A HISTORY OF *ASARUM* AND *HEXASTYLIS* (ARISTOLOCHIACEAE)

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The plants commonly known as wild ginger and heartleaf have undergone various changes in their taxonomic classification. Today, in Europe and the United States of America, wild ginger is classified as the genus *Asarum* and heartleaf is classified as the genus *Hexastylis*. There have been no comparative studies between American and Asian specimens to establish the similarities between them. However, there have been many recent studies to classify these plants within Asia. This paper reviews the taxonomic characters of *Asarum* and *Hexastylis* and compares the taxonomic classification systems of at least ten different botanists throughout modern history. Recent technology for use in plant classification is also discussed.

The history of *Asarum* and *Hexastylis* is long and varied. Many botanists throughout the years have disagreed as to whether *Hexastylis* is a distinct genus or a subgroup of *Asarum*. *Asarum* has been viewed in a broad sense (sensu lato) as having about 85 species, including the species that have been referred to as *Hexastylis*. *Asarum* has also been recognized in the restricted sense (sensu stricto) with about 17 species. Under these circumstances, *Hexastylis* is considered a segregate genus with about nine species (Kelly 1998). *Asarum* is commonly known as wild ginger and *Hexastylis* is commonly known as heartleaf. These groups belong to

the family Aristolochiaceae, which is commonly known as the pipevine family or the birthwort family.

Aristolochiaceae is composed of woody and herbaceous perennials that are often aromatic. The woody plants are twining lianas and the herbaceous plants are frequently rhizomatous. *Asarum* and *Hexastylis* are both low growing, non-twining herbs with rhizomes (Huber 1993). The stems of Aristolochiaceae are branched (Mesler & Lu 1993) but in some genera, like *Asarum* and *Hexastylis*, the stems are nearly completely underground so that they appear stemless (Wofford 1989). The leaves are simple, entire, basal and cauline (Mesler & Lu 1993). The leaves of *Asarum* are deciduous and pubescent while the leaves of *Hexastylis* are evergreen and glabrous (Wofford 1989). Flowers are solitary and perfect (bisexual). The ovaries are mostly inferior (epigynous), though they are sometimes half-inferior or almost superior (hypogynous) (Huber 1993). The flowers are radial or bilateral. There are three free or fused sepals and no petals. There is usually one pistil and 6 to 12 stamens that can be free or fused to the style (Mesler & Lu 1993). The fruit is usually capsular, septicidal, or irregularly dehiscent. The abundant seeds are oily and have a starch-free endosperm (Huber 1993). The seeds have nutrient filled elaiosomes to encourage ant-dispersal since they have no other means of long-distance dispersal and they desiccate quickly (Kelly 1998). The embryo is very small but well developed (Huber 1993). Members of the Aristolochiaceae family are principally tropical; however, *Asarum* and *Hexastylis* grow primarily in the north temperate zone (Kelly 1997).

The latest research on the classification of these two groups was published by Kelly in 2001. He utilized modern cladistic methods to analyze morphological data and nuclear ribosomal DNA (internal transcribed spacer, ITS) sequences. He also reviewed the historical precedence. Kelly believes that *Hexastylis* and several other groups should be combined under *Asarum* in a broad sense. He claims that *Asarum* sensu lato is monophyletic. The characters that make *Asarum* sensu lato distinct from the rest of Aristolochiaceae are Adeterminate seasonal growth, simple leaf bases, cataphylls, preformed flowers and leaves, and fleshy, irregularly dehiscent

fruits@ (Kelly 2001). Kelly divides *Asarum* into two subgenera, *Asarum* and *Heterotropa*. Within subgenus *Asarum* are the two sections *Asarum* and *Geotaenium* and within subgenus *Heterotropa* are the two sections *Heterotropa* and *Asiasarum*. Kelly places *Hexastylis* as a series within section *Heterotropa*. The subgenus *Asarum* is characterized by connate styles and inferior ovaries while the subgenus *Heterotropa* is represented with sculptured sepals, superior ovaries, separate styles, dorsal stigmas, and bifid style extensions (Kelly 2001).

Kelly=s conclusions were reached with a sampling of species from within segregate genera, including *Asarum* Linnaeus (1753), *Hexastylis* Rafinesque (1825), *Heterotropa* Morren & Decaisne (1834), *Japonasarum* Nakai (1936), *Asiasarum* Maekawa (1936) and *Geotaenium* Maekawa (1953). See Appendix Table 1 for a listing of all of the species used by Kelly in his 1997 and 1998 analyses. To this date, no one has done a taxonomic treatment of *Asarum* sensu lato on a global level. Kelly utilized information from other sources to broaden the number of similar species; however, he did not take into consideration all of the species from these groups. He did have a greater personal sampling of *Asarum* sensu stricto (Kelly 1997). If Kelly=s methods were to be applied to all of the species involved and from all locations including eastern Asia, North America and Europe, perhaps the results would differ or perhaps Kelly=s hypothesis would be validated.

Kelly=s taxonomic classification varies from the traditionally accepted classification of Blomquist (1957), who like some of his predecessors and followers, examined only the species of North America. Kelly, however, was not the first to compare the species of North America and eastern Asia. These comparisons began as botanists proceeded to explore far-away places. Some authors split species into multiple genera and other authors lumped the species into sections within fewer genera. There is no single precedence of classification for *Asarum* sensu lato and to this day, none of them have been absolutely verified for all of the species concerned. This history of classification begins in pre-Linnaean times and continues to the present.

