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A Brief Review of Recent Controversies in the Taxonomy and Nomenclature of *Sambucus nigra sensu lato*

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Abstract

The genus *Sambucus* is widespread and morphologically difficult, and as a result, no taxonomic treatment to date has been entirely satisfactory. The only modern revision, by Bolli, reduced the number of recognized species worldwide from over 30 to nine. In Bolli's treatment, five taxa formerly considered to be distinct species, including *S. canadensis*, *S. cerulea*, *S. peruviana*, and the endemic island taxa *S. maderensis* and *S. palmensis*, were placed within *S. nigra* as subspecies. Available data relating to these taxa are briefly reviewed. It is suggested that, while the recognition of the American elder as *S. nigra* subsp. *canadensis* is reasonable, *S. cerulea* and possibly *S. peruviana* would be better treated as distinct species; the best classification of the other two taxa remains uncertain. The preferred family assignment for *Sambucus* is *Adoxaceae*, though the name of this family may change in future depending upon the ultimate disposition of published nomenclatural proposals now in process.

Keywords

American elder; blue elder; European elder; *Sambucus canadensis*; *Sambucus cerulea*

INTRODUCTION

Taxonomy of the elderberry genus, *Sambucus* L., has been complicated by the fact that the genus is both geographically widespread and morphologically complicated, often showing great variability within species that have broad ranges. The former has meant that most authors have dealt only with the species of a single region or section of interest, without addressing the remainder of the group. The latter has led to overdescription of species, with numerous synonyms published for some variable species, as well as the publication of large numbers of putative infraspecific taxa (subspecies, varieties or forms) that have little or no biological significance. The last worldwide revisionary study before that of Bolli (1994) was by von Schwerin (1920), who tentatively recognized 28 species and numerous varieties. Several later publications of new species, mostly Asian, were by authors who dealt only with portions of the genus. Some of the species recognized even in recent treatments are likely to be overdescribed.

Infrageneric classification has also been controversial, as the range of variation has encouraged authors to recognize infrageneric taxa despite the relatively small number of species involved. The earliest major treatments of the modern era (Fritsch, 1897; von Schwerin, 1909, 1920) recognized seven sections. Some later authors have favored

combining some of these into fewer sections (Rehder, 1913; Weberling, 1966; Hara, 1983), while others have favored recognition of both subgenera and sections (Samutina, 1986) or both sections and series (Fukuoka, 1987). The level of disagreement among classifications has continued to reflect considerable uncertainty regarding relationships among the major lineages. For example, Samutina (1986) treated *Sambucus ebulus* L. as the sole member of *Sambucus* subg. *Ebulus* (Spach) M.L. Samutina, indicating a belief that it was extremely distinctive, whereas Fukuoka (1987) placed it with *S. africana* in *Sambucus* sect. *Ebulus* Spach ser. *Ebulus*.

Bolli's (1994) Ph.D. dissertation, which provides the only modern revisionary or monographic treatment of all species of *Sambucus* worldwide, makes a dramatic break from the past, admittedly problematic traditional approach to the genus. Bolli's dissertation was validly published as a volume of *Dissertationes Botanicae* bearing an ISBN (cf. Art. 30.8 and Art. 30, Note 4 in the International Code of Nomenclature [ICN; McNeill et al., 2012]). In that volume, he reduced the number of recognized species to a mere nine, in view of which division of the genus into sections was superfluous. This reduction of perhaps 65 to 75% in the number of species recognized worldwide was accomplished by treating many formerly recognized species as mere synonyms of other species or, less often, recognizing them only at the subspecific level. The European or black elder (*S. nigra* L.), the American elder native to eastern North America and Central America (*S. canadensis* L., which itself encompasses great morphological variation), the western American blue elder (*S. cerulea* Raf.), the South American "Peruvian" elder (*S. peruviana* H.B.K.), and two Old World island taxa (*S. maderensis* Lowe and *S. palmensis* Link) were always before treated as distinct species, except that *S. maderensis* was once named as a variety of European elder, *S. nigra* var. *lanceolata* Lowe. According to Bolli, those six taxa should be treated as subspecies of a single, extremely widespread and variable species: *S. nigra* subsp. *nigra* (an autonym not to be attributed to Bolli) for the European elder, *S. nigra* subsp. *canadensis* (L.) Bolli for the American elder, *S. nigra* subsp. *cerulea* (Raf.) Bolli for the blue elder, and so forth. As Bolli's is the only modern revisionary treatment of the genus, his classification may be presumed by some users of literature to be the best available. However, there is reason to suspect that while some of Bolli's radical changes improved the taxonomy of the genus, others did not. With regard to *Sambucus nigra*, the taxon of interest to this short review, it may be that some of the taxa treated by Bolli as subspecies of *S. nigra* are appropriately so treated, while others are better recognized as distinct species.

