# JUSTIFICATION FOR SUBSPECIES
# IN *ARCEUTHOBIUM CAMPYLOPODUM* (VISCACEAE)

**DANIEL L. NICKRENT**
Department of Plant Biology
Southern Illinois University
Carbondale, Illinois 62901-6509
nickrent@plant.siu.edu

## ABSTRACT

In the dwarf mistletoes (*Arceuthobium*, Viscaceae), sect. *Campylopoda* was previously considered to include entities treated at the rank of species: *A. abietinum*, *A. apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, *A. laricis*, *A. littorum*, *A. microcarpum*, *A. monticola*, *A. occidentale*, *A. siskiyouense*, and *A. tsugense*. Morphology, host associations, levels of sympatry and genetic evidence are reviewed here and, in contrast, it is concluded that these taxa are best viewed as ecotypes of a single variable species. Formal nomenclature treating these taxa at the rank of subspecies is presented, following previous conventions for recognizing infraspecific taxa in dwarf mistletoes.

**KEY WORDS**: *Arceuthobium campylopodum*, dwarf mistletoe, ecotype, subspecies, Viscaceae

*Arceuthobium* (dwarf mistletoes, Viscaceae) has been of great interest to American plant morphologists, pathologists, and systematists since the late 1800s. This is the only genus in Viscaceae that naturally occurs in both the Old and New World. In contrast to most viscaceous mistletoes such as *Viscum* and *Phoradendron*, *Arceuthobium* is morphologically reduced with scale leaves (squamate habit) and small monochlamydeous flowers whose morphology varies little between species. The explosively dehiscent fruits are unique in the family and allow population expansion without requiring bird vectors. The adult shoots produce only a small amount of carbohydrate through photosynthesis, thus these mistletoes approach the holoparasitic condition (Nickrent & García 2009).

Dwarf mistletoes are often referred to as being host specific. In reality, host specificity varies tremendously among different species. In a broad sense, all New World dwarf mistletoes are more specific than their Old World counterparts because they occur only on Pinaceae whereas the latter parasitize both Pinaceae and Cupressaceae.

The taxonomy of American dwarf mistletoes has experienced many changes since the early 1900s. Gill (1935) applied a host form concept such that *Arceuthobium* names were determined by the host being parasitized. That method introduced problems when one dwarf mistletoe species occurred on several hosts and had to be given different names. The first comprehensive monograph of *Arceuthobium* was by Hawksworth and Wiens (1972). They rejected the host form concept, stating that the morphological integrity of mistletoe species was maintained even when it was found on non-principal hosts. This basic tenet was retained in the newer monograph (Hawksworth & Wiens 1996), which included descriptions of several new species.

Certainly one of the more taxonomically difficult groups in the genus *Arceuthobium* is a complex centered around *A. campylopodum*. In the 1972 monograph (Hawksworth & Wiens 1972), sect. *Campylopoda* Hawksw. & Wiens included 16 species in three Series. In the later monograph, a revised classification of the genus was proposed based upon DNA evidence (Chapter 15, Molecular

Systematics, Nickrent 1996). Here, taxa in series *Rubra* and *Stricta* from Hawksworth and Wiens (1972) were removed from sect. *Campylopoda* and placed in sect. *Vaginata*. This move was supported by molecular as well as morphological and biogeographic data. The newly constituted sect. *Campylopoda* was then essentially the same as series *Campylopoda* from Hawksworth and Wiens (1972) and included the following ten species: *A. abietinum*, *A. apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, *A. laricis*, *A. microcarpum*, *A. occidentale*, and *A. tsugense* as well as three more recently named species: *A. littorum*, *A. monticola*, and *A. siskiyouense*.

Although the above classification utilized data from nuclear ribosomal ITS sequences, sampling was incomplete (no Old World taxa were sampled) and included only four species from sect. *Campylopoda* (*A. abietinum*, *A. apachecum*, *A. campylopodum*, and *A. microcarpum*). This situation was rectified by Nickrent et al. (2004), where ITS sequences were obtained from all species in the genus as well as chloroplast *trnL* region sequences from New World species. The resulting ITS maximum parsimony tree showed that all but one of the 13 species of sect. *Campylopoda* had identical to nearly identical ITS sequences. The most genetically divergent member, *A. blumeri*, was considered to be a "transitional" species between the mainly USA sect. *Campylopoda* species and the mainly Mexican and central American subg. *Vaginata* species (Nickrent et al. 2004). The results from analyzing the chloroplast sequences were the same as with ITS. The high genetic similarity seen between species in sect. *Campylopoda* contrasted with values seen between other species in the genus where a greater number of substitutions was observed (longer branches on phylograms). For these reasons, a phylogenetic classification was proposed where all 13 species were considered to be part of a more broadly defined *A. campylopodum*.