Asarum was first described in pre-Linnaean times. *Asarum europaeum* L., then known as *Asaron*, was described and illustrated in the 1574 herbal by Dodoen. It was also mentioned in Parkinson=s 1640 herbal and Tournefort=s 1694 and 1698 herbals (Kelly 2001). The species that was then considered the second species of *Asarum*, and later considered by some as the first species of *Hexastylis*, was collected by John Clayton in eastern Virginia before 1730 and so was called *Virginicum* (Blomquist 1957). *Asaron* (*Asarum europaeum* L.) from Europe and *Virginicum* [*Asarum virginicum* L. later known as *Hexastylis virginica* (L.) Rafinesque] from North America were mentioned in Parkinson=s 1640 herbal Theatrum Botanicum (Kelly, 2001). *Virginicum* was later described by Gronovius in 1739 in his Flora Virginia and then it was renamed by Linnaeus in 1753 to *Asarum virginicum* (Blomquist 1957). Linnaeus included four species in the genus *Asarum* in his Species Plantarum. These were *A. europaeum, A. canadense, A. virginicum* and *A. hypocistis. Asarum hypocistis* was later moved and became *Cytinus hypocistis* (Kelly 2001).

The second species of the later named genus *Hexastylis* was discovered in 1803 by André Michaux in South Carolina. He named it *Asarum arifolium* in his Flora Boreali-Americana (Blomquist 1957). Rafinesque was the first to suggest a restricted delimitation for *Asarum* in 1825. The two species of *Asarum* in North America, *A. virginicum* and *A. arifolium*, were redesignated by Rafinesque to the genus *Hexastylis*. The distinguishing characters of *Hexastylis* were connate sepals, sessile anthers, half-superior ovaries, and free styles with a bifurcate apex. Rafinesque noted that *Hexastylis* had more in common with *Siphisia* (*Aristolochia*) than *Asarum* when the flowers were seen alive (Kelly 2001). Rafinesque=s new genus *Hexastylis* was not used by American taxonomists until 1903 when Small adopted the name in the first edition of his Flora of the Southeastern United States (Blomquist 1957).

Oriental floras became known to western taxonomists when Siebold and Zuccarini issued the series of papers Flora Japonica between the years 1826 and 1870 (Li 1952). In 1834, Morren and Decaisne named the new genus *Heterotropa* to contain one Asian

species *Heterotropa asaroides*. Morren and Decaisne recognized the similarities between *Heterotropa* and *Asarum* but they emphasized the differences between the two genera. Their list of distinguishing characteristics was almost identical to Rafinesque=s list describing *Hexastylis*. Over the next century, taxonomists ignored both *Heterotropa* and *Hexastylis* as new species were discovered either because they were not aware of these genera or because they disagreed with separating the species concerned from the genus *Asarum* (Kelly 2001).

In 1840, Asa Gray published his first paper in response to Siebold and Zuccarini=s Flora Japonica. Although Halen, a student of Linnaeus, mentioned the similarities of the floras of Asia and North America in 1750, Asa Gray wrote a series of papers in the 1840s that began the foundations of plant geography as a science. In the 1850s, Asa Gray received many plant specimens from Japan and reported that the new species and genera from Japan were Aidentical, analogous, or nearly related@ (Li 1952) to species in eastern North America. Li (1952) stated that the species in eastern North America had been isolated from the species in eastern Asia long enough to develop distinct morphological characters. However, there were many identical or nearly related species in both northeastern Asia and western North America. Tiffney (1985) contributed this to the continuous rather than discontinuous distributions across the Bering land bridge. Li says that the species related between the colder regions of eastern Asia and the western part of North America are more recent and are mostly herbaceous plants. The discontinuous distribution between eastern Asia and eastern North America is relatively older and more peculiar. The species are distinct but many genera are identical and the genera are found only in these two regions (Li 1952). Asa Gray did not recognize the genus *Hexastylis* in 1842. He emended the genus *Heterotropa* that had been named by Morren and Decaisne in 1834 to include *Asarum virginicum* and *Asarum arifolium* and placed these species in the new section *Homotropa* (Blomquist 1957).

In 1841, Rugel discovered the third species of the genus that later became known as *Hexastylis*. It was found in North Carolina near

the French Broad River. It was named *Asarum* (*Monotropa*) *macranthum* by Shuttleworth but it had only been written in a message distributed by Rugel in 1841 and was not properly published. The name was changed several times due to the fact that each revision was a homonym with some other name until Britten and Baker renamed the species to *Asarum shuttleworthii* in 1898 (Blomquist 1957). In 1984, Galle collected some clumps of what became known as *Hexastylis shuttleworthii* (Britten & Baker) Small var. *harperi* Gaddy from a private garden in Decatur, Georgia and transplanted it to Calloway Gardens in Pine Mountain, Georgia and then called his cultivar ACalloway,@ (Gaddy 1987a) by which it is known in the horticultural trade (Barringer 1993).

Rafinesque=s *Hexastylis* and Morren and Decaisne=s *Heterotropa* were placed into synonymy by Braun in 1861. Braun then recognized *Asarum* in the broad sense and divided it into three sections, namely *Ceratasarum*, *Heterotropa*, and *Euasarum.* *Hexastylis* had been changed to *Ceratasarum.* Section *Ceratasarum* included the two North American species *Asarum virginicum* L. and *Asarum arifolium* Michx. as well as the one Japanese species *Asarum variegatum* Braun and Bouché. Section *Heterotropa* contained *Asarum asaroides* (Morren & Decaisne) Braun. Section *Euasarum* contained *A. canadense* L., *A. hookeri* Fielding & Gardner (= *Asarum caudatum* Lindl.), *A. himalaicum* J. D. Hook. & Th. Thomson ex Klotzsch, and *A. europaeum* L. The defining characters of section *Euasarum* were inferior ovaries, connate styles, terminal stigmas, and long anther connectives (Kelly 2001).