CRITICAL EVALUATION OF BOLLI'S TREATMENT

It must be acknowledged that species circumscription is necessarily subjective. In zoology, the biological species concept (Mayr, 1942, 1957), whereby populations are considered to be the same species if they are capable of interbreeding successfully, has been popular for several decades – with the caveat that since hybridization experiments have not been feasible for many taxa, morphological differentiation is commonly used as a proxy for presumed reproductive isolation. This concept is not useful for plants, many of which hybridize freely, at one extreme, or reproduce by apomixis at the other extreme. Various genetically or evolutionarily based species concepts have been proposed, all of which have been argued to have philosophical or practical problems not limited to, for many taxa, the practical

impossibility of obtaining adequate molecular data to apply them. Therefore, the most widely used concept in plant taxonomy remains the taxonomic species concept, which considers a species to be a group of populations possessing a combination of morphological characters that distinguishes them from all other populations (e.g., van Steenis, 1957; Grant, 1981). This method unavoidably depends upon the ability of the taxonomist to observe as many characters as possible and recognize which are important in a given genus or family. An author may specify that three fixed morphological differences suffice to recognize groups at the species level, but whether two, three, or four such differences are perceived in the herbarium may depend upon both the quality of observation and the quality and number of available specimens.

The result is that differences of taxonomic opinion, whereby one taxonomist sees two or more species and another sees a single variable species or a single species with multiple subspecies and/or varieties, have been relatively common in botanical taxonomy. Taxonomists who have a bias towards recognizing every variant as a species are called “splitters”, while those who have a bias towards encompassing large ranges of variation within a single name are called “lumpers.” Because in the most problematic groups there is no definitive right or wrong answer, those whose bias is toward splitting may refuse to accept a highly lumped classification and vice versa. It is not mandatory to adopt the most recent classification, and classifications that are too different from mainstream opinion may be largely or totally rejected.

Bolli’s classification of *Sambucus* reflects a strong bias toward lumping. At one point (Bolli, 1994) he stated that “The geographical races, in the following defined as subspecies, turned out to be the biological units in *Sambucus*.” Others with an opposite bias might have been inclined to recognize “biological units” at the species level. He explained further (Bolli, 1994) that a subspecies to him represented a “morphologically homogenous group of populations” distinguished from others by both geography and morphology (or if necessary karyology, palynology, etc.), whereas a species to him was a “morphologically unique group of populations” distinguished by “discontinuities in growth habit, inflorescence architecture, as well as number, structure, and distribution of the floral organs.” Groups of populations with identical floral morphology and “biogeographical connections” would be included within a single species. Since there are many genera in which “good” species have identical floral morphology and can be distinguished only by vegetative and/or fruit characters, that principle creates a bias toward potentially excessive lumping. Furthermore, it is not clear that Bolli required species with multiple subspecies to be putatively natural groups; there are occasional indirect indications to the contrary.

