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Pitcher Plants (*Sarracenia*) Provide a 21st-Century Perspective on Intraspecific Ranks and Interspecific Hybrids: A Modest Proposal* for Appropriate Recognition and Usage

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Abstract—The taxonomic use of infraspecific ranks (subspecies, variety, subvariety, form, and subform), and the formal recognition of interspecific hybrid taxa, is permitted by the International Code of Nomenclature for algae, fungi, and plants. However, considerable confusion regarding the biological and systematic merits is caused by current practice in the use of infraspecific ranks, which obscures the meaningful variability on which natural selection operates, and by the formal recognition of those interspecific hybrids that lack the potential for inter-lineage gene flow. These issues also may have pragmatic and legal consequences, especially regarding the legal delimitation and management of threatened and endangered species. A detailed comparison of three contemporary floras highlights the degree to which infraspecific and interspecific variation are treated inconsistently. An in-depth analysis of taxonomy of the North American flowering plant genus *Sarracenia* (Sarraceniaceae) provides an ideal case study illustrating the confusion that can arise from inconsistent and apparently arbitrary designation of infraspecific ranks and hybrid taxa. To alleviate these problems, we propose the abandonment of infraspecific ranks of “variety” and “form,” and discourage naming of sterile interspecific hybrids except for use in the horticultural or agronomic trade. Our recommendations for taxonomic practice are in accord with the objectives proposed in the Systematics Agenda 2000, Systematics Agenda 2020, and the Global Strategy for Plant Conservation.

Keywords—Flora, nomenclature, *Sarracenia*, species concept, systematics.

“My first task would certainly be to rectify the names. ...If the names are not correct, if they do not match realities, language has no object. If language is without an object, action becomes impossible—and therefore, all human affairs disintegrate and their management becomes pointless and impossible. Hence the very first task of a true statesman is to rectify the names.”

From *The Analects of Confucius*, tr. Simon Leys (1997)

Systematists have long struggled with the appropriate designation of infraspecific taxa (subspecies (subsp.), variety (var.), subvarieties (subvar.), form (forma), and subforms) and interspecific hybrids (e.g. Hamilton and Reichard 1992; Stebbins 1993; McDade 1995). The botanical literature is replete with such designations, as early botanists and taxonomists, including Linnaeus, were influenced by the concept of special creation and sought to catalog the seemingly infinite range of phenotypic diversity found in nature (Reveal and Pringle 1993). This tendency has been particularly prevalent in the horticultural and agronomic literature, due in part to the economic incentive for providing a range of commercial offerings with desirable traits for ornamental or practical use (see also Hettterscheid and Brandenburg 1995). The generation of interspecific hybrids also has long been a common practice in agronomy (Kingsbury 2009); modern agribusiness often takes advantage of the infertility of vigorously growing hybrids (e.g. proprietary strains of F₁ hybrid maize) to ensure a reliable supply of customers from year-to-year (e.g. Sonka 2001).

Darwin’s (1859) observation that natural selection acts on infraspecific variation brought a new cognitive perspective to

evolutionary biology and systematics that is well reflected in contemporary approaches to phylogenetic analysis and evolutionary systematics (e.g. Bateman 2011). Many taxonomists, however, continue to treat infraspecific taxa and interspecific hybrids in ways that fail to account for ongoing dynamics that are continually occurring in the field. Although new DNA sequencing techniques are identifying genetic variability at increasingly finer scales, these differences may not reflect infraspecific distinctions. Rather, such genetic variation may better be viewed as the historical fragmentation and coalescence of genotypic possibilities that Maddison (1997) summarized in his concept of a phylogeny as a model of the change of interbreeding probabilities through time (a “cloud of gene histories”).

Even though the International Code of Nomenclature (ICN) for algae, fungi, and plants continues to recognize the validity of infraspecific ranks, there remains little consensus as to how or when to distinguish infraspecific taxa from true species. Stebbins (1993: 240) proposed a pluralistic consensus: “[i]n local floras, some authors recognize as separate species, sympatric populations that in many regions keep distinct from each other but that elsewhere form localized hybrid swarms. Other authors designate them as ‘varieties.’” But Stebbins’ (1993) consensus leads to inconsistent taxonomy. A single entity (i.e. a species, a subspecies, or a hybrid) should be the same thing wherever it occurs. It cannot logically be a species in one location, for example, and a subspecies in another.

On the other hand, the suggestion of a strictly phylogenetic nomenclature consisting of a formal, albeit rank-free, classification system with named but unranked uninomials (Mishler 1999), continues to be fraught by debates over the special status of species relative to other taxonomic ranks (summarized in Cellinese et al. 2012). Systems of phylogenetic

*With apologies to Jonathan Swift

nomenclature with named but unranked uninomials conflate the discrete goal of nomenclature (communication about taxa among individuals in a variety of scientific disciplines; Schuh 2003; Valleau 2004) with the two goals of systematics: taxonomic recognition of species (i.e. using understanding of variation to produce a falsifiable system of classification; Mayr 1992; Gaston and Mound 1993) and the identification of their hypothesized phylogenetic relationships (see also Wortley et al. 2002).

A third alternative to classical nomenclatural codes and phycodes was suggested by de Queiroz (2007), who built on Mayr's biological species concept. de Queiroz (2007) suggested that a species can be geometrically represented as a line (lineage) consisting of a continuous series of connected (often overlapping) points. Information transfer (i.e. genotypes) proceeds through time from ancestor (e.g. parent) to descendent (e.g. offspring). A species exhibits persistence through time, for which the duration is greater than a single generation of a representative individual. A sterile or otherwise non-self-sustaining hybrid, in contrast, can be represented as a point, because ancestor-descendent information transfer is not possible. The temporal duration of a sterile hybrid equals its generational time. A parental species and a sterile hybrid resulting from inter-lineage gene flow are not evolutionarily equivalent, and, in our opinion, the latter deserves less recognition than reproductive species because it does not have the potential for persistent transfer of genetic information. Sterile hybrids may be commercially successful, but they are better viewed from a systematic perspective as short-lived interconnections within Maddison's (1997) cloud of gene histories within a given lineage.