Braun in 1861, Duchartre in 1864 and Schmidt in 1935 did not recognize the genus *Hexastylis* and considered the species within *Hexastylis* to be *Asarum* section *Ceratasarum* (Barringer 1993). Duchartre added a fourth section, *Aschidasarum*, under which he placed the newly described Japanese species *A. elegans* Duch. (Kelly 2001). In 1893, Solereder repeated Duchartre=s sectional classification in the first edition of Engler and Prantl (Blomquist 1957). In 1933, Schmidt also repeated the four sections given by Duchartre in the second edition of Engler and Prantl. Schmidt placed these sections into two subgenera: *Heterotropa* and

Ceratasarum. Sections *Heterotropa* and *Euasarum* were placed in *Asarum* subgenus *Heterotropa* and sections *Aschidasarum* and *Ceratasarum* were placed in *Asarum* subgenus *Ceratasarum* (Kelly 2001). He had elevated *Ceratasarum* from the rank of section as given by Braun in 1861 to the rank of subgenus with *Ceratasarum* also listed as a section within the subgenus (Blomquist 1957). By 1933, *Asarum* section *Euasarum* held six species, including *A. caudigerum* Hance, the first member of the group from China (Kelly 2001).

In 1897, Small described *Asarum callifolium* from Florida. It had already been collected by Chapman about fifty years earlier and he identified it as *Asarum arifolium* Michx (Blomquist 1957). Barringer later placed *A. callifolium* Small as a variety under *A. arifolium* Michx. because Blomquist (1957) and Gaddy (1987b) demonstrated that it was actually a Gulf Coast variety of *Hexastylis arifolium* (Michx.) Small with large flowers. Also in 1897, Ashe discovered *Asarum ruthii, A. memmingeri, A. heterophyllum,* and *A. minus.* He complained that the description given by Gronovius in 1739 did not give enough information to distinguish *Asarum virginicum* from any of its close relatives. Ashe Athought it preferable to follow the practice of several European botanists and ignore, in such a case of uncertainty, the Linnaean name, as it represents a group of at least four species rather than a single plant@ (Ashe 1897). Ashe had someone make a comparison between *A. minus* and the Gronovius specimen of *A. virginicum* in the British museum. Although *A. minus* was a smaller plant with a smaller flower, Ashe admitted that *A. minus* could actually be *A. virginicum* (Ashe 1897). Barringer (1993) later placed *A. ruthii* as a variety under *A. arifolium* because Blomquist (1957) recognized it as a variety under *Hexastylis arifolia* (Michx.) Small.

Between the years 1886 and 1905, Chinese plants became available to the scientific world when Forbes and Hemsley published their Index Florae Sinensis. Between 1900 and 1901, Diels published his Die Flora von Central-China. The areas covered in this publication were the upper and middle Yangtze valley. These are the areas where the largest concentration of species that appear related to species from eastern North America occurs (Li 1952). It is

interesting to note that the habitats in which *Asarum* sensu lato have been found are nearly the same on both sides of the world. The mountain-riparian areas are similar among Japan, the Yangtze valley of China and the Appalachian region of North America.

In 1933, Maekawa studied the Japanese flora and he preferred to use the segregates of *Asarum* instead of lumping all of the species into one single genus. Maekawa moved about 45 species from *Asarum* to the segregate genus *Heterotropa*. Over the next several decades, he described and named many new species, renamed existing species, and set up additional segregate genera. In 1936, Maekawa suggested that *Asiasarum* is similar to *Heterotropa* except that *Asiasarum* has long stamen filaments and lacks the shelf of tissue that lies along the inner surface of the calyx (Kelly 2001). That same year, he divided *Asarum* into five segregate genera. The first genus *Asarum* sensu stricto contains a combination of European, North American and Asian species. The genera *Asiasarum, Geotaenium,* and *Heterotropa* all have species found exclusively in the orient. The fifth genus *Hexastylis* has species found only in the southeastern United States (Gaddy 1987b).

In 1933, Small published his Manual of the Southeastern Flora. He divided the family Asaraceae into three genera: *Hexastylis*, *Asarum* and *Aristolochia*. He listed eight species of *Hexastylis* and four species of *Asarum*. See Appendix Table 2a for the list of these two genera. He separated *Aristolochia* into three sections: *Hastatae* with three species, *Pentandrae* with one species and *Macrophyllae* with two species. Small distinguished *Hexastylis* by its superior ovary, distinct styles, filaments that are shorter than the anthers, and evergreen leaves. He distinguished *Asarum* by its inferior ovary, united styles, filaments that are longer than the anthers, and deciduous leaves (Small 1933).

Roland Harper discovered a new species in south central Alabama in 1924 and he named it *Hexastylis speciosa* because of its showy flowers (Harper 1924). Fernald discovered a new species of *Asarum* in 1943. He and Lewis found *A. lewisii* but Fernald named it. When Fernald published the eighth edition of Gray=s Manual of Botany in 1950, he did not recognize *Hexastylis* as a separate genus as Small had done (Blomquist 1957) but instead, he included all of

the wild ginger and heartleaf species in the genus *Asarum* (Wilson and Brown 1981).

