### Measurements and taxonomy in Arceuthobium (Viscaceae).

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# ABSTRACT

The population complexities within *Arceuthobium campylopodum* sensu Gill (1935) have led to two recent analyses reaching different conclusions even though mainly or at least in part based on standardized internodal measurements. These measurements cannot be utilized to formulate taxonomic conclusions because stem internodes continue to elongate from year to year. It is recommended to refrain from using infraspecific categories until the relevant variation patterns, both in hosts and parasite populations, are better known. *Phytologia* 98(3): 186-189 (July 6, 2016). ISSN 030319430.

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The complex of populations representing *Arceuthobium campylopodum* Engelm