**Species concepts and *Arceuthobium* sect. *Campylopoda***

The species problem has been the focus of much discussion and conflict in the biological and philosophical literature. Species concepts include the biological, morphological, evolutionary, phylogenetic, and ecological, where each focuses upon different aspects of a broad spectrum of interrelated attributes and processes. Proponents of one or another concept often have specific requirements and objectives. From a philosophical perspective, Pigliucci (2003) discusses how "species" is a family resemblance (cluster) concept that can only be defined by a series of characteristics. Hawksworth and Wiens (1972, 1996) maintained that species of sect. *Campylopoda* could be distinguished by morphological characters (e.g. shoot dimensions, shoot color, width of the staminate flower, etc.), physiological characters (flowering and fruiting times), as well as principal host species. The purpose of this article is to examine some of the empirical evidence that bears upon a meaningful species concept for the *Arceuthobium campylopodum* complex.

*Morphological differentiation.* The monograph by Hawksworth and Wiens (1996) reported quantitative (continuous) morphological characters for all 13 members of sect. *Campylopoda*, and five of the characters used are depicted graphically in Figure 1. It should be stated that no sample sizes nor variances in the measurements were reported. Looking at the first four characters, although the mean values differ between some taxa, there is much overlap in the numerical ranges. There appears to be very little variation in staminate flower width between the taxa. To date no multivariate studies have been conducted to determine whether the characters used to differentiate species in sect. *Campylopoda* are statistically valid.

*Reproductive isolation.* The biological species concept (Mayr 1942) emphasizes reproductive isolation. In plants, reproductive isolating mechanisms may evolve because of geographical isolation, ecological niche segregation, temporal variation in flowering times, behavioral traits of pollinators (ethological differences), and genetic (e.g. interspecific incompatibility) factors. Hawksworth and Wiens (1972, 1996) indicated that there is no evidence of hybridization between any species of *Arceuthobium*. But detecting hybridization would be difficult because all members of the genus have
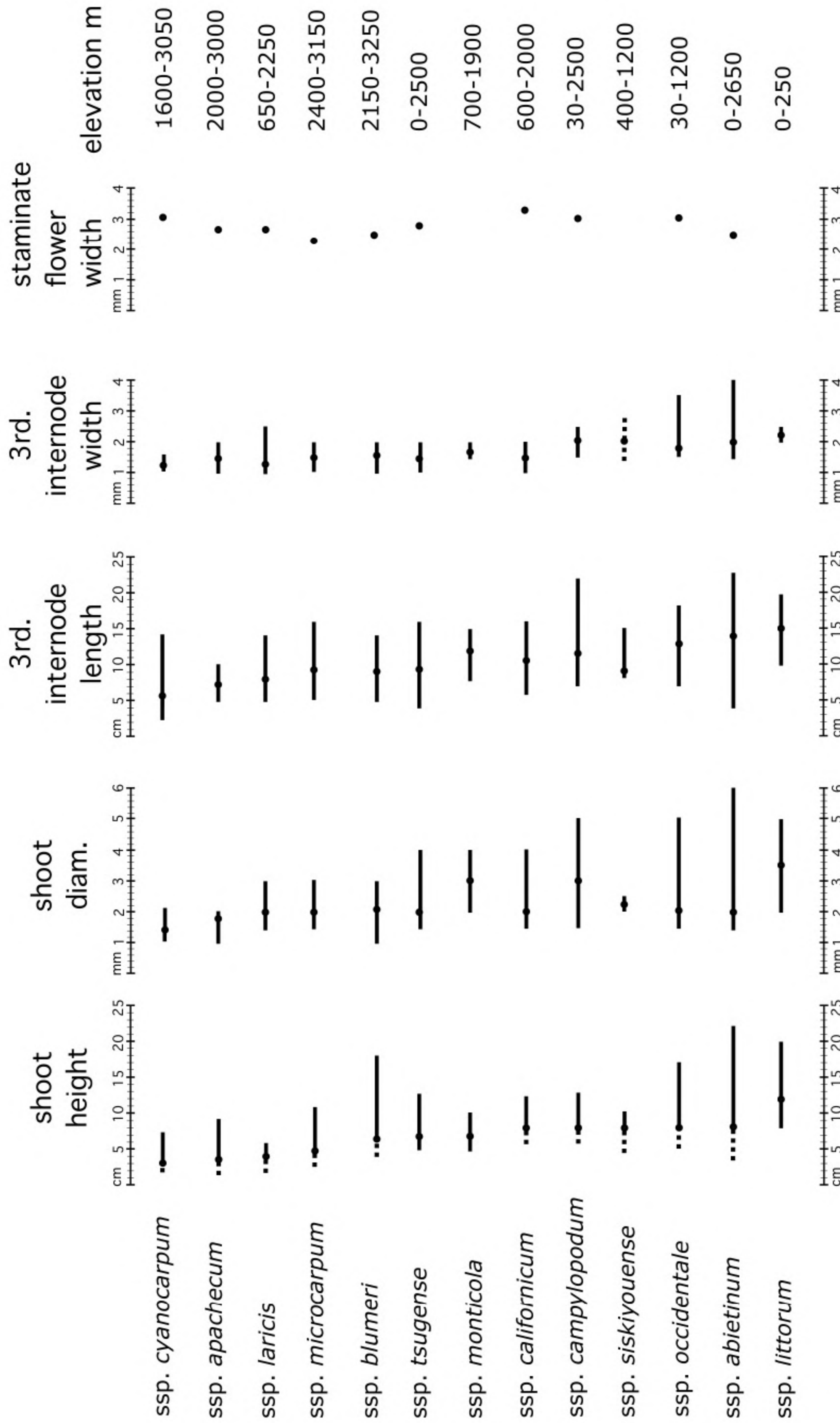
Fig. 1. Values for five morphological characters used in Hawksworth and Wiens (1996) for the 13 subspecies of *Arceuthobium campylopodum*. The solid lines represent the ranges of values reported and the dot the mean. Dashed lines indicate that no minimum (or for subsp. *siskiyouense* third internode width minimum or maximum) values were reported. Staminate flower widths were not reported for subsp. *littorum*, subsp. *monticola*, and subsp. *siskiyouense*. Also shown are the altitudinal ranges for each taxon.