Our focus here is on assessing the nature and utility of infraspecific ranks and naming of sterile hybrids. We first build upon work by Hamilton and Reichard (1992) and McDade (1995), and examine the use of infraspecific ranks and hybrids in several classic and contemporary North American regional floristic treatments. We then explore in more detail the confusion generated by the proliferation of infraspecific designations through a case study of the genus *Sarracenia* Linnaeus (Sarraceniaceae), the Western Hemisphere pitcher plants. Our analysis and case study reinforce several recommendations previously articulated by other systematists and evolutionary biologists, but also provide additional considerations based on our experiences working with this group of plants, which exhibits marked levels of local phenotypic variation that have been recognized taxonomically.

Infraspecific Ranks and Hybrids in Past and Contemporary Floras—The use of infraspecific ranks and hybrids is widespread in many North American floristic manuals and guides (Table 1) and in the horticultural literature (e.g. Bailey 1924; L. H. Bailey Hortorium 1976). Although the ICN also allows the designation of subvariety and subform, we did not analyze these rarely-used ranks, but our discussion similarly applies to these cases. The use of infraspecific ranks varies among users and treatments; Stebbins (1993) notes that it is inconsistent even in "standard" manuals. For example, for 31 flowering plant genera found in the northeastern U. S. A. and Canada, Fernald (1950), Gleason and Cronquist (1991), and Haines (2011) differ considerably in their recognition and use of infraspecific taxa (Table 2, in which we divide the number of infraspecific and hybrid taxa by the total number of taxa recognized in each of these floras to account for their different geographic coverage). At one extreme, Fernald (1950) recognized 32% of the total flora as infraspecific taxa. At the other, Haines (2011) recognized only 16% of the taxa as such. This supports previous observations that more geographically

TABLE 2. Numbers of subspecies, varieties, forms, and hybrids recognized by Fernald (1950), Gleason and Cronquist (1991), and Haines (2011) in 31 genera of vascular land plants: *Asplenium* L. (Polypodiaceae; Aspleniaceae in Haines); *Osmunda* L. (Osmundaceae); *Nuphar* J. E. Smith (Nymphaeaceae); *Carex* L. (Cyperaceae); *Cyperus* L. (Cyperaceae); *Juncus* L. (Juncaceae); *Potamogeton* L. (Potamogetonaceae); *Cypripedium* L. (Orchidaceae); *Habenaria* Willd. (*Platanthera* Rich in Haines) (Orchidaceae); *Aster* L. (*Symphotrichum* Nees in Haines) (Asteraceae); *Lactuca* L. (Asteraceae); *Liatris* Gaertn. ex Schreb. (Asteraceae); *Prenanthes* L. (*Nabalus* Cassini in Haines) (Asteraceae); *Solidago* L. (Asteraceae); *Betula* L. (Betulaceae); *Lonicera* L. (Caprifoliaceae); *Cornus* L. (*Swida* Opiz in Haines) (Cornaceae); *Baptisia* Vent. (Fabaceae); *Lespedeza* Michx. (Fabaceae); *Quercus* L. (Fagaceae); *Carya* Nutt. (Juglandaceae); *Myrica* L. (Myricaceae); *Lysimachia* L. (Myrsinaceae); *Geum* L. (Rosaceae); *Crataegus* Tourm. ex L. (Rosaceae); *Pyrus* L. (Rosaceae); *Linaria* Miller (Plantaginaceae); *Populus* L. (Salicaceae); *Salix* L. (Salicaceae); *Acer* L. (Sapindaceae); *Viola* L. (Violaceae). The categories of subspecies and forms were not used by Gleason and Cronquist (1991). The parenthetical values are the % of the total taxa recognized as infraspecific taxa and hybrids. The complete dataset is provided in Table S1.

| | Fernald | Gleason and Cronquist | Haines |
|------------------------------|--------------|-----------------------|------------|
| Total taxa recognized | 1,767 | 1,102 | 884 |
| Species | 1,009 (57.1) | 768 (69.7) | 608 (68.8) |
| Subspecies | 6 (0.3) | — | 44 (5.0) |
| Varieties | 411 (23.3) | 255 (23.1) | 100 (11.3) |
| Forms | 145 (8.2) | — | — |
| Hybrids | 196 (11.1) | 79 (7.2) | 132 (14.9) |

TABLE 1. Use of hybrids and the infraspecific ranks of subspecies, form and variety by different North American floras. Y = rank used; N = rank not used in the flora.

| Manual | Author(s) | Year | Subspecies | Variety | Form | Hybrid |
|--|--|----------------|------------|---------|------|--------|
| <i>Manual of the Vascular Flora of the Carolinas</i> | Radford, Ahles, Bell | 1968 | Y | Y | N | Y |
| <i>Gray's Manual of Botany</i> | Fernald | 1950 | Y | Y | Y | Y |
| <i>Flora of the Pacific Northwest</i> | Hitchcock and Cronquist | 1973 | N | Y | N | N |
| <i>Manual of Vascular Plants of Northeastern United States and Adjacent Canada</i> | Gleason and Cronquist | 1991 | N | Y | N | Y |
| <i>Field Manual of Michigan Flora</i> | Voss and Reznicek | 2012 | Y | Y | N | Y |
| <i>Vascular Plants of California, second edition (Jepson Manual)</i> | Baldwin et al. | 2012 | Y | Y | N | Y |
| <i>Flora Novae-Angliae</i> | Haines | 2011 | Y | Y | N | Y |
| <i>Intermountain Flora: Vascular Plants of the Intermountain West, U. S. A.</i> | NYBG | 1972–2012 | Y | Y | N | Y |
| <i>Flora of North America</i> | Flora of North America Editorial Committee | 1993 – present | Y | Y | N | Y |