In 1945, Blomquist found a new species of *Hexastylis* in North Carolina and named it *H. pilosiflora*, but in his later publication of 1957 he recognized it as *H. lewisii* (Fernald) Blomquist & Oosting. He said that the plant had two different kinds of rhizomes. Some rhizomes are elongate and have many leaves that are reduced to vestiges of petioles. Other rhizomes are short and usually have flowers. In addition to the elongate rhizomes, the most distinctive characters are long colorless hairs that are found inside of the calyx lobes as well as the longitudinal ridges inside of the lower part of the tube. Although other species of *Hexastylis* have hairs inside the calyx, this one has the longest and most uniformly colorless hairs. Blomquist also described the natural habitat of *H. virginica* (L.) Small and *H. arifolia* (Michx.) Small. *H. virginica* is restricted to steep streams and river bluffs while *H. arifolia* grows openly on wooded slopes near streams. He said that they occasionally grow together on some bluffs but they flower at different times (Blomquist 1945). In 1986, Gaddy stated that no natural hybrids of *Hexastylis* had ever been reported. However, Wyatt had succeeded in hybridizing *Hexastylis arifolia* with *H. virginica* in a laboratory in 1954 (Gaddy 1986).

In addition to morphological characters, some botanists began to use the information from DNA testing to distinguish between species. Different gene sequences can be used to study phylogenetic relationships at various taxonomic levels. To study distantly related organisms, a sequence that evolves slowly is needed such as the nuclear small-subunit ribosomal DNA sequences (16S-like). To study organisms at the family level, mitochondrial rRNA genes are more useful since they evolve more rapidly. The quickest evolving genes are the internal transcribed spacer region and intergenic spacer of the nuclear rRNA repeat units, which are most appropriate for comparing taxa at the species level (White et al. 1990). In 1914, Samuelson gave the earliest chromosome report on Aristolochiaceae. In 1918, Tackholm and Söderberg found that the chromosomes of *Asarum* are larger than the chromosomes of *Aristolochia* (Gregory

1956) and that the large chromosomes of *Asarum* resembled the chromosomes of monocotyledons (Huber 1993).

Maekawa was utilizing chromosome numbers in his classifications in 1953. He named a new genus, *Geotaenium*, to include the two Asian species, *Asarum geophilum* Hemsl. and *Asarum epigynum* Hayata, because of their unusual diploid chromosome number of 2*n* = 12. However, he was the only one to advocate recognition of this genus even into the 1990s (Kelly 2001). As discussed earlier, Maekawa preferred to split the species into separate genera but others like Schmidt and Araki preferred to lump the species into the single genus *Asarum* (Gaddy 1987b).

In 1937 and 1953, Araki produced an Ainfrageneric classification for *Asarum* that formed a strong basis for the current taxonomy of the group@ (Kelly 2001). He divided two subgenera into nine sections Abased on characters related to sepal morphology, leaf persistence, and shape of the anther connectives@ (Kelly 2001). The two subgenera were *Asarum* subgenus *Asarum*, which was characterized by the Asepals being free above the base and forming a pseudotube,@ (Barringer 1993) and *Asarum* subgenus *Heterotropa* (Morren and Decaisne) Schmidt, which was distinguished by the Asepals being fused into a tube@ (Barringer 1993). He placed the sections *Ceratasarum* (*Hexastylis*) Braun, *Heterotropa* (Morren and Decaisne) Braun, and *Asiasarum* (Maekawa) Araki together in the subgenus *Heterotropa.* Then he placed the remaining North American species in subgenus *Asarum* (Barringer 1993). When Blomquist wrote his influential revision of *Hexastylis* in 1957, he overlooked Araki=s classification (Barringer 1993).

Blomquist wrote his well known revision of *Hexastylis* of North America in 1957. Though he did recognize some species that Small had recognized in 1933, Blomquist did not recognize the same ones that Small had listed for the segregate genus *Hexastylis* (Wilson and Brown 1981). See Appendix Tables 2a-c for the listing of these species as well as a comparison of other classifications. He divided the taxa of *Hexastylis*, which occurs in the southeastern United States, into three distinct groups: *Arifolia, Speciosa,* and *Virginica.* See Table 1 for the key to these three groups:

Table 1. Blomquist=s botanical key to the groups *Arifolia, Speciosa,* and *Virginica* under the genus *Hexastylis*.

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1. Style-extensions above the stigmas *bifid to the stigmas,* the lobes usually divergent at anthesis; leaf-blades triangular- to ovate-sagittate or -subhastate, when variegated, the light green areas *between* the principal veins.
    2. Calyces narrowly to broadly flask-shaped or ovate, the lobes erect or more or less spreading, without a flange above and smooth within the tube. B **group *Arifolia***.
    2. Calyces elongate-cut-shaped below, expanding abruptly above into an expansive flange and ridged-reticulate inside the tube. B **group *Speciosa***.
1. Style-extensions above the stigmas *not bifid to the stigmas,* mostly only notched at the apex; leaf-blades cordate to orbicular-cordate or retuse, when variegated, the light green areas *along* the principal veins; calyces ridged or ridged-reticulate inside the tube. B **group *Virginica*** (Blomquist 1957).

Blomquist pointed out that Ageneric concepts are formulated on the basis of personal experience and judgement@ (Blomquist 1957). Heuristic methods were utilized in this traditional phylogenetic approach to taxonomy in which there is a non-rigorous procedure for comparing relationships. This kind of taxonomic classification leads to many disagreements particularly when there is not enough information on all of the species concerned. Blomquist believed that if there were a more thorough, monographic study of *Asarum* sensu lato, there would be a general division of it into even more genera. He said that since the Oriental species were still relatively unknown at the time, his system only applied to the North American species.

However, he listed some of the Oriental species that could be placed in *Hexastylis*, namely: *A. variegatum* Braun and Bouche, *A. maximum* Hemsl., *A. macranthum* Hook. f., and *A. sieboldii* Miq. (Blomquist 1957). Blomquist did, however, overlook more than thirty Asiatic species that had been published by 1957 (Kelly 1997).