the same chromosome number (n = 14) and similar chromosome morphology. Moreover, given the overlap in the ranges of morphological characters among members of sect. *Campylopoda*, it would be difficult to identify a hybrid individual based on intermediate morphology. Many nonparasitic angiosperm species have been tested for reproductive isolation by conducting artificial cross-pollinations, either under field, common garden, or laboratory conditions. Such crossing experiments usually document a range of outcomes for the next generations, from complete genetic barriers (no successful crosses) to partially fertile or fully fertile $F_1$ or $F_2$ progeny. Unfortunately, very few interspecific cross-pollination experiments have been conducted with *Arceuthobium*. Mathiasen (1982) crossed staminate *A. blumeri* with carpellate *A. apachecum* and obtained no fruits; however, the control pollinations also had low fruit set. No study involving cross-pollination of all taxa of *Arceuthobium* sect. *Campylopoda* has been published, thus compatibility data are generally lacking.

***Geographical isolation and sympatry.*** The degree of sympatry present among species of dwarf mistletoe was discussed in Hawksworth and Wiens (1996), with proximity categories set at within 30 m, 400 m, and 2 km. Comparing subspecies of sect. *Campylopoda* (Table 1) using these criteria, all but two are sympatric with at least one other member of the section (the exceptions being *A. campylopodum* subsp. *blumeri* and subsp. *littorum*). *Arceuthobium* pollen is dispersed by both insects and wind, and the latter may account for long-range pollen dispersal. For example, Leopold (1967) found dwarf mistletoe pollen in traps where the nearest population was 16 km away. Given that distance, the number of sympatric species in sect. *Campylopoda* would increase. The two taxa with the highest number of sympatric species are *A. campylopodum* subsp. *abietinum* and subsp. *campylopodum*, with eight and seven species, respectively. For *A. campylopodum* subsp. *campylopodum* and subsp. *occidentale*, a number of populations exist where both principal hosts (*P. ponderosa* and *P. sabiniana*, respectively) are being parasitized, and here the mistletoes are morphologically and genetically indistinguishable (Nickrent 1987).

Table 1. Degree of sympatry among subspecies of *Arceuthobium campylopodum*. [1]

| Taxon (abbreviation) | 30, 400 m | 2 km | # 30, 400 m | # 2 km | Total |
|---|---|---|---|---|---|
| subsp. *abietinum* (ABI) | CAL, CAM, CYA, OCC, TSU | LAR, MIC, TSU | 5 | 3 | 8 |
| subsp. *apachecum* (APA) | MIC | | 1 | 0 | 1 |
| subsp. *blumeri* (BLU) | | | 0 | 0 | 0 |
| subsp. *californicum* (CAL) | ABI | CAM | 1 | 1 | 2 |
| subsp. *campylopodum* (CAM) | ABI, CYA, LAR, MON, OCC, SIS | CAL | 6 | 1 | 7 |
| subsp. *cyanocarpum* (CYA) | ABI, CAM | | 2 | 0 | 2 |
| subsp. *laricis* (LAR) | CAM | ABI | 1 | 1 | 2 |
| subsp. *littorum* (LIT) | | | 0 | 0 | 0 |
| subsp. *microcarpum* (MIC) | APA | ABI | 1 | 1 | 2 |
| subsp. *monticola* (MON) | CAM, SIS | | 2 | 0 | 2 |
| subsp. *occidentale* (OCC) | ABI, CAM | | 2 | 0 | 2 |
| subsp. *siskiyouense* (SIS) | CAM, MON | | 2 | 0 | 2 |
| subsp. *tsugense* (TSU) | ABI | | 1 | 0 | 1 |

[1] Data derived from Hawksworth and Wiens (1996).