Thus, users of taxonomy with less inclination towards lumping might reasonably wish to scrutinize each of Bolli’s taxonomic decisions individually rather than adopting them wholesale. A few recent floristic treatments explicitly reject portions of Bolli’s taxonomy in using traditional species circumscriptions (e.g., Solomon, 2001; Kaul et al., 2006; Whittemore, 2006); on the other hand, Turner et al. (2003) accepted Bolli’s species circumscription and reduced the two North American taxa to varieties of *Sambucus nigra*, in accordance with his general preference for the rank of varieties over that of subspecies. None of the recent local or regional treatments has conducted a complete re-evaluation of

the genus, and given the numerous challenges involved in doing so to a high standard, such work may not be expected to be repeated soon. Herein, the evidence for and against Bolli's expanded circumscription of *S. nigra* will be briefly reviewed and tentative recommendations regarding some of the taxa involved will be made.

Morphology and Palynology

Bolli (1994) noted that all six subspecies included in his broad concept of *Sambucus nigra* were quite similar morphologically, especially in floral morphology, in which there are no consistent differences among subspecies. The variation in vegetative morphology within subspecies is great enough that most subspecies are not reliably distinguishable. Bolli observes at one point that specimens from most parts of the species' range can be identified to subspecies by their geographic origin. Bolli (1994) also states that "Without detailed information about the fruit colour it is often impossible to distinguish between" subsp. *nigra*, *canadensis*, *cerulea*, and *maderensis*, adding that subsp. *nigra* and *canadensis* are morphologically most similar. Those two may also differ in characters that are not readily observable in herbarium material, such as typical habit, but many herbarium specimens of subsp. *nigra* and *canadensis* indeed cannot be reliably distinguished from one another by morphology. Bolli's key made note of minor but, if consistent, useful vegetative characters by which subsp. *peruviana* and *palmensis* could be recognized. However, the statement that subsp. *cerulea* may be indistinguishable without information on the fruit is contradicted by his key, in which that subspecies is separated first from the other five by the whitish waxy coat on the annual shoots and fruit and the elongated lenticels on the bark (which is often silver-gray).

Bolli (1994) provided high-quality SEM images of the pollen of many taxa. He seemed hesitant to treat pollen as a source of important taxonomic characters at the species level, remarking that exine sculpturing was reported to be variable within species of certain other genera. Pollen characters are rarely used in revisionary studies, primarily because they cannot be observed either in the field with a hand lens or in the herbarium with a dissecting microscope; therefore they cannot serve as the basis for a taxon circumscription or key that would be useful in practice. However, prominent differences in pollen morphology (or other characters visible to the naked eye, such as genetic markers or chemical content) can be used as supporting evidence to help to justify recognition at the species level of taxa that are morphologically distinguishable but similar enough to be of uncertain status. Bolli recognized five categories of pollen in *Sambucus*: four types with reticulate surfaces, distinguished by the distribution and apparent coarseness of the reticulum, and one with a foveolate (slightly pitted) to nearly smooth surface. The former four categories might not be unambiguously distinguishable, but the qualitative distinction between reticulate and foveolate/smooth pollen types is conspicuous. *Sambucus nigra* subsp. *nigra*, *canadensis* and *peruviana* have pollen that is reticulate over most of the surface, while *S. nigra* subsp. *cerulea*, *maderensis* and *palmensis* have pollen that is foveolate to nearly smooth.

Karyology and Interfertility

Chromosome number varies within *Sambucus nigra* as circumscribed by Bolli. Numerous references agree that the European elder, *S. nigra* sensu stricto, has a sporophytic

chromosome count of $2n = 36$ (e.g., Ourecky, 1970; Murin, 1976; D'Ovidio, 1984; Benko-Iseppon, 1992; Hollingsworth et al., 1992; Lövgqvist and Hultgård, 1999). The same also appears to be true of *S. nigra* subsp. *canadensis*, based on the most reliable reports (Ourecky, 1970; Harriman, 1981; Benko-Iseppon, 1992), and the taxa formerly known as *S. palmensis* and *S. maderensis* (Benko-Iseppon, 1992). However, chromosome counts have been reported of $2n = 38$ for *S. cerulea* (Ourecky, 1970; Benko-Iseppon, 1992) and $2n = \text{ca. } 72$ for *S. peruviana*, which is therefore a tetraploid (Benko-Iseppon, 1992).