Radford, Ahles and Bell (1968) recognized eight species of *Hexastylis*, one species of *Asarum*, and two species of *Aristolochia* in their influential Manual of the Vascular Flora of the Carolinas as listed in Appendix Table 2b. However, the disagreements between the treatments of *Hexastylis* and *Asarum* continued. In the same year, Rickett used the name *Asarum* for most of the species that others recognized under *Hexastylis* except for two very rare species (Wilson and Brown 1981).

In 1981, Sugawara conducted cytotaxonomic (karyotypes and C-banding patterns) analyses on 14 species of *Asarum* sensu stricto, *Asiasarum* and *Heterotropa*. He reiterated the hypothesis of Maekawa from 1963 that the chromosome number 2n=26, which is characteristic of most species of *Asarum* sensu stricto, *Asiasarum* and *Hexastylis*, may be the ancestral condition and that the chromosome number 2n=24, which is characteristic of all species of *Heterotropa*, may be a derivation due to chromosomal reduction. Then he stated that there was no evidence in his study to support that hypothesis and that the evolutionary significance of the chromosome numbers and the generic relationships should be reconsidered (Sugawara 1981).

In 1982, Sugawara extended his studies to *Hexastylis ruthii* (Ashe) Small [2n=26], *Hexastylis speciosa* Harper[2n=26], and *Asarum epigynum* Hayata [2n=12]. *Asarum epigynum* is different from the other groups in *Asarum* sensu lato in chromosome number and karyotype. Sugawara refuted Blomquist=s subdivision of *Hexastylis* into the groups *Arifolia*, *Speciosa* and *Virginica*, which was based on the shape of the pistil. He found no difference in the karyotype or C-banding pattern between *H. ruthii* of group *Arifolia* and *H. speciosa* of group *Speciosa*. However, he did find significant differences between the genera *Hexastylis* and *Asarum*. Earlier studies by Ono in 1960 showed a close relationship between *Hexastylis* and *Asarum* due to the number of chromosomal pairs but

the two species of *Hexastylis* studied by Sugawara had a different number of chromosomal pairs from those of *Asarum* sp. He concluded that these species of *Hexastylis* were actually more similar to *Asiasarum*. However, there were obvious differences between *Asiasarum* and *Hexastylis* in the C-banded chromosomes (Sugawara 1982).

In 1983, Cheng and Yang utilized *Asarum* in the broad sense in their taxonomic classifications of Chinese species as did Hatusima and Yamahata in 1988 with the Japanese species (Barringer 1993). They followed Araki=s initial hierarchy with a few changes. Huber also followed Araki=s lead in placing all of the species of *Asarum*, *Hexastylis* and *Heterotropa* under *Asarum* sensu lato (Huber 1993). Cheng and Yang (1983) divided *Asarum* sensu lato into the same two subgenera that Araki established: *Asarum* and *Heterotropa*. The difference lies in the sections and series beneath these subgenera. See Appendix Table 4 for this classification. The distinguishing characters of *Asarum* subgenus *Asarum* and subgenus *Heterotropa* are given by Cheng and Yang (1983) in Appendix Table 5c along with the character descriptions of several other taxonomists in Appendix Tables 5a-c.

In 1984, Soltis noted the differences in the karyotypic data between Sugawara in 1982 and Maekawa and Ono in 1965; so he reinvestigated the same species of *Asarum* plus three additional species of *Hexastylis* in order to represent all of the groups recognized by Blomquist in 1957. These species were *Asarum canadense* L., *Asarum caudatum* Lindl., *Hexastylis arifolia* (Michaux) Small, *Hexastylis lewisii* (Fernald) Blomquist and Oosting, and *Hexastylis virginica* (L.) Small. The data on the species of *Asarum* found by Soltis was in agreement with that found by Sugawara. The combined data of Soltis and Sugawara show no apparent differences in the karyotypes among the species of the three subgeneric groups of *Hexastylis* as recognized by Blomquist. Soltis disagreed with Maekawa and Ono in their assessment of the karyotypes of *Asarum* and *Hexastylis*. They found that the karyotypes were nearly identical, indicating a close relationship. Alternatively, Soltis did agree with Sugawara in finding that *Hexastylis* and *Asarum* are karyotypically different (Soltis, 1984).

In 1987, Gaddy made a review of the taxonomy and biogeography of *Hexastylis.* He decided to follow Blomquist and Soltis in recognizing *Hexastylis* as a distinct genus. Gaddy maintains the three groups set forth by Blomquist: *Arifolia*, *Speciosa* and *Virginica.* Gaddy departs from Blomquist by going further into dividing group *Virginica* into subgroups: *Virginica, Shuttleworthii* and *Heterophylla*. See Appendix Table 2c for the complete listing of species and varieties. Gaddy perpetuated a correction made by Bell in Radford et al. in 1968. *Hexastylis minor* was originally named by Ashe in 1897 as *Asarum minus* and when Blomquist renamed it *Hexastylis minus*, he maintained the masculine spelling of *minus*. Although *Asarum* is masculine, *Hexastylis* is feminine and so it needed to be corrected to the feminine form of *minor* (Gaddy 1987b).

Sugawara wrote a third taxonomic study of *Asarum* sensu lato in 1987. In addition to the cytological comparisons by which he previously established generic distinctness, he also compared the floral anatomies of twelve species from the five related genera: *Asarum*, *Geotaenium*, *Hexastylis*, *Asiasarum* and *Heterotropa.* By looking at the gynoecial vasculature, Sugawara was able to find differences between *Asarum-Geotaenium* and *Asiasarum-Heterotropa-Hexastylis*. He found that the ventral bundles of *Hexastylis* differed from those of *Asiasarum-Heterotropa* and *Asarum-Geotaenium* but the floral structure and vasculature of *Hexastylis* was closer to *Asiasarum-Heterotropa*. Sugawara also pointed out that since more emphasis is placed on floral structure and vasculature than on chromosomal evolution as relation indicators, the different chromosome numbers among the species must have evolved separately within the two lines: *Asarum* [2n=24] B *Geotaenium* [2n=12] and *Asiasarum* [2n=26] B *Heterotropa* [2n=24] B *Hexastylis* [2n=26] (Sugawara, 1987).