FIG. 1. Examples of different species of *Sarracenia*. Top row: *Sarracenia purpurea* (left); *S. rosea* (right). Middle row: *S. alata* (left); *S. flava* (right). Bottom row: *S. alabamensis* subsp. *wherryi* (left); *S. leucophylla* (right). All photographs by R. F. C. Naczi.

limited floras tend to recognize less variability within a taxon (i.e. overestimate endemism because the range of variability across the entire species range is not recognized in regional floras), while underestimating synonymy (Mabberley 1991; Scotland and Wortley 2003). However, 15% of Haines' (2011) flora was considered to be hybrids, whereas only 11% and 7% of Fernald's (1950) and Gleason and Cronquist's (1991) floras, respectively, were hybrids. All three floras recognize varieties, Fernald (1970) and Haines (2011) recognize subspecies, but only Fernald (1950) recognizes forms. Gleason and Cronquist (1991) were more likely to confer species rank than either Haines (2011) or Fernald (1950), whereas Haines (2011) was more likely to identify regional subspecies. In the most recent floras (e.g. NYBG 1972–2012; Flora of North America Editorial Committee 1993–present; Haines 2011; Baldwin et al. 2012), there is consistent recognition of subspecies, varieties, and hybrids, all of which are accorded full taxonomic status (Baldwin et al. 2012), but forms are no longer used (Table 1).

The proliferation of many infraspecific names and the persistence of named hybrid taxa under different taxonomic ranks in the botanical literature of the early 20th century (Table 1) correspond with the lack of an enforced uniform Code of Nomenclature prior to 1930 (although the first attempt at a uniform code occurred nearly 75 yr earlier: see de Candolle [1867]). Presently, Division II, Chapter III, Article 24 of the Melbourne Code (McNeill et al. 2012) provides clear structures for the proper naming of infraspecific taxa, such as subsp., var., and forma. Article H3 and Recommendation H3A in Appendix I provide guidelines for the proper naming of hybrid taxa (but see Hettterscheid and Brandenburg 1995). In contrast, the International Code of Zoological Nomenclature (ICZN 2012) does not provide for formal recognition of infrasubspecific groups, but subspecies are considered acceptable as part of a "species group" (Chapter 10, Article 45; ICZN 2012). In the ICZN, subspecies normally are written as trinomials.

All nomenclatural codes facilitate the naming process but none dictate what information should be included in a taxonomic description or flora (but see Article 38.2 of the Melbourne Code, especially Ex. 4, regarding diagnoses). Because the current rate of extinction is rising sharply (Leakey and Lewin 1995), some have argued that it is critical to assign names and ranks to as many undescribed taxa as possible (e.g. Hopkins and Freckleton 2002; Mace 2004; Dobson 2005; Kim and Byrne 2006; Scheffers et al. 2012; Costello et al. 2013). However, the effort to rapidly assign names tends to ride roughshod over the fact that species designations are falsifiable hypotheses (Gaston and Mound 1993) and may artificially inflate the true number of species (Scotland and Wortley 2003). Further, as noted by Bateman (2011) and Tripp and Hoagland (2013), rapid description often precludes inclusion of detailed morphologic, genetic, or phylogenetic information, thus making it difficult to test the hypothesis that a new entity described from only a small number of herbarium specimens is, in fact, a defensible new taxon. Thus, we gently suggest that botanists be more circumspect in identifying infraspecific taxa and that the requirements for recognition of a new species be more stringent. We elaborate on these ideas using a case-study of a small genus we know well: the North American pitcher plants in the genus *Sarracenia* (e.g. Naczi et al. 1999; Ellison 2001; Ellison et al. 2004, 2012; Dahlem and Naczi 2006; Ellison and Gotelli 2009; Oswald et al. 2011).

Sarracenia: A Case Study—The carnivorous plant genus *Sarracenia* (Fig. 1) offers an ideal case study illustrating the taxonomic confusion that affects researchers studying the ecology, evolution, and natural history of the genus as well as regulatory agencies charged with protecting endangered *Sarracenia* species. The two most current treatments of the genus, published within 18 mo of each other, disagree in many respects (Table 3). The review by Mellichamp and Case (2009) in *Flora of North America* recognizes only 17 non-hybrid taxa: 11 species, plus two subspecies each of *S. alabamensis*, *S. purpurea*, and *S. rubra*. In contrast, McPherson and Schnell (2011) recognize 49 non-hybrid taxa: eight species, six subspecies, 24 varieties, and 11 forms (Table 3). How has this great disparity in taxonomic recognition arisen?

In the first full treatise on carnivorous plants (Darwin 1875), there is scant detail on pitcher plants (not only *Sarracenia* and *Heliamphora*, as well as the unrelated Asian *Nepenthes* and the Australian *Cephalotus*). However, by the end of the 19th century, *Sarracenia* was of broad interest in England and across Europe, where amateur botanists and horticulturalists were hard at work propagating, cultivating, and crossing species (Veitch 1906; Macfarlane 1908). Indeed, since the late 1800s, the production and propagation of hybrid individuals has spurred considerable horticultural interest in these plants (Moore 1874; Masters 1881; Veitch 1906; for current examples, see McPherson and Schnell 2011; D'Amato 2013). The commercial interest in this genus may have resulted in the recognition of a large number of infraspecific taxa, but the number of infraspecific taxa in *Sarracenia* is not unusual compared with other groups (Table 2; full dataset in Table S1).

Initial identification keys and treatments of *Sarracenia* generally recognized seven or eight species: *S. alata* (as *S. sledgei* Macfarlane), *S. flava*, *S. leucophylla* (as *S. drummondii* Croom), *S. minor* (as *S. variolaris* Michaux), *S. oreophila* (initially as a nomen nudum variety of *S. flava*; see McDaniel 1971), *S. psittacina*, *S. purpurea*, and *S. rubra* (Macfarlane 1908; Harper 1918; Small 1933). Wherry (1935) included *S. jonesii* Wherry in his review of the genus, but reassessments and revisionary treatments by Bell (1949) and McDaniel (1971) synonymized *S. jonesii* with *S. rubra*.