Bolli (1994) did not consider variations in chromosome number to justify recognition at the species level. As he noted, infraspecific variation in chromosome number is already known to occur in *Sambucus*, as both $2n = 36$ and $2n = 38$ have been repeatedly reported from the similarly widespread species *Sambucus racemosa* L., as traditionally defined (e.g., Murin, 1974; Ceschmedjiev, 1976; Javurkova, 1981; Benko-Iseppon, 1992). In difficult polyploid complexes, e.g., that of yarrow (*Achillea millefolium*), it is also not infrequent for taxonomic treatments even to include multiple ploidy levels within a species for the sake of a usable taxonomy, and occasionally gene flow is known to occur among ploidy levels. However, in a simpler case in which a tetraploid is geographically separated from the presumed diploid progenitor and distinguishable from it even by minor morphological characters, many taxonomists would feel that the difference in ploidy levels favored recognition at the species level.

Sambucus nigra subsp. *nigra* and *S. nigra* subsp. *canadensis* hybridize readily, with probable hybrids being described in the literature as early as 1868 (Carrière, 1868). However, meiotic abnormalities have been reported in diploid hybrids (Ourecky, 1970) and though crosses may set seed, few of the seeds germinate (Chia, 1975). A cross of *S. nigra* \times *S. cerulea* has been reported to be semi-fertile, producing eight seedlings from 58 seeds (Chia, 1975). Hybridization between more distantly related elderberry taxa is much less successful. For example, natural hybrids between *S. nigra* and *S. racemosa* L. are very rare even though the species are sympatric over large areas; hybrids' pollen development is poor, and their seeds seldom appear viable and essentially never germinate (e.g., Winge, 1994; Koncalová et al., 1983; Nilsson, 1987). Therefore, the relative ease and success of hybridization between some subspecies of *S. nigra* sensu Bolli does suggest close genetic relatedness. It should also be noted that even in non-hybrid elderberries, many ovules may remain undeveloped and seed germination rates, which are always very low without stratification, can be relatively poor even with elaborate stratification regimes involving lengthy periods at specific temperatures (e.g., Conrad and McDonough, 1972; Brinkman, 1974; Clergeau, 1992; Bolli, 1994; Jinadasa, 2000; Atkinson and Atkinson, 2002). There probably are incomplete reproductive barriers between subsp. *nigra* and subsp. *canadensis*, but this does not necessarily support recognition at the species level; there are many other species in which reproduction between subspecies is impaired (e.g., Harushima et al., 2002; Nanni et al., 2004; Grundt et al., 2006; Nosrati et al., 2011).

Phytochemical and Molecular Data

Numerous studies reporting chemical constituents of *Sambucus* species have been conducted, but most do not directly compare multiple taxa. Bolli (1994) carried out some

TLC and HPLC analyses and reported considerable variation within subspecies of *S. nigra* in the number of anthocyanins present in an individual; however, subsp. *canadensis* was consistently distinguished by the presence of anthocyanins not found in other subspecies. He also reported that subspp. *cerulea* and *peruviana* were sometimes not distinguishable, and that subspp. *nigra* and *maderensis* were similar; no data were available from subsp. *palmensis*. Lee and Finn (2007) confirmed that subsp. *canadensis* not only has distinctive anthocyanin content as compared to subsp. *nigra*, but contains a greater number of polyphenolic compounds in substantial quantity. Perhaps as a result, the fruits of subsp. *canadensis* may have more potent anticarcinogenic activity than those of subsp. *nigra* (Thole et al., 2006). The presence of multiple chemotypes within a species is, however, common and often correlated with geography.