In 1990, Sugawara, Ogisu, and Cheng described a new species of *Asarum* from southwestern China, *Asarum yunnanense* T. Sugawara, M. Ogisu & C. Y. Cheng. It is most closely related to *A. geophilum* and *A. epigynum* because they share the same chromosome number of 2n=12 as well as some floral characters such as an urceolate calyx-tube that spreads above the gynoecium. However, it is

different from the other two species in that it has longer filaments, differently shaped leaves and a symmetrical karyotype versus an asymmetrical karyotype. Sugawara et al. were reluctant to split *Asarum* into separate genera even when they are as different as what others have categorized as the segregate genus *Geotaenium*, which contains *A. geophilum* and *A. epigynum*. Therefore, they placed the new species as well as the other two species mentioned above into the genus *Asarum* until the relationships between all of the species within *Asarum* sensu lato have been studied (Sugawara et al. 1990).

In 1993, Barringer recombined the North American genus *Asarum* in the broad sense. He does not list all of the species of *Asarum* because they are already listed elsewhere. He also does not list all of the species previously segregated into *Hexastylis* because the unlisted species already have valid names in *Asarum* or they are considered synonyms. For instance, Barringer eliminated the name *Hexastylis rhombiformis* Gaddy because the original description given by Gaddy shows the flower shape of a typical *Hexastylis contracta* Blomquist. Blomquist was aware of the degrees of variability in this species and described this in his review of *Hexastylis* in 1957. Barringer considered these two species names synonyms and changed both of them to *Asarum contractum* (Blomquist) Barringer (Barringer 1993). See Appendix Table 2c for Barringer=s list of new *Asarum* species.

In 1997, Kelly reiterated the fact that the relationships between the five segregate genera previously mentioned are unclear and that their monophyly had not yet been tested. Kelly was the first to apply cladistical analysis to *Asarum* sensu lato. Kelly=s data supported the formation of two major clades within *Asarum* sensu lato which parallel the groups established by Sugawara. Though, Kelly disagrees with the hypothesis of Sugawara in 1981 and Yinger in 1983 that the first chromosomal number was 2n=12 then doubled to 2n=24 and then progressed to 2n=26 by aneuploid increase. Kelly supports Maewaka=s hypothesis from 1963 that an aneuploid reduction occurred between the various species of *Asarum* sensu lato from 2n=26 to 2n=24 and then to 2n=12 (Kelly 1997).

In 1998, Kelly tested the phylogenetic relationships within *Asarum* sensu lato based on morphological characters and ITS sequences. He confirmed his previously described two clade system. Based on ITS data alone he concluded that *Asarum* sensu stricto is monophyletic. *Heterotropa* is also monophyletic and *Hexastylis* is paraphyletic, but *Heterotropa* plus *Hexastylis* are monophyletic (Kelly 1998). In his 2001 taxonomic treatment, Kelly placed *Hexastylis* as a series within section *Heterotropa* (Kelly 2001). When the ITS data and morphology data were combined, Kelly found better resolution between the large groups. He could see that *Geotaenium* was a sister group to *Asarum* sensu stricto and that *Asiasarum* was a sister group to *Heterotropa-Hexastylis*. Kelly has decided to treat *Asarum* in the broad sense for a couple of reasons. If he were to recognize the two clades as segregate genera, he would have to name one of them *Hexastylis* as required by priority and he would have to make about fifty new combinations in the process. Another reason to maintain all of the species under a single genus is to highlight the morphological unity of *Asarum* sensu lato within Aristolochiaceae (Kelly 1998).

In reflecting on evolutionary developments, it is important to examine the possibilities of hybridization via cross-pollination. Kelly determined, based on floral characters and pollination activities, that autonomous self-pollination is evolutionarily ancestral to herkogamous outcrossing. Although cross-pollination can occur during the female phase of flowering, the species of *Asarum* sensu lato that were observed rely more heavily on self-pollination. He admits that as new data are gathered on the unsampled herkogamous species, the prevalence of outcrossing in *Hexastylis* and *Heterotropa* may be underestimated (Kelly 1997). Araki (1953), Cheng & Yang (1983), and Kelly (2001) segregate *Asarum* sensu lato into the two subgenera *Asarum* and *Heterotropa*. All of them have reviewed species from Asia and North America and have listed some distinguishing characteristics of these two genera but they do not all have the same lists as can be seen in Appendix Tables 5a-c. At least two of the authors agree on two points. One is that subgenus *Asarum* has free sepals that form a short tube while subgenus *Heterotropa* has fused sepals that form variously shaped tubes.

Second is that subgenus *Asarum* has connate styles that form a column while subgenus *Heterotropa* has separate styles.

It is evident that more studies need to be conducted to determine the validity of the most recent taxonomic classifications and whether these groups truly belong within *Asarum* sensu lato or a number of segregate species. It seems safer to lump the species into a single genus and then further segregate them into various groupings within that genus until it can be proven that the species should be put into segregate genera based on their evolutionary history as more knowledge comes to light. The biogeographical evidence suggests that all of the species discussed thus far in *Asarum* sensu lato are most likely closely related but various groups evolved separately beyond some certain time in the past. Some authors have based their taxonomic groupings on a sampling of species that were collected from a relatively small area on the planet while other authors have chosen to include a sampling from as many areas around the globe as are representative of the genus *Asarum* sensu lato. Morphological characters have been traditionally used for centuries to classify plants, but modern techniques in the study of DNA have added a valuable tool in the equally modern cladistical approach to taxonomic classifications. It is best to take all things into consideration and to maintain an open mind as small steps are taken to prove or disprove each hypothesis as it arises.