Table 2. Hosts of the subspecies of *Arceuthobium campylopodum* [1]

| Host | subsp. *abietinum* | subsp. *apachecum* | subsp. *blumeri* | subsp. *californicum* | subsp. *campylopodum* | subsp. *cyanocarpum* |
|---|---|---|---|---|---|---|
| *Abies amabilis* | 0.33 [2] | | | | | |
| *Abies concolor* | 1 | | | | | |
| *Abies durangensis* | 1 | | | | | |
| *Abies grandis* | 1 | | | | | |
| *Abies lasiocarpa* | 0.5 | | | | | |
| *Abies magnifica* | 1 | | | | | |
| *Abies procera* | | | | | | |
| *Larix occidentalis* | | | | | | |
| *Picea breweriana* | 0.5 | | | | | |
| *Picea engelmannii* | | | | | | 0.25 |
| *Picea pungens* | | | | | | |
| *Picea sitchensis* | | | | | | |
| *Pinus albicaulis* | | | | | | 1 |
| *Pinus aristata* | | | | | | 1 |
| *Pinus ayacahuite* | 0.33 | | 1 | | | |
| *Pinus attenuata* | | | | | 0.5 | |
| *Pinus balfouriana* | | | | | | 0.33 |
| *Pinus contorta* | 0.33 | | | | 0.33 | 0.25 |
| *Pinus coulteri* | | | | | 0.5 | |
| *Pinus flexilis* | | | | | | 1 |
| *Pinus jeffreyi* | | | | | 1 | |
| *Pinus lambertiana* | 0.33 | | | 1 | 0.25 | |
| *Pinus longaeva* | | | | | | 1 |
| *Pinus monticola* | 0.33 | | | 0.5 | | 0.5 |
| *Pinus muricata* | | | | | | |
| *Pinus ponderosa* | | | | | 1 | 0.25 |
| *Pinus radiata* | | | | | | |
| *Pinus sabiniana* | | | | | 0.33 | |
| *Pinus strobiformis* | | 1 | 1 | | | |
| *Pseudotsuga menziesii* | | | | | | |
| *Tsuga heterophylla* | | | | | | |
| *Tsuga mertensiana* | | | | | | 0.5 |
| **Inverse specificity** | 6.65 | 1 | 2 | 1.5 | 3.91 | 6.08 |
| **Number of principal hosts** | 4 | 1 | 2 | 1 | 2 | 4 |

Table 2, cont.

| Host | subsp. *laricis* | subsp. *littorum* | subsp. *microcarpum* | subsp. *monticola* | subsp. *occidentale* | subsp. *siskiyouense* | subsp. *tsugense* |
|---|---|---|---|---|---|---|---|
| *Abies amabilis* | | | | | | | 1 |
| *Abies concolor* | | | | | | | |
| *Abies durangensis* | | | | | | | |
| *Abies grandis* | 0.25 | | | | | | 0.33 |
| *Abies lasiocarpa* | 0.33 | | 0.25 | | | | 1 |
| *Abies magnifica* | | | | | | | |
| *Abies procera* | | | | | | | 1 |
| *Larix occidentalis* | 1 | | | | | | |
| *Picea breweriana* | | | | 0.33 | | | 0.25 |
| *Picea engelmannii* | 0.25 | | 1 | | | | 0.25 |
| *Picea pungens* | | | 1 | | | | |
| *Picea sitchensis* | | | | | | | 0.25 |
| *Pinus albicaulis* | 0.25 | | | | | | 0.5 |
| *Pinus aristata* | | | 1 | | | | |
| *Pinus ayacahuite* | | | | | | | |
| *Pinus attenuata* | | | | | 0.5 | 1 | |
| *Pinus balfouriana* | | | | | | | |
| *Pinus contorta* | 0.5 | 0.33 | | | | 0.25 | 1 |
| *Pinus coulteri* | | | | | 0.5 | | |
| *Pinus flexilis* | | | | | | | |
| *Pinus jeffreyi* | | | | 0.25 | 0.33 | 0.25 | |
| *Pinus lambertiana* | | | | 0.5 | | | |
| *Pinus longaeva* | | | | | | | |
| *Pinus monticola* | 0.25 | | | 1 | | | 0.33 |
| *Pinus muricata* | | 1 | | | | | |
| *Pinus ponderosa* | 0.33 | | | | 0.33 | 0.25 | |
| *Pinus radiata* | | 1 | | | *[3] | | |
| *Pinus sabiniana* | | | | | 1 | | |
| *Pinus strobiformis* | | | 0.25 | | | | |
| *Pseudotsuga menziesii* | | | | | | | 0.25 |
| *Tsuga heterophylla* | | | | | | | 1 |
| *Tsuga mertensiana* | 1 | | | | | | 1 |
| **Inverse specificity** | 4.16 | 2.33 | 3.5 | 2.08 | 2.66 | 1.75 | 8.16 |
| **Number of principal hosts** | 1 | 2 | 3 | 1 | 1 | 1 | 6 |

[1] Data derived from Hawksworth and Wiens (1996), [2] 1 = principal host, 0.5 = secondary, 0.33 = occasional, 0.25 = rare
[3] *A. campylopodum* subsp. *occidentale* parasitizes cultivated *Pinus radiata*.