Finally, three years after Bolli's dissertation was completed, Eriksson and Donoghue (1997) published a phylogenetic study of *Sambucus* based on ITS sequences and cladistic analysis of limited morphological data that included five of the six species Bolli had placed within *S. nigra* sensu lato. Unfortunately, those data did not provide strong support for any hypotheses regarding evolutionary relationships. However, they did suggest that four of the taxa of interest, including *S. nigra*, *S. canadensis*, *S. peruviana*, and *S. maderensis*, might form a natural group, while the fifth, *S. cerulea*, might not be included within that group. More sequence data might be very helpful.

Tentative Conclusions

Difficulties in classification of *Sambucus* species may derive from at least two distinct factors. First, desirable forms of evidence are often unavailable; for example, if existing literature included more genetic data for the island taxa *S. maderensis* and *S. palmensis* and results of hybridization experiments crossing them with *S. nigra* subsp. *nigra*, their ideal status might be easier to determine. Second, patterns of variation in some species or species complexes, even when carefully studied using adequate material, are so complicated that neither lumping all populations into a single species nor dividing them into multiple species seems to adequately reflect the nature of observable variation. White (1962) termed this sort of group an ochlopecies, from a Greek root meaning "irregular crowd, mob" or "annoyance." Cronk (1998) defined ochlopecies as being characterized primarily by variation that is strongly polymorphic but not hierarchical nor fully correlated with geography or ecology, involving characters that vary independently rather than in suites of co-occurring features; their variability must not be attributable to hybridization or to divergence of asexually reproducing "microspecies", and usually they should be geographically and/or ecologically widespread and have variants that may be consistently distinguishable locally but not globally. Arguably, *Sambucus nigra* sensu lato may fall into this category of problematic taxa, which (to the extent that they are real phenomena rather than sampling artefacts, a debated question) are not well handled by Linnean nomenclature. Cronk (1998) argued in favor of using single binomials to cover very broad groups and applying only informal names to major morphotypes. However, since formal names, whether specific or infraspecific, are so widely used as keys to available information, it seems most conservative to continue to formally recognize distinguishable, geographically correlated

groups of populations at some level pending a more complete understanding of the relationships among them.

Considering the currently available evidence, it seems (at least to this author, who is inclined to be a moderate lumpner) that Bolli's choice to treat the former *S. canadensis* as *S. nigra* subsp. *canadensis* is reasonable. The two are certainly closely related and are so similar in morphology that specimens cannot always be unambiguously identified, which argues against recognition at the species level. By contrast, the treatment of *S. cerulea* as a subspecies of *S. nigra* appears less appropriate. The degree of reproductive isolation between *S. cerulea* and *S. nigra* might not be any greater than that between *S. nigra* subsp. *nigra* and *S. nigra* subsp. *canadensis*. However, *S. cerulea* is better distinguished from *S. nigra* sensu stricto by differences in morphology (especially the waxy indument of young twigs), chromosome number, and pollen type; the cladistic analyses by Eriksson and Donoghue (1997) that reported it to be excluded from the main group of *S. nigra*-affiliated taxa are, though weakly supported, also worthy of some consideration. Continued recognition of this taxon at the species level therefore seems (to this author) easier to justify at this time than reduction to a subspecies. Such a partial acceptance of Bolli's treatment of *S. nigra* sensu lato was implicitly adopted by McGuffin et al. (2000), who specified Standardized Common Names for use in American commerce for taxa that they named *S. nigra*, *S. nigra* subsp. *canadensis*, and *S. cerulea*.

The ideal disposition of the other three taxa is unclear. *Sambucus peruviana* is not particularly distinctive, except in being tetraploid; its morphology is barely distinguishable from that of *S. nigra* subsp. *nigra* and subsp. *canadensis*, from the latter of which it may have arisen as an autopolyploid. Bolli (1994) speculated on whether subsp. *peruviana* and subsp. *canadensis* might be able to hybridize where their current ranges overlap in Central America, but this has not been shown to occur, and given the poor fertility of diploid hybrids in this genus, it is not reasonable to assume that there would be significant gene flow across ploidy levels. Since subsp. *peruviana* can be presumed to be reproductively isolated and for the most part occupies a different range (and hence, as Bolli notes, can be identified by geography!), many taxonomists might prefer to recognize it at the species level.

