horticulture.* Vol. 7. Garland Publishing, New York.

French, J. C. 1987. Structure of ovular and placental trichomes of Araceae. *Bot. Gaz.* 148:198–208.

Godfrey, R. K. & J. W. Wooten. 1979. *Aquatic and Wetland Plants of Southeastern United States. Monocotyledons.* Univ. of Georgia Press, Athens.

Grayum, M. H. 1985. Evolutionary and ecological significance of starch storage in pollen of the Araceae. *Amer. J. Bot.* 72:1565–1577.

———. 1986. Correlations between pollination biology and pollen morphology in the Araceae, with some implications for angiosperm evolution. *In* S. Blackmore and I. K. Ferguson (eds.), *Pollen and Spores: Form and Function,* 313–327. Academic Press, New York.

———. 1990. Evolution and phylogeny of the Araceae. *Ann. Missouri Bot. Gard.* 77:628–697.

Grear, J. W., Jr. 1966. Cytogeography of *Orontium aquaticum* (Araceae). *Rhodora* 68:25–34.

———. 1973. Observations on the stomatal apparatus of *Orontium aquaticum* (Araceae). *Bot. Gaz.* 134:151–153.

Greening, H. S. & J. Gerritsen. 1987. Changes in macrophyte community structure following drought in the Okefenokee Swamp, Georgia, U.S.A. *Aquatic Bot.* 28:113–128.

Harshberger, J. W. [1916] 1970. *The Vegetation of the New Jersey Pine-Barrens.* Dover Publications, New York.

Hellquist, C. B. & G. E. Crow. 1982. Aquatic vascular plants of New England: Part 5. Araceae, Lemnaceae, Xyridaceae, Eriocaulaceae, and Pontederiaceae. *Bulletin 523, New Hampshire Agricultural Experiment Station,* Durham.

Hotta, M. 1971. Study of the family Araceae. General remarks. *Jap. J. Bot.* 20: 269–310.

Hough, M. Y. 1983. *New Jersey Wild Plants.* Harmony Press, Harmony, NJ.

Huttleston, D. G. 1953. A taxonomic study of the temperate North American Araceae. Ph.D. Thesis, Cornell University, Ithaca, NY.

Krause, K. 1908. Araceae–Calloideae. *In* A. Engler (ed.), *Das Pflanzenreich.* IV, 23B (Heft 37):140–155. Wilhelm Engelmann, Leipzig.

Muenscher, W. C. 1944. *Aquatic Plants of the United States.* Comstock Publishing Co., Ithaca, NY.

Ogden, E. C. 1974. Anatomical patterns of some aquatic vascular plants of New York. *Bulletin 424, New York State Museum and Science Service,* Albany.

Peterson, L. 1978. *A Field Guide to Edible*

Wild Plants of Eastern and Central North America. Houghton Mifflin, Boston.

Radford, A. E., H. E. Ahles, & C. R. Bell. 1968. *Manual of the Vascular Flora of the Carolinas.* Univ. of North Carolina Press, Chapel Hill.

Raffill, C. P. 1946. Bog and water garden: *Orontium aquaticum. Gardeners' Chronicle* 119 (April 6):159.

Rawlinson, E. S. & L. G. Carr. 1937. Plants of Spring Pond, Augusta County, Virginia. *Claytonia* 3:36–40.

Ray, T. S. 1987. Diversity of shoot organization in the Araceae. *Amer. J. Bot.* 74:1373–1387.

———. 1988. Survey of shoot organization in the Araceae. *Amer. J. Bot.* 75: 56–84.

Ridley, H. N. 1930. *The Dispersal of Plants throughout the World.* L. Reeve, Ashford, UK.

Schaffner, J. H. 1937. The flowers of the golden-club. *American Botanist* 43:98–103.

Sculthorpe, C. D. 1967. *The Biology of Aquatic Vascular Plants.* St. Martin's Press, New York.

Stone, W. 1910. Report of the plants of southern New Jersey, with especial reference to the flora of the Pine Barrens. *Ann. Report of the New Jersey State Museum,* Trenton.

Strausbaugh, P. D. & E. L Core. 1977. *Flora of West Virginia,* 2nd ed. Seneca Books, Grantsville, WV.

Tiner, R. W., Jr. 1988. *Field Guide to Nontidal Wetland Identification.* Maryland Dept. of Natural Resources, Annapolis, MD and U.S. Fish and Wildlife Service, Newton Corner, MA.

Tomlinson, P. B. 1986. *The Botany of Mangroves.* Cambridge University Press, New York.

Weatherbee, P. B. & G. E. Crow. 1990. Phytogeography of Berkshire County, Massachusetts. *Rhodora* 92:232–256.

Wilson, K. A. 1960. The genera of the Arales in the southeastern United States. *J. Arnold Arboretum* 41:47–72.

Additional technical references on the morphology, anatomy, embryology, and cytology of *Orontium*:

Barabé, D. and M. Labrecque. 1985. Vascularisation de la fleur d'*Orontium aquaticum* L. (Aracées). *Bull. Soc. Bot. Fr.,* 132, Lettres bot., 1985:133–145.

Engler, A. [1877] 1990. Comparative studies on the morphology of the Araceae. Part II. On leaf placement and shoot organization of Araceae. (Translated and annotated by T. S. Ray and S. S. Brenner). Botanischer Garten and Botanisches Museum, Berlin, Dahlem.

French, J. C. 1986. Ovular vasculature in Araceae. *Bot. Gaz.* 147:478–495.

———. 1988. Systematic occurrence of anastomosing laticifers in Araceae. *Bot. Gaz.* 149:71–81.

——— & P. B. Tomlinson. 1981. Vascular patterns in stems of Araceae: subfamilies Calloideae and Lasioideae. *Bot. Gaz.* 142:366–381.

Grayum, M. H. 1984. Palynology and phylogeny of the Araceae. Ph.D. Thesis, University of Massachusetts, Amherst.

———. 1991. Systematic embryology of the Araceae. *Bot. Rev.* 57:167–203.

Marchant, C. J. 1973. Chromosome variation in *Araceae*: V. Acoreae to Lasieae. *Kew Bulletin* 28:199–210.

Petersen, G. 1989. Cytology and systematics of Araceae. *Nordic J. Bot.* 9:119–166.

Ray, T. S. 1987. Leaf types in the Araceae. *Amer. J. Bot.* 74:1359–1372.