***Host relationships***.  Looking at specificity from the host perspective, nearly all Pinaceae species are principal host for just one *Arceuthobium* taxon (Table 2).  Exceptions include *Pinus strobiformis* and *Tsuga mertensiana*, which serve as principal hosts for two dwarf mistletoe taxa.  When viewed from the parasite perspective, 7 of the 13 subspecies of sect. *Campylopoda* have more than one principal host (Table 2).  Some taxa, such as *A. campylopodum* subsp. *abietinum*, subsp. *cyanocarpum*, and subsp. *tsugense* have four or more principal hosts and broad host ranges overall.  The latter is recorded from five different genera of conifers: *Abies, Picea, Pinus, Pseudotsuga,* and *Tsuga*.  Although occasional or rare occurrences could be dismissed as insignificant when viewing the preponderance of mistletoes found on principal hosts, these occurrences likely provide some evidence that these species at least have the genetic propensity for being generalists.  A measure of generality ("inverse specificity") is shown in Table 2, calculated as the sum of successively down-weighted secondary, occasional, and rare hosts.  Although phylogenetic data do not yet allow inference on this matter, the ancestor to all species of sect. *Campylopoda* could have been a generalist (the plesiomorphic state).  From that ancestor, capable of parasitizing a number of host species, populations evolved with greater specialization along host lines.

***Genetic divergence***.  Given the absence of empirical cross-pollination data testing interspecific compatibility in *Arceuthobium*, the next best approach is to directly measure genetic divergence among the species.  The first tests of interspecific genetic differences between species of sect. *Campylopoda* utilized isozymes, where all members of the section had greater than 80% Nei's unbiased genetic identity values (Nickrent et al. 1984; Nickrent 1986).  Moreover, these isozyme analyses did not result in clusters corresponding to species in sect. *Campylopoda* as defined by Hawksworth and Wiens (1972) or with similarity values consistent with other members of the genus.  A more detailed isozyme analysis conducted using 500 individuals of *A. campylopodum* and *A. occidentale* showed no consistent difference between these two taxa (Nickrent 1987).

As stated above, both ITS and *trnT-L* region DNA sequences showed identity to near identity among all species of sect. *Campylopoda*.  Moreover, all these species share a unique 156 bp deletion in the *trnT-L* spacer.  Both of these spacers have been used with many other angiosperms in studies of species relationships.  Although ITS may not be ideal for some taxonomic groups or biological situations (Alvarez & Wendel 2003), it continues to be a useful phylogenetic marker for a vast array of plants and it cannot be discounted as being too problematic.  Along with chloroplast *rbcL* and *matK*, it can be used as a barcode sequence for seed plants (China Plant BOL Group 2011) and indeed among the markers tested showed the greatest ability to discriminate species (67.2%).

**The concept of ecotype and *Arceuthobium* sect. *Campylopoda***

As used by ecological geneticists, ecotypes represents populations that have fixed genotypic adaptations to particular ecological niches.  The work on ecotypes by Clausen et al. (1940) has been supported and extended into the modern genomic era by work on model plants such as *Arabidopsis* (Park et al. 2009).  That study compared protein patterns among three *Arabidopsis* ecotypes and showed that their genetic diversity was reflected in quantitative differences in the protein expression patterns.  A more explicit enumeration of terms describing microevolutionary units took place with the development of the "deme" concept (Briggs & Block 1981).  For both ecotypes and demes, the names assigned to these units were not intended to be ranks within formal botanical nomenclature.  That said, infraspecific variation in plants is frequently documented using the ranks "variety" and "subspecies."  For example, the classic study of ecotypes in *Potentilla glandulosa* (Clausen et al. 1940) involved four subspecies: *glandulosa* (*typica*), *reflexa, hanseni,* and *nevadensis*.

In the case of *Arceuthobium*, the most important environmental component is the host tree.  As with *Potentilla glandulosa*, native to Stanford but succumbing when grown at Timberline, seeds of *Arceuthobium campylopodum* derived from parasites on one particular host species may not

survive as seedlings on a host tree of another species. It seems that taxa within the *A. campylopodum* complex conform to the concept of ecotype. In addition to the host, whose distribution is correlated with elevation, such a correlation may also exist in *Arceuthobium*. The 13 taxa of sect. *Campylopoda* were arranged according to shoot height (Fig. 1), and it appears that the tallest shoots are at lower elevations and the smaller shoots at higher elevations. It is also likely that flowering and fruiting times have a strong elevational component. The exception seems to be *A. blumeri*, which is the most dissimilar genetically within the entire section.

## Subspecific ranks for *Arceuthobium campylopodum*

In plants, the ranks of variety and subspecies have approximately equal, albeit somewhat regional, usage (variety favored in the USA, subspecies elsewhere). Attempts to arrive at a consensus as to what conditions can be used to precisely define these two ranks have mostly failed (Hamilton & Reichard 1992). It is often assumed that subspecies is more associated with biogeographically separate population clusters, but this usage appears more consistent among animal as opposed to plant taxonomists. As stated by Raven (1974) "it is clearly not possible to assume from the fact the category 'subspecies' or 'variety' has been applied within a given species that a certain pattern of variation is present; only, in either case, that the species has been subdivided."