The taxa traditionally called *Sambucus maderensis* and *S. palmensis*, which are native to Madeira and the Canaries respectively, can be morphologically separated from *S. nigra* subsp. *nigra* only by minor characters, but they do, like *S. cerulea*, have a different pollen type. The phytochemical content of *S. maderensis*, once treated as a variety of *S. nigra* sensu stricto, is similar to that of *S. nigra* subsp. *nigra*. *Sambucus* species are often dispersed by birds (e.g., Stiles, 1980; Malmberg and Willson, 1988); since dispersal by birds to these islands from Europe would certainly be much easier than dispersal from the New World, given the distances involved, it is plausible that the closest affinities of the island endemics may be with the European subspecies. However, since detailed genetic data and crossing studies are lacking, the degree to which these taxa have become genetically differentiated is unknown. Both are endangered, and Bolli (1994) reports that *S. nigra* subsp. *maderensis* is threatened with extinction in part because, unlike *S. nigra* subsp. *nigra*, it cannot spread from its severely reduced native habitat into secondary vegetation; this difference in habitat preferences could be viewed as evidence of genetic distinctiveness. Some taxonomists feel

that it is preferable to maintain endangered taxa of uncertain status at the species level on the grounds that erroneous reduction to a subspecies or variety might have the serious consequence of discouraging conservation efforts.

FAMILY ASSIGNMENT OF *SAMBUCUS*

Sambucus was traditionally placed within *Caprifoliaceae*, or occasionally segregated into *Sambucaceae*. DNA sequence data (Donoghue et al., 1992; Bell et al., 2001; Donoghue et al., 2001; Zhang et al., 2003) demonstrated that it and a few other genera, primarily *Viburnum* L. and *Adoxa* L., formed a monophyletic group that was clearly separated from the remainder of *Caprifoliaceae*. The removal of those genera from *Caprifoliaceae* could be accomplished either by placing each of the key genera involved into its own segregate family (*Sambucaceae*, *Viburnaceae* and *Adoxaceae*) or by placing all three into a single family, which under the rules of nomenclature is named *Adoxaceae*. Both of those family circumscriptions have come into relatively widespread use in the past two decades. However, the current recommendation of the influential Angiosperm Phylogeny Group (Bremer et al., 2009) to place all of the involved genera into *Adoxaceae* has been swaying opinion in favor of a single-family classification. Hence, *Adoxaceae* should be regarded as the preferred family assignment.

It is possible that this name will change shortly if certain nomenclatural actions are taken. *Adoxaceae* is the correct name for the combined family, even though it is the youngest of the three family names, because it is the only one of the three that has been included in the list of family names that automatically have priority over non-conserved names (Appendix IIB of the International Code of Nomenclature; cf. Art. 14.5 of the ICN [McNeill et al., 2012]). Reveal (2008) discovered that a never-used, obsolete family name, *Tinaceae* (based on *Tinus* Mill., a synonym of *Viburnum*), was slightly older than *Viburnaceae* and ought to replace it if the three-family classification is used. To avoid this undesirable outcome, he published a nomenclatural proposal that sought to add *Viburnaceae* to the list of conserved family names. Doing so would also make *Viburnaceae* the correct name if the single-family classification was used. Since Reveal felt that to be an undesirable change, he made two additional, alternative proposals, one of which would “superconserve” *Adoxaceae* and the other of which would conserve *Sambucaceae*, making that the correct name. These proposals have been very controversial, and the first committee tasked with making recommendations regarding them, the Nomenclature Committee for Vascular Plants, has had difficulty in achieving consensus for or against any of them. Whatever recommendations that committee ultimately makes will then be voted upon by the General Committee, which may have opinions of its own, and whose votes will finally be subject to the approval of the Nomenclature Section of the next International Botanical Congress (in Shenzhen, China, in 2017).

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