Appendix Table 1. Species of *Asarum* sensu lato included in Kelly=s cladistical analyses of 1997 and 1998.

Asarum sensu stricto

Section *Asarum*

A. canadense L.
A. europaeum L.
A. lemmonii S. Watson
A. marmoratum Piper

Section *Calidasarum* Araki

A. caudatum Lindl.
A. caudigerum Hance
A. hartwegii S. Watson

Section *Japonasarum* (Nakai) Araki
A. caulescens Maxim.
A. pulchellum Hemsl.
Section *Brevituba* Cheng & Yang
A. caudigerellum Cheng & Yang
A. debile Franch.
A. himalaicum Hook & Thomson
Segregate *Geotaenium* [*Asarum* **section** *Geotaenium* (2001)]
A. epigynum Hayata
Segregate *Asiasarum* [*Asarum* **section** *Asiasarum* (2001)]
A. sieboldii Miq.
Segregate *Heterotropa* [*Asarum* **section** *Heterotropa* (2001)]
Section *Bicornes* Araki
A. blumei Duch.
A. forbesii Maxim.
A. fudsinoi Ito
A. gelasinum (F. Maek.) Hatus.
A. hatsushimae Hatus. & Hamada
A. savatieri Franch.
A. takaoi F. Maek.
A. yakusimense Masam.
Section *Aschidasarum* Duch.
A. asperum F. Maek.
A. crassum F. Maek.
A. minimitanianum Hatus.
Section *Longiflora* Cheng & Yang [listed only in 1997]
Section *Heterotropa* (Morren & Decne.) Braun
A. asaroides (Morren & Decne.) Makino
A. satsumense F. Maek.
Segregate *Hexastylis* [*Asarum* **section** *Heterotropa* **series** *Hexastylis* (2001)]
A. arifolium Michx.
A. shuttleworthii Britten & Baker
A. speciosum Harper
A. virginicum L.
A. minor Ashe [listed only in 1998]

Appendix Table 2a. Taxonomic Classifications of *Hexastylis* and/or *Asarum*

Blomquist (1957)	Small (1933)
Genus *Hexastylis*	**Genus** *Hexastylis*
Group *Arifolia*	
H. arifolia (Michx.) Small	*H. arifolia* (Michx.) Small
var. *arifolia*	
var. *ruthii* (Ashe) Blomquist	*H. ruthii* (Ashe) Small
var. *callifolia* (Small) Blomquist	*H. callifolia* Small
Group *Speciosa*	
H. speciosa Harper	*H. speciosa* Harper
Group *Virginica*	
H. shuttleworthii (Britten & Baker) Small	*H. shuttleworthii* (Britten & Baker) Small
H. heterophylla (Ashe) Small	*H. heterophylla* (Ashe) Small
H. virginica (L.) Small	*H. virginica* (L.) Small
H. minus (Ashe) Blomquist	*H. memmingeri* (Ashe) Small
H. lewisii (Fernald) Blomquist & Oosting	**Genus** *Asarum*
H. naniflora Blomquist	*A. reflexum* Bicknell
H. contracta Blomquist	*A. canadense* L.
	A. accuminatum (Ashe) Bicknell
	*A. rubracinctum*Peattie
	Genus *Aristolochia*
	8 species

Appendix Table 2b. Taxonomic Classifications of *Hexastylis* and/or *Asarum*

Radford et al. (1968)	Radford continued
Genus *Hexastylis*	**Genus** *Asarum*
H. arifolia (Michx.) Small	*A. canadense* L.
H. shuttleworthii (Britten & Baker) Small	**Genus** *Aristolochia*
H. heterophylla (Ashe) Small	2 species

H. virginica (L.) Small
H. minor (Ashe) Blomquist
H. lewisii (Fernald) Blomquist & Oosting
H. naniflora Blomquist
H. contracta Blomquist

Appendix Table 2c. Taxonomic Classifications of *Hexastylis* and/or *Asarum*

Gaddy (1987)	Barringer (1993)
Genus *Hexastylis*	**Genus** *Asarum*
Group *Arifolia*	
H. arifolia (Michx.) Small	*A. arifolium* Michaux
var. *arifolia*	
var. *ruthii* (Ashe) Blomquist	**var**. *ruthii* (Ashe) Barringer
var. *callifolia* (Small) Blomquist	**var**. *callifolium* (Small) Barringer
Group *Speciosa*	
H. speciosa Harper	*A. speciosum* (Harper) Barringer
Group *Virginica*	
Subgroup *Shuttleworthii*	
H. shuttleworthii (Britten & Baker) Small	*A. shuttleworthii* Britten & Baker
var. *shuttleworthii*	
var. *harperi* Gaddy	**var**. *harperi* (Gaddy) Barringer
H. lewisii (Fernald) Blomquist	
Subgroup *Heterophylla*	
H. heterophylla (Ashe) Small	
H. minor (Ashe) Blomquist	
H. naniflora Blomquist	
H. contracta Blomquist	
Subgroup *Virginica*	
H. virginica (L.) Small	
H. rhombiformis Gaddy	

Appendix Table 3a. Taxonomic Classifications of *Asarum* sensu lato and/or the segregates of *Asarum* sensu stricto B excluding those listed in Appendix Tables 2a-c.