The phylogenetic classification of *Arceuthobium campylopodum* (Nickrent et al. 2004) did not specify subspecific ranks within this species. Given that these 13 taxa have been recognized as species in previous classifications and the importance of these mistletoes in North American forestry, these infraspecific taxa within sect. *Campylopoda* will be formally recognized here at the rank of subspecies. This rank is already being used for *A. vaginatum* subsp. *vaginatum* and *A. vaginatum* subsp. *cryptopodum*. The former is widespread in Mexico whereas the latter is most common in the western USA. The two subspecies are parapatric, coming into contact in Sinaloa, Mexico. The rank of subspecies has also been used in *A. tsugense*. Thus, to retain consistency within the genus, subspecies will be used instead of the rank of variety.

In terms of geographic distributions, the 13 subspecies of *A. campylopodum* show varying associations with each other, these ranging from complete allopatry to parapatry and finally sympatry. If one translates the data shown in Table 1 to a 13 X 13 matrix, 78 cells result as possible cases of sympatry. Of these, 15 cells are occupied, thus less than 20% of the time are cases reported for sympatry among these subspecies. The two taxa that show the highest levels of sympatry are *A. campylopodum* subsp. *abietinum* and *A. campylopodum* subsp. *campylopodum*. Looking at the overall distributions, one could suggest four general categories based on geography that could be used to define four subspecies: California (subspecies *californicum*, *campylopodum*, *littorum*, *monticola*, *occidentale*, and *siskyouense*), Northwest (subspecies *laricis* and *tsugense*), Southwest (subspecies *apachecum*, *blumeri*, and *microcarpum*) and Western USA (*abietinum* and *cyanocarpum*). This approach will not be recommended here because (1) there is no phylogenetic evidence that the subspecies placed in these categories are more similar to one another than to other subspecies of *A. campylopodum*, (2) the members of these categories do not appear to have any morphologically coherent features, and (3) these categories do not have any correlation with ecological conditions or host species. For these reasons, and to retain some connection to the species names currently being used by various applied fields (such as forestry, which follows the Hawksworth and Wiens system), 13 subspecific names will be used.

## Nomenclature

For the taxa in sect. *Campylopoda*, a number of species of Hawksworth and Wiens (1972, 1996) had previously been recognized as varieties of *A. campylopodum*. These are here being recognized at the rank of subspecies (stat. nov.).

*ARCEUTHOBIUM CAMPYLOPODUM* Engelm. in A. Gray, Boston J. Nat. Hist. 6: 214. 1850.

1. ***Arceuthobium campylopodum*** subsp. ***campylopodum***.
*Arceuthobium campylopodum* Engelm. forma *typicum* L.S. Gill, Trans. Connecticut Acad. Arts 32: 185. 1935.
*Arceuthobium campylopodum* Engelm. var. *brachyarthron* Engelm. in A. Gray, Boston J. Nat. Hist. (Pl. Lindheim. pt. 2) 6: 214. 1850.
*Arceuthobium campylopodum* Engelm. var. *macrarthron* Engelm. in A. Gray, Boston J. Nat. Hist. (Pl. Lindheim. pt. 2) 6: 214. 1850.
*Razoumofskya campylopoda* (Engelm.) Kuntze, Revis. Gen. Pl. 2: 587. 1891.

2. ***Arceuthobium campylopodum*** subsp. ***abietinum*** (Engelm.) Nickrent, **comb. & stat. nov.** *Arceuthobium douglasii* Engelm. var. *abietinum* Engelm. in S. Wats., Bot. California 2: 106. 1880.
*Arceuthobium abietinum* (Engelm.) Hawksw. & Wiens, Brittonia 22: 68. 1970.
*Arceuthobium abietinum* (Engelm.) Hawksw. & Wiens forma speciales *concoloris* Hawksw. & Wiens, Brittonia 22: 267. 1970.
*Arceuthobium abietinum* (Engelm.) Hawksw. & Wiens forma speciales *magnificae* Hawksw. & Wiens, Brittonia 22: 268. 1970.
*Arceuthobium campylopodum* Engelm. forma *abietinum* L.S. Gill, Trans. Connecticut Acad. Arts 32: 195. 1935.
*Razoumofskya abietina* (Engelm.) Abrams, Ill. Fl. Pacific States 1: 530. 1923.
*Razoumofskya abietina* (Engelm.) Abrams forma *parvula* Tubeuf [nomen nudum], Naturwiss. Z. Forst Landw. 17: 219. 1919. .
*Razoumofskya abietina* (Engelm.) Abrams forma *magna* Tubeuf [nomen nudum], Naturwiss. Z. Forst Landw. 17: 220. 1919.
*Razoumofskya douglasii* (Engelm.) Kuntze var. *abietina* (Engelm.) Greene, Fl. Francisc. 3: 341. 1892.
*Arceuthobium occidentale* Engelm. var. *abietinum* Engelm. in S. Watson, Bot. California 2: 107. 1880.