Among these early systematic treatments, the recognition of infraspecific taxa was relatively uncommon. Macfarlane (1908) recognized no subspecies or forms, but did recognize seven varieties of *S. flava* differentiated by leaf size and color, and one variety of *S. purpurea*, var. *heterophylla*, recognized by its complete lack of red pigmentation (now known to be caused by a single-locus mutation: Sheridan and Mills 1998). The only infraspecific taxon recognized by Harper (1918) was *S. flava* var. *oreophila*, at the time a nomen nudum for a rarely collected species. Bell (1949) considered *S. jonesii* a form of *S. rubra* and also recognized *S. purpurea* forma *heterophylla*, but otherwise synonymized all infraspecific taxa within the eight aforementioned species. McDaniel (1971), like Gleason and Cronquist over a quarter-century later (Gleason and Cronquist 1991), concurred with Bell (1949) that subspecific and varietal subdivisions of *S. purpurea* were undesirable. McDaniel (1971) similarly recognized no subspecies or varieties of any *Sarracenia* species, but did recognize *S. purpurea* forma *heterophylla*. Most recently, in their treatment of the genus for *Flora of North America*, Mellichamp and Case (2009) eliminated varieties and forms altogether, and recognized only six subspecies in the genus.

TABLE 3. Current treatments of *Sarracenia*. The 11 species recognized by Mellichamp and Case (2009) in *Flora of North America* are listed in the first column. Mellichamp and Case (2009) also recognize six subspecies but neither varieties nor forms, whereas McPherson and Schnell (2011) recognize six subspecies, 24 varieties, 11 forms. Note also that McPherson and Schnell (2011) consider *S. alabamensis* and *S. jonesii* to be subspecies of *S. rubra*, and consider *S. rosea* to be variety *burkii* of *S. purpurea* subsp. *venosa*.

| Species | Infraspecific taxa | |
|--|---|--|
| | Mellichamp and Case (2009) | McPherson and Schnell (2011) |
| <i>alabamensis</i> Case & Case | subsp. <i>alabamensis</i> subsp. <i>wherryi</i> (D. E. Schnell) Case & Case | |
| <i>alata</i> (Wood) Wood | | var. <i>alata</i> var. <i>atrorubra</i> McPherson & Schnell var. <i>cuprea</i> McPherson & Schnell var. <i>nigropurpurea</i> D'Amato ex McPherson & Schnell var. <i>ornata</i> McPherson & Schnell var. <i>rubrioperculata</i> McPherson & Schnell f. <i>viridescens</i> McPherson & Schnell |
| <i>flava</i> Linneaus | | var. <i>flava</i> var. <i>atropurpurea</i> (Hort Bull ex Mast.) Hort. Bull ex Robinson var. <i>cuprea</i> Schnell var. <i>maxima</i> Hort. Bull ex Mast. var. <i>ornata</i> Hort. Bull ex Robinson var. <i>rubricorpora</i> Schnell var. <i>rugelii</i> (Shuttlew. ex DC.) Mast. f. <i>viridescens</i> McPherson & Schnell |
| <i>jonesii</i> Wherry <i>leucophylla</i> Rafinesque | | var. <i>leucophylla</i> var. <i>alba</i> (Hort. Baines ex Hogg & Moore) Pietropaolo & Pietropaolo ex McPherson & Schnell f. <i>viridescens</i> McPherson & Schnell |
| <i>minor</i> Walter | | var. <i>minor</i> var. <i>okefenokeensis</i> Schnell f. <i>viridescens</i> S. McPherson & Schnell |
| <i>oreophila</i> Wherry | | var. <i>oreophila</i> var. <i>ornata</i> McPherson & Schnell |
| <i>psittacina</i> Michaux | | var. <i>psittacina</i> var. <i>okefenokeensis</i> McPherson & Schnell var. <i>psittacina</i> f. <i>viridescens</i> McPherson & Schnell var. <i>okefenokeensis</i> f. <i>luteoviridis</i> McPherson & Schnell |
| <i>purpurea</i> Linneaus | subsp. <i>purpurea</i> subsp. <i>venosa</i> (Rafinesque) Wherry | subsp. <i>purpurea</i> subsp. <i>venosa</i> var. <i>venosa</i> (Rafinesque) Wherry subsp. <i>venosa</i> var. <i>burkii</i> Schnell subsp. <i>venosa</i> var. <i>montana</i> Schnell & Determann subsp. <i>purpurea</i> f. <i>heterophylla</i> (Eaton) Fern. subsp. <i>venosa</i> var. <i>venosa</i> f. <i>pallidiflora</i> McPherson & Schnell subsp. <i>venosa</i> var. <i>burkii</i> f. <i>luteola</i> Hanrahan & Miller |
| <i>rosea</i> Naczi, Case & Case | | |
| <i>rubra</i> Walter | subsp. <i>rubra</i> subsp. <i>gulfensis</i> Schnell | subsp. <i>rubra</i> subsp. <i>gulfensis</i> Schnell subsp. <i>alabamensis</i> (Case & Case) McPherson & Schnell subsp. <i>jonesii</i> (Wherry) Wherry subsp. <i>wherryi</i> (Case & Case) Schnell subsp. <i>gulfensis</i> f. <i>heteroviridis</i> McPherson & Schnell subsp. <i>jonesii</i> f. <i>viridescens</i> McPherson & Schnell |

During the same early years of the 20th century, botanical surveys expanded in North America and a number of putative naturally-occurring hybrids were observed and described (Table 4, Fig. 2; see reviews in McDaniel 1971; Bell 1949, 1952; Bell and Case 1956; Mellichamp and Case 2009; McPherson and Schnell 2011). Two taxa now recognized as hybrids, *S. × catesbaei* and *S. × swaniana*, were originally described as species. Natural hybrids are now known for every named *Sarracenia* species except for *S. oreophila* (Table 4, Fig. 2), and data in Ellison et al. (2012) also suggest the possibility that

what has been recognized as *S. purpurea* subsp. *venosa* var. *montana* arose through hybridization (or at least plastid exchange) between *S. oreophila* and *S. purpurea* var. *venosa*. Although this provides an example of Maddison's (1997) "historical genetic potentiality," we note that Mellichamp and Case (2009) consider *S. purpurea* subsp. *venosa* var. *montana* simply to be *S. purpurea* subsp. *venosa* at the southwest edge of its geographic range. Further research is needed to determine if this taxon should be recognized as a unique subspecies or a fertile hybrid.