Maekawa (1953)	Araki (1953)
divided *Asarum* sensu lato into 5 segregate genera	divided *Asarum* sensu lato into 2 subgenera
Genus *Asarum* sensu stricto	**Genus** *Asarum* sensu lato
Genus *Asiasarum*	**Subgenus** *Heterotropa*
Genus *Geotaenium*	**Section** *Ceratasarum* Braun [*Hexastylis*]
Genus *Heterotropa*	**Section** *Asiasarum* (Maekawa)Araki
Genus *Hexastylis*	**Section** *Heterotropa* (Morren & Decaisne) Braun
	Subgenus *Asarum* Remainder of the North American species

Appendix Table 3b. Taxonomic Classifications of *Asarum* sensu lato and/or the segregates of *Asarum* sensu stricto B excluding those listed in Appendix Tables 2a-c.

Sugawara (1987) & Kelly (2001)	Kelly (2001)
Divided *Asarum* sensu lato into 2 clades	**Genus** *Asarum* sensu lato
Genus *Asarum* sensu lato	**Subgenus** *Asarum*
Asarum-Geotaenium clade	**Section** *Asarum*
Asiasarum-Heterotropa-Hexastylis clade	**Section** *Geotaenium*
	Subgenus *Heterotropa*
	Section *Heterotropa*
	Series *Hexastylis*
	Section *Asiasarum*

Appendix Table 4. The Chinese species of *Asarum* sensu lato included in Cheng & Yang=s taxonomic classification.

Genus *Asarum*
Subgenus *Asarum*
Section *Asarum*
Series *Calidasarum* (Araki) Cheng & Yang
A. caudigerum Hance
var. *caudigerum*
var. *cardiophyllum* (Franchet) Cheng & Yang
A. renicordatum Cheng & Yang
Series *Japonasarum* (Nakai) Cheng & Yang
A. pulchellum Hemsley
A. caulescens Maxim.
Section *Brevituba* Cheng & Yang
A. caudigerellum Cheng & Yang
A. debile Franchet
A. himalaicum Hooker & Thomson ex Klotzsch
A. geophyllum Hemsley
A. epigynum Hayata
Subgenus *Heterotropa*
Section *Asiasarum* (Maekawa) Araki
A. sieboldii Miq.
A. sieboldii Miq. f. *seoulense* (Nakai) Cheng & Yang
A. heterotropoides Schmidt
var. *mandshuricum* (Maxim.) Kitagawa
Section *Heterotropa* (Morren & Decne.) Braun
Series *Achidasarum* (Duchartre) Cheng & Yang
A. chinense Franchet
A. ichangense Cheng & Yang
A. fukienense Cheng & Yang
Series *Bicorne* Araki
A. chingchengense Cheng & Yang
A. forbesii Maxim.
A. taitonense Hayata

A. infrapurpureum Hayata
A. macranthum Hooker
A. crispulatum Cheng & Yang
A. delavayi Franchet
A. porphyronotum Cheng & Yang
var. *atrovirens* Cheng & Yang
A. inflatum Cheng & Yang
A. maximum Hemsley
A. insigne Diels
A. nanchuanense Cheng & Yang
A. sagittarioides C. F. Liang
A. longerhizomatosum C. F. Liang & C. S. Yang
A. wulingense C. F. Liang

Section *Longiflora* Cheng & Yang
A. magnificum Tsiang ex Cheng & Yang
var. *dinghuense* Cheng & Yang
A. petelotii Schmidt

Appendix Table 5a. Morphological Characters of *Hexastylis* and/or *Asarum* sensu lato and/or *Asarum* sensu stricto

Small (1933)	Barringer (1993)
Genus *Hexastylis*	**Genus** *Asarum* sensu lato
B superior ovary	B low herbs
B distinct styles	B creeping stems
B filaments shorter than anthers	B a few cordate-reniform leaves
B evergreen leaves	B flowers are radially symmetrical
Genus *Asarum* sensu stricto	B 3-lobed calyx
B inferior ovary	B 12 or 15 stamens
B united styles	B 6 styles
B filaments longer than anthers	B fruits are fleshy capsules
- deciduous leaves	B many flattened,

cordate, arillate seeds

Appendix Table 5b. Morphological Characters of *Hexastylis* and/or *Asarum* sensu lato and/or *Asarum* sensu stricto

Maekawa (1933)	Araki (1953)
Genus *Asiasarum*	*Asarum* sensu lato
- long stamen filaments	**Subgenus** *Asarum*
- no shelf of tissue along inner surface of calyx as in Heterotropa	- sepals free above base forming a Pseudotube
	Subgenus Heterotropa
	-sepals fused into a tube

Appendix Table 5c. Morphological characters of *Hexastylis* and/or *Asarum* sensu lato and/or *Asarum* sensu stricto

Kelly (2001)	Cheng & Yang (1983)
Asarum sensu lato	*Asarum* sensu lato
B determinate seasonal growth	Chinese species
B simple leaf bases	**Subgenus** *Asarum*
B cataphylls	B perianth lobes free or united only at the base forming a short tube
B preformed flowers and leaves	B stamens with filaments that are usually longer than anthers
B fleshy, irregularly dehiscent fruits	B styles united into a column
Subgenus *Asarum*	B 6-lobed at the apex
B connate styles	B stigmas mostly terminal
B inferior ovaries	**Subgenus** *Heterotropa*
Subgenus *Heterotropa*	B perianth lobes united above the ovary forming variously shaped tubes
B separate styles	B stamens with very short filaments or subsessile
B superior ovaries	
Bsculptured sepals	
B dorsal stigmas	
B bifid style extensions	

- styles are often free, rarely short and subconnate (in Japanese species)
- lobes often bifid at the apex
- rarely subentire

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