3. ***Arceuthobium campylopodum*** subsp. ***blumeri*** (A. Nelson) Nickrent, **comb. & stat. nov.** *Arceuthobium blumeri* A. Nelson, Bot. Gaz.56: 65. 1913.
*Arceuthobium campylopodum* Engelm. forma *blumeri* (Engelm.) L.S. Gill, Trans. Connecticut Acad. Arts 32: 207. 1935.
*Razoumofskya blumeri* (A. Nelson) Standley, Proc. Biol. Soc. Washington 29: 86. 1916.

The argument could be made that this taxon should be recognized as a distinct species (*A. blumeri*) because it differs genetically from others in sect. *Campylopoda* and is completely allopatric from all of them. But given its high morphological similarity to other members of the section, it is here considered one of the 13 subspecies of *A. campylopodum*.

4. ***Arceuthobium campylopodum*** subsp. ***cyanocarpum*** (A. Nelson ex Rydb.) Nickrent, **comb. & stat. nov.** *Razoumofskya cyanocarpa* A. Nelson ex Rydb., Fl. Colorado 100, 101. 1906.
*Arceuthobium campylopodum* Engelm. forma *cyanocarpum* L.S. Gill, Trans. Connecticut Acad. Arts 32: 204. 1935.
*Arceuthobium cyanocarpum* (A. Nelson ex Rydb.) J.M. Coult. & A. Nelson, New Man. Bot. Centr. Rocky Mts. 146. 1909.

5. ***Arceuthobium campylopodum*** subsp. ***laricis*** (M.E. Jones) Nickrent, **comb. & stat. nov.** *Arceuthobium douglasii* Engelm. var. *laricis* M.E. Jones, Bull. Montana Univ., Biol. Ser. 15: 25. 1910.

*Arceuthobium laricis* (Piper) H. St. John, Fl. Southeastern Washington 115. 1936.

*Arceuthobium campylopodum* Engelm. forma *laricis* (Piper) L.S. Gill, Trans. Connecticut Acad. Arts. 32: 202. 1935.

*Razoumofskya douglasii* (Engelm.) Kuntze subsp. *laricis* Piper [nomen nudum], Contr. U.S. Natl. Herb. 11: 223. 1906.

*Razoumofskya laricis* Piper in Piper and Beattie, Fl. Southeast. Washington 80. 1914.

6. ***Arceuthobium campylopodum*** subsp. ***microcarpum*** (Engelm.) Nickrent, **comb. & stat. nov.** *Arceuthobium douglasii* Engelm. "var.?" *microcarpum* Engelm. in Rothrock, Rep. U.S. Geogr. Surv., Wheeler 6: 253. 1878.

*Arceuthobium microcarpum* (Engelm.) Hawksw. & Wiens, Brittonia 22: 268. 1970.

*Arceuthobium campylopodum* Engelm. forma *microcarpum* (Engelm.) L.S. Gill, Trans. Connecticut Acad. Arts 32: 209. 1935.

*Razoumofskya douglasii* (Engelm.) Kuntze var. *microcarpa* (Engelm.) Tubeuf [nomen nudum?], Naturwiss. Z. Forst Landw. 17: 216. 1919.

*Razoumofskya microcarpa* (Engelm.) Wooton & Standley, Contr. U.S. Natl. Herb. 19: 179. 1915.

7. ***Arceuthobium campylopodum*** subsp. ***tsugense*** (Rosend.) Nickrent, **comb. & stat. nov.** *Razoumofskya tsugensis* Rosend., Minnesota Bot. Stud. 3: 272, pl. 27, 28. 1903.

*Arceuthobium tsugense* (Rosend.) G.N. Jones subsp. *amabilae* Mathiasen & C.M. Daugherty, Novon 17: 223. 2007.

*Arceuthobium tsugense* (Rosend.) G.N. Jones subsp. *contortae* Wass & Mathiasen, Novon 13: 269. 2003.

*Arceuthobium tsugense* (Rosend.) G.N. Jones subsp. *mertensianae* Hawksw. & Nickrent, Novon 2: 209. 1992.

*Arceuthobium tsugense* (Rosend.) G.N. Jones, Univ. Wash. Publ. Biol. 5: 139. 1936.

*Arceuthobium campylopodum* forma *tsugensis* L.S. Gill, Trans. Connecticut Acad. Arts 32: 200. 1935.

8. ***Arceuthobium campylopodum*** subsp. ***apachecum*** (Hawksw. & Wiens) Nickrent, **comb. & stat. nov.** *Arceuthobium apachecum* Hawksw. & Wiens, Brittonia 22: 266. 1970.

9. ***Arceuthobium campylopodum*** subsp. ***californicum*** (Hawksw. & Wiens) Nickrent, **comb. & stat. nov.** *Arceuthobium californicum* Hawksw. & Wiens, Brittonia 22: 266. 1970.

*Arceuthobium campylopodum* Engelm. var. *cryptopodum* (Engelm.) Jepson, Man. Fl. Pl. Calif. 284. 1925.

10. ***Arceuthobium campylopodum*** subsp. ***littorum*** (Hawksw, Wiens & Nickrent) Nickrent, **comb. & stat. nov.** *Arceuthobium littorum* Hawksw., Wiens & Nickrent, Novon 2: 206. 1992.