TABLE 4. Recognized hybrids of known wild origin of *Sarracenia*. Note that *S.* × *catesbaei* was originally described as a species.

| nothospecies | cross | Recognized by | | | | | |
|-----------------------------------|--|-------------------|---------------|-------------------|-----------------|----------------------------|------------------------------|
| | | Macfarlane (1908) | Harper (1918) | Bell (1949, 1952) | McDaniel (1971) | Mellichamp and Case (2009) | McPherson and Schnell (2011) |
| × <i>areolata</i> Macfarlane | <i>alata</i> × <i>leucophylla</i> | | | ✓ | ✓ | ✓ | ✓ |
| <none> | <i>alata</i> × <i>psittacina</i> | | | | ✓ | | ✓ |
| × <i>exornata</i> Nicholson | <i>alata</i> × <i>purpurea</i> | | | ✓ | ✓ | ✓ | ✓ |
| × <i>ahlesii</i> Bell & Case | <i>alata</i> × <i>rubra</i> | | | | ✓ | ✓ | ✓ |
| × <i>moorei</i> Masters | <i>flava</i> × <i>leucophylla</i> | ✓ | | ✓ | ✓ | ✓ | ✓ |
| × <i>harperi</i> Bell | <i>flava</i> × <i>minor</i> | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| × <i>catesbaei</i> Elliott | <i>flava</i> × <i>purpurea</i> | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| × <i>naczii</i> Mellichamp | <i>flava</i> × <i>rosea</i> | | | | | ✓ | |
| × <i>popei</i> Hort. | <i>flava</i> × <i>rubra</i> | | | ✓ | | ✓ | |
| × <i>excellens</i> Nicholson | <i>leucophylla</i> × <i>minor</i> | ✓ | | | | | ✓ |
| × <i>wrigleyana</i> (S. G.) Bell | <i>leucophylla</i> × <i>psittacina</i> | ✓ | | ✓ | ✓ | ✓ | ✓ |
| × <i>mitchelliana</i> Nicholson | <i>leucophylla</i> × <i>purpurea</i> | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| × <i>readii</i> Bell | <i>leucophylla</i> × <i>rubra</i> | | | ✓ | | ✓ | ✓ |
| × <i>bellii</i> Mellichamp | <i>leucophylla</i> × <i>rubra</i> subsp. <i>gulfensis</i> | | | | | ✓ | |
| × <i>ormosa</i> Veitch ex Mast. | <i>minor</i> × <i>psittacina</i> | ✓ | ✓ | ✓ | ✓ | | ✓ |
| × <i>swaniana</i> Robinson | <i>minor</i> × <i>purpurea</i> | ✓ | | ✓ | ✓ | ✓ | ✓ |
| × <i>rhederi</i> Bell | <i>minor</i> × <i>rubra</i> | | | ✓ | ✓ | ✓ | ✓ |
| × <i>caseii</i> Mellichamp | <i>psittacina</i> × <i>alabemensis</i> subsp. <i>wherryi</i> | | | | ✓ | ✓ | ✓ |
| × <i>courtii</i> Hort. | <i>psittacina</i> × <i>purpurea</i> | ✓ | | | | ✓ | ✓ |
| × <i>gilpini</i> Bell & Case | <i>psittacina</i> × <i>rubra</i> | | | | | ✓ | ✓ |
| × <i>charlesmoorei</i> Mellichamp | <i>purpurea</i> × <i>jonesii</i> | | | ✓ | | ✓ | ✓ |
| × <i>chelsonii</i> Masters | <i>purpurea</i> × <i>rubra</i> | ✓ | | ✓ | ✓ | ✓ | ✓ |
| Total | 22 | 11 | 5 | 14 | 13 | 19 | 18 |

Although systematic treatments of the entire genus emphasize species and hybrids while de-emphasizing infraspecific taxa, regional treatments (e.g. Fernald 1950; Radford et al. 1968; Gleason and Cronquist 1991; Haines 2011), field guides (e.g. Sorrie 2011), and general reviews aimed at hobbyists and horticulturalists (e.g. Schnell 2002; McPherson 2007; McPherson and Schnell 2011) continue to identify, and even formally describe, infraspecific taxa (Small [1933] is a notable exception to this rule). Although a handful of subspecies and varieties are geographic isolates, the vast majority of infraspecific taxa are based on variation in a single phenotypic trait, most frequently leaf color (Table 5). In fact,

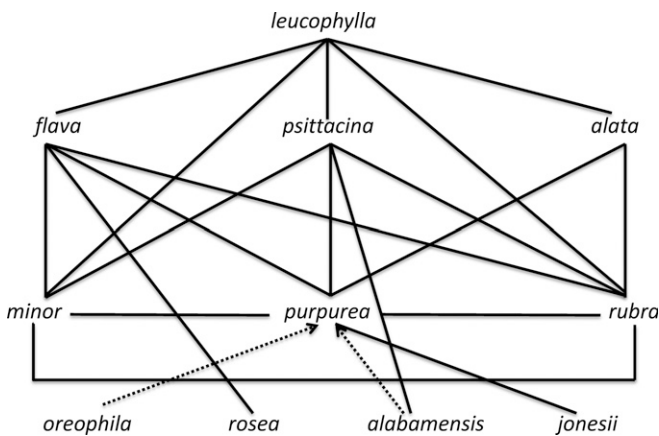


FIG. 2. Diagram of observed natural hybrids among different *Sarracenia* species (based on taxonomic treatments in Bell 1949; Bell and Case 1956; McDaniel 1971; Mellichamp and Case 2009). Although no naturally occurring hybrids yet have been documented in the literature involving *S. oreophila*, chloroplast DNA sequences suggest the hypothesis that plastids in *S. purpurea* subsp. *venosa* var. *montana* may have resulted from introgression (dotted lines) into this variety from *S. oreophila* (or perhaps *S. alabamensis*) (see Fig. 2a in Ellison et al. 2012).