11. ***Arceuthobium campylopodum*** subsp. ***monticola*** (Hawksw., Wiens & Nickrent) Nickrent, **comb. & stat. nov.** *Arceuthobium monticola* Hawksw., Wiens & Nickrent, Novon 2: 205. 1992.

12. ***Arceuthobium campylopodum*** subsp. ***occidentale*** (Engelm.) Nickrent, **comb. & stat. nov.** *Arceuthobium occidentale* Engelm., U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6: 375. 1878.

*Razoumofskya occidentale* (Engelm.) Kuntze, Revis. Gen. Pl. 2: 587. 1891.

13. ***Arceuthobium campylopodum*** subsp. ***siskiyouense*** (Hawksw., Wiens & Nickrent) Nickrent, **comb. & stat. nov.** *Arceuthobium siskiyouense* Hawksw., Wiens & Nickrent, Novon 2: 204. 1992.

## LITERATURE CITED

Alvarez, I. and J.F. Wendel. 2003. Ribosomal ITS sequences and plant phylogenetic inference. Molec. Phylogen. Evol. 29: 417–434.

Briggs, D. and M. Block. 1981. An investigation into the use of the '-deme' terminology. New Phytologist 89: 729-735.

Clausen, J., D.D. Keck, and W.W. Hiesey. 1940. Experimental studies on the nature of species. Carnegie Inst. Washington Publications.

Gill, LS. 1935. *Arceuthobium* in the United States. Trans. Connecticut Acad. Arts. 32: 111–245.

Hawksworth, F.G. and D. Wiens. 1972. Biology and Classification of Dwarf Mistletoes (*Arceuthobium*). USDA Forest Service, Agric. Handbook 401. Washington, D.C.

Hawksworth, F.G. and D. Wiens. 1996. Dwarf Mistletoes: Biology, Pathology, and Systematics. USDA Forest Service, Agric. Handbook 709. Washington D.C.

Leopold, E.B. 1967. Late-Cenozoic patterns of plant extinction. Pp. 203–246 *in* P.S. Martin and H.E. Wright (eds.). Pleistocene Extinctions: The Search For a Cause. Yale Univ. Press, New Haven, Connecticut.

Chinese Plant Barcode of Life Group (China Plant BOL Group), including D.-Z. Li and 19 coauthors. 2011. Comparative analysis of a large dataset indicates that internal transcribed spacer (ITS) should be incorporated into the core barcode for seed plants. Proc. Natl. Acad. Sci. USA 108: 19641–19646.

Hamilton, C.W. and S.H. Reichard. 1992. Current practice in the use of subspecies, variety, and forma in the classification of wild plants. Taxon 41: 485-498.

Mathiasen, R. 1982. Taxonomic studies of dwarf mistletoes (*Arceuthobium* spp.) parasitizing *Pinus strobiformis*. Great Basin Naturalist 42: 120–127.

Mayr, E. 1942. Systematics and the Origin of Species From the Viewpoint of a Zoologist. Columbia Univ. Press. New York.

Nickrent, D.L. 1986. Genetic polymorphism in the morphologically reduced dwarf mistletoes (*Arceuthobium*, Viscaceae): an electrophoretic study. Amer. J. Bot. 73: 1492–1502.

Nickrent, D.L. 1987. Systematics and population biology of two sibling species of *Arceuthobium* (dwarf mistletoes, Viscaceae). Pp. 597–611 *in* H.C. Weber and W. Forstreuter (eds.). Proc. 4th Interntl. Symposium on Parasitic Flowering Plants. Philipps-Univ., Marburg, West Germany.

Nickrent, D.L., S.I. Guttman, and W.H. Eshbaugh. 1984. Biosystematic and evolutionary relationships among selected taxa of *Arceuthobium*. Pp. 20–35 *in* F.G. Hawksworth and R. Scharpf (techn. coords.). Biology of Dwarf Mistletoes: Proceedings of the Symposium. USDA Forest Service, General Tech. Report RM-111. Ft. Collins, Colorado.

Nickrent, D.L. and M.A. García. 2009. On the brink of holoparasitism: plastome evolution in dwarf mistletoes (*Arceuthobium*, Viscaceae). J. Molec. Evol. 68: 603–615.

Nickrent, D.L., M.A. García, M.P. Martín and R.L. Mathiasen. 2004. A phylogeny of all species of *Arceuthobium* (Viscaceae) using nuclear and chloroplast DNA sequences. Amer. J. Bot. 91: 125–138.

Park, K.M., Y.H. Choi, W.M. Park, H.J. Na, Y.J. Na, D.H. Lee, W.I. Chung, and D.S. Kim. 2009. Proteomic pattern-based identification of molecular phenotypes from *Arabidopsis thaliana* ecotypes. Pl. Sci. 177: 7–18.

Pigliucci, M. 2003. Species as family resemblance concepts: the (dis-)solution of the species problem? BioEssays 25: 596–602.