all 11 forms recognized by McPherson and Schnell (2011) are color-morphs characterized by the lack of production of anthocyanins (Sheridan and Mills 1998). Students of *Sarracenia* have long noted little systematic value of color (Bell 1949), and even McPherson and Schnell's treatment illustrates a wide range of variability in colors within varieties defined by color. Evidence from allozyme and sequence data also repeatedly demonstrates a lack of clear differentiation among recognized infraspecific taxa (Bayer et al. 1996; Godt and Hamrick 1996, 1998, 1999; Neyland and Merchant 2006; Ellison et al. 2012). At the other extreme, Zellmer et al. (2012) used pyrosequence data to show that morphologically similar populations of *S. alata* on either side of the Mississippi River have been reproductively isolated for ~60,000 generations. However, Zellmer et al. (2012) did not proceed to describe the eastern and western populations as subspecies or varieties but see Carstens and Satler 2013.

As in many plant taxa, interspecific hybridization is also common in *Sarracenia* (Fig. 2), and names for many hybrid taxa have been published (Table 4). Many of these remain contested and most lack types (Bell 1952; Nelson 1986). Hybridization in the genus is not surprising, however, because most *Sarracenia* species diverged from one another less than three million years ago, likely due to late Neogene, and especially more recent Pleistocene, glaciation (Ellison et al. 2012). Hybrid swarms are common in the field, and molecular markers are being developed that may help to better identify hybrids and their parents (Rogers et al. 2010), and to assess the fertility of *Sarracenia* hybrids.

This inconsistent nomenclature, i.e. "lumping" in peer-reviewed articles and national floras, "splitting" in regional floras, field guides, and popular works (cf. Mabberley 1991; Scotland and Wortley 2003), continues to plague the taxonomy of *Sarracenia* (see reviews in Reveal 1993; Ellison 2001; Mellichamp and Case 2009). Ecologists, physiologists, conservation biologists, and others whose work depends on stable

TABLE 5. Summary of key characters used by Mellichamp and Case (2009) and McPherson and Schnell (2011) to distinguish infraspecific taxa of *Sarracenia*.

| Species | subspecies | variety | form | distinguished by |
|---|--|---|---------------------|---|
| <i>alabamensis</i> (fide Mellichamp and Case) | <i>alabamensis</i> | | | Pitchers trimorphic, soft, yellow-green to red, venation weakly pronounced; central Alabama |
| | <i>wherryi</i> | | | Monomorphic dull-green pitchers; southwestern Alabama, adjacent Mississippi, and Florida |
| <i>alata</i> | | <i>alata</i> | | Yellowish-green pitchers; minimally-colored leaf vein |
| | | <i>alata</i> | <i>viridescens</i> | No red coloration (anthocyanin-free mutant) |
| | | <i>atrorubra</i> | | Dark red pitchers |
| | | <i>cuprea</i> | | Copper-colored pitcher lid |
| | | <i>nigropurpurea</i> | | Purplish-black pitchers |
| | | <i>ornata</i> | | Dense, red leaf veins |
| | | <i>rubriperculata</i> | | Red-to-purple coloration of the underside of the pitcher lid |
| <i>flava</i> | | <i>flava</i> | | Yellowish-green to buttery yellow; darkly pigmented veins on lower surface of the lid and column |
| | | <i>flava</i> | <i>viridescens</i> | No red coloration (anthocyanin-free mutant) |
| | | <i>atropurpurea</i> | | Deep red/purple/maroon pitchers |
| | | <i>cuprea</i> | | Copper-colored pitcher lid |
| | | <i>maxima</i> | | Pure yellow-green leaves (but not anthocyanin-free – note red scale at petiole base) |
| | | <i>ornata</i> | | Dense, red leaf veins |
| | | <i>rubricorpora</i> | | Red pitchers, hood and nectar roll yellow |
| | | <i>rugelii</i> | | Pure yellow-green leaves except for red-to-purple patch on the interior surface of the pitcher column, near its junction with the hood |
| <i>leucophylla</i> | | <i>leucophylla</i> | | Pitchers red to green, top of pitcher and hood white/translucent with red veins |
| | | <i>leucophylla</i> <i>alba</i> | <i>viridescens</i> | No red coloration (anthocyanin-free mutant) Upper parts of pitcher pure white, no discernible venation on the interior of the pitcher opening |
| <i>minor</i> | | <i>minor</i> | | Pitchers short, yellowish-green, with white translucent areolation |
| | | <i>minor</i> <i>okefenokeensis</i> | <i>viridescens</i> | No red coloration (anthocyanin-free mutant) Collected in the Okefenokee National Wildlife Refuge; taller, narrower pitchers than var. <i>minor</i> . |
| <i>oreophila</i> | | <i>oreophila</i> <i>ornata</i> | | Yellowish-green to golden-yellow pitchers, red venation thin, light Dense, red leaf veins |
| <i>psittacina</i> | | <i>psittacina</i> <i>psittacina</i> <i>okefenokeensis</i> | <i>viridescens</i> | Pitchers recumbent, yellowish-green or red, with orange or red hoods No red coloration (anthocyanin-free mutant) Collected in the Okefenokee National Wildlife Refuge; very large pitchers |
| | | <i>okefenokeensis</i> | <i>luteoviridis</i> | No red coloration (anthocyanin-free mutant) Geographically defined: north of Maryland; pitchers dark red, flowers dark red to maroon; pitcher venation fine |
| <i>purpurea</i> | <i>purpurea</i> | | | No red coloration (anthocyanin-free mutant) |
| | <i>purpurea</i> <i>venosa</i> | <i>venosa</i> | <i>heterophylla</i> | No red coloration (anthocyanin-free mutant) Geographically defined: south of extent of Wisconsin Glaciation; pitchers dark red, flowers bright red; pitcher venation coarse |
| | <i>venosa</i> <i>venosa</i> | <i>venosa</i> <i>burkii</i> | <i>pallidiflora</i> | No red coloration (anthocyanin-free mutant) Geographic isolate (Gulf of Mexico drainage); pink petals |
| | <i>venosa</i> | <i>burkii</i> (sensu McPherson & Schnell) | <i>luteola</i> | No red coloration (anthocyanin-free mutant) |
| | <i>venosa</i> | <i>burkii</i> (sensu McPherson & Schnell) | | |
| <i>rosea</i> (sensu Naczi, Case & Case) | <i>venosa</i> | <i>montana</i> | | Geographic isolate (Appalachian mountain seepage bogs) |
| <i>rubra</i> | <i>rubra</i> | | | Pitchers firm, green to red to maroon; relatively short, tapering |
| | <i>alabamensis</i> (sensu McPherson & Schnell) | | | Pitchers trimorphic, soft, yellow-green to red, venation weakly pronounced; central Alabama |
| | <i>gulfensis</i> | | | Geographic isolate (Florida panhandle); |
| | <i>gulfensis</i> | | <i>luteoviridis</i> | No red coloration (anthocyanin-free mutant) |
| | <i>jonesii</i> | | | Pitchers relatively tall, bulging |
| | <i>jonesii</i> <i>wherryi</i> (sensu McPherson & Schnell) | | <i>viridescens</i> | No red coloration (anthocyanin-free mutant) Monomorphic dull-green pitchers, southwestern Alabama, adjacent Mississippi, and Florida |

and reliable taxonomy, but who usually have insufficient background to distinguish among divergent taxonomic treatments, often have no easy way to decide which taxon they are studying (of course, this problem extends to numerous taxa besides *Sarracenia*).

But this is not simply an academic problem; as suggested by the epigraph, this instability presents difficulties for managing the rare and endangered taxa of *Sarracenia* that often inhabit threatened wetland habitats. For example, the U. S. Fish and Wildlife Service (Department of the Interior 2012) lists three taxa, *S. oreophila*, *S. rubra* subsp. *alabamensis*, and *S. rubra* subsp. *jonesii*, as “endangered.” The Convention on International Trade in Endangered Species of Wild Fauna and Flora includes the same three species in its Appendix I (“species that are the most endangered...threatened with extinction,” and for which international trade is prohibited; CITES 2012). The treatment of *Sarracenia* in *Flora of North America* (Mellichamp and Case 2009) does not recognize either *S. rubra* subsp. *jonesii* or *S. rubra* subsp. *alabamensis* as valid taxa. Rather, Mellichamp and Case (2009) consider both *S. jonesii* and *S. alabamensis* to be distinct species; the latter with two subspecies. This raises the obvious question. Are any or all of these protected either by CITES or by the U. S. Endangered Species Act, or does protection depend on the flora in question? Absent reliable taxonomy, legal challenges to listing status or management plans are inevitable. For example, if *S. jonesii* is recognized as a “full” species, does it have legal protection as *S. rubra* subsp. *jonesii*?

DISCUSSION

On Intraspecific Taxa—The issues that we have raised in our summary of existing floras and in the taxonomy and nomenclature of *Sarracenia* are not new. For example, Hamilton and Reichard (1992), in their survey of a four-year sample of taxonomic monographs, revisions, and notes from 26 journals regarding ferns, gymnosperms, and flowering plants, determined that the use of infraspecific taxa “...is healthy and viable in the eyes of many taxonomists.” The ranks of subsp. and var. were the most widely employed infraspecific categories, with little consistency or agreement in their circumscription or taxonomic application among the surveyed taxonomic works. They also noted a strong regional or international bias toward certain categories, possibly reflective of historical perspectives. Similarly, McDade (1995) reported that the most common infraspecific categories in botanical monographs were subspecies and variety, but that the use of “form” had declined through time.

We identified a similarly wide usage of subspecies and varieties, but little use of forms, in northeastern North American floras (Table 2). However, many practitioners use the terms “subspecies” and “variety” interchangeably (McDade 1995), leading to confusion and inconsistent use of these designations across groups. We, along with Hamilton and Reichard (1992) and McDade (1995), continue to see a lack of a proper circumscription of the particular use of the rank “subspecies” by most plant taxonomists and systematists. This omission is also an issue in zoological taxonomy and nomenclature (Braby et al. 2012). We thus conclude that, absent the adoption of a uninomial phylocode (e.g. Cellinese et al. 2012) that applies to species and infraspecific taxa, there is a need for uniformity in usage of terms denoting infraspecific taxa that consist of biologically (i.e. evolutionarily)

meaningful and distinctive, but incompletely differentiated, groups of lineage-specific individuals.

There has been, over time, an evolution of thought regarding the appropriate use of infraspecific taxonomic categories. A number of treatises on the art and science of taxonomy and systematics have ranged from a simple listing of the hierarchy of infraspecific categories (e.g. Davis and Heywood 1973; Radford et al. 1974; Simpson 2006) to a comprehensive discussion of the history and biology of these categories (e.g. Stuessy 2009). Following from these, we propose that botanists adopt a (modified) concept of subspecies suggested by Braby et al. (2012; our modifications in italics):

“Subspecies comprise evolving populations that represent partially isolated lineages of a *well-defined* species that are *either* allopatric *or sympatric*, phenotypically distinct, have at least one fixed diagnosable character state, and that these character differences are, or are assumed to be, correlated with *at least partial* evolutionary independence according to population genetic structure.”

At the same time, we strongly discourage continued use of varieties and forms (as well as the allowed, albeit rarely used, subvarieties and subforms). Our conclusion is mirrored in the more recent general trend we identified to deemphasize, or outright discourage, the use of ranks lower than subspecies. As Stuessy (2009: 154) noted, “the usage of subspecies, variety, and form has changed over the years, which has confounded attempts to use the concepts in a consistent fashion.” Stuessy (2009) did support the use of both subspecies and varieties in those cases where such designations have proven useful in specific groups, but states “[o]ne suggestion toward uniformity would be to set a future start date, e.g. the year 2011, for the use of only one infraspecific category (preferably the subspecies),” which is the approach used in the most recent and comprehensive treatment of *Sarracenia* (Mellichamp and Case 2009).

This advice has parallels elsewhere. Among zoologists, Simpson stated that “[o]ne of the commonest and most abused terms in taxonomy has been *variety*” (Simpson 1961: 177; italics in the original). Simpson also discounted the use of the category “form” and averred (1961: 180) that “[i]n present classification, however, the *only* acceptable infraspecific *category* [i.e., rank] is the subspecies.” In fact, the current ICZN states that “[n]ames published after 1960 with the term “variety” or “form” [are] excluded” and are not regulated by the Code (ICZN 2012, Article 15.2).

On Hybrids—In the cases where two fertile species, over time, give rise either through hybridization or introgression to demonstrably self-sustaining (e.g. sexually fertile, apomictic, etc.) offspring that constitute a distinctive lineage, then formal naming of the hybrid lineage as a new species would be warranted because it exhibits the same geometric and logical properties as a fertile species (e.g. persistence through generational time, transfer of genetic information). We note that determination of the sterility or fertility of a hybrid taxon is rarely possible from herbarium specimens. Rather, field observations and other supporting information would be needed for conclusive demonstration of fertility. We recognize that obtaining such information can take time, but we suggest that improved taxonomic clarity is well worth the effort (e.g. Mayr 1992; Helgen et al. 2013).

Evolution as an Organizing Theme—The emphasis on evolution as a driving process and organizing theme of international efforts also can bring increased focus to the role of

systematics in biology, education, and public affairs (Systematics Agenda 2000 [SA2K] 1994; Daly et al. 2012). The goals of both SA2K and Systematics Agenda 2020 (Daly et al. 2012) include the analysis and synthesis of information derived from research on the history of life; and the evolutionary origin, maintenance, and loss of biological diversity. Similarly, the Global Strategy for Plant Conservation (GSPC) 2011–2020 (Conference of the Parties to the Convention on Biological Diversity 2010) includes the understanding, documentation, and recognition of plant diversity (Objective I), as well as awareness of the importance of plant diversity (Objective IV). Meeting these objectives is not possible without knowing the names of plants. In fact, the first target of the GSPC is the development of a widely accessible (i.e. online) working list of all known plants, including the compilation of synthesis of existing knowledge of nomenclature and synonymy.

The key to fulfilling any of the goals and objectives of the Systematics Agendas or GSPC is a hypothesis-driven (Gaston and Mound 1993), predictive classification system (Bateman 2011) and the ability to clearly communicate and apply this knowledge to science and society (Daly et al. 2012). We maintain that the proliferation and propagation of names for sterile, non-self-sustaining hybrids and infraspecific names below the subspecies rank does little to shed insight into the evolutionary processes at work in said lineages. Furthermore, inconsistent taxonomy and nomenclature adds confusion and inhibits proper and effective communication regarding the true nature of the taxa involved, including in many cases, their conservation, protection, and preservation. A consistent, evolutionarily-based taxonomic system is also needed to ensure that burgeoning citizen-science initiatives aimed at documenting patterns of biodiversity and their rapid changes provide consistent and accurate data (e.g. Hochachka et al. 2012).

Recommendations—We offer the following recommendations (some having been stated by previous authors as cited below).

1) For new descriptions of infraspecific taxa, we encourage the single term “subspecies” as the sole infraspecific designation below the rank of species. This term should be applied to a group of individuals only in cases where there is strong supporting evidence of incomplete differentiation, distinct geographic distribution, at least one clearly fixed phenotypic difference, or genetic differentiation that confers the possible evolutionary potential for speciation to occur (e.g. de Queiroz 2007).

2) The use of the infraspecific designations of “form” and “variety” should be abandoned in plant taxonomy and systematics. The International Code of Zoological Nomenclature (ICZN 2012) disallows the use of such categories, and there has been a historical decline in botanical systematics in the use of the category of “form” (Table 1) and the rank of “variety” (e.g. Table 2). In terms of describing or elucidating the nature of the evolutionary process, neither of these terms is of scientific value, and their continued usage only promotes confusion.

3) For those groups in which the infraspecific rank “variety” has been used in the past, we suggest that revisionary treatments should encompass infrasubspecific variation in descriptions of species or subspecies. Following Stuessy (2009), we also strongly discourage elevating a “variety” to a “subspecies,” unless there is sufficient scientific evidence to warrant such an elevation. Varieties, forms, and other

infraspecific ranks should be included in accounts of synonymy since it is crucial to provide continuity with earlier taxonomic treatments.

4) Only self-sustaining (e.g. through sexual reproduction, apomixis, etc.) populations of interspecific hybrids should be provided with formal taxonomic names. Sterile hybrids that arise through occasional syngamy from two distinct species should not be named. The ability of different species to form sterile hybrids could be noted in their written descriptions. Because it is difficult to determine from herbarium specimens whether a hybrid taxon can form a self-sustaining population, field observations and other supporting information should be sought to support (or reject) formal taxonomic or nomenclatural recognition.

5) The use and retention of “variety” and “form” (as well as “cultivar” or “cultivated variety” and infertile hybrids) should be allowed only for horticultural, agricultural, and ornamental purposes. These terms should only be used to designate desirable phenotypes that have been artificially selected for their practical (i.e. human) use or direct economic benefit, both of which need a clear communication system that reflects commercially desirable phenotypes (see also Hettterscheid and Brandenburg 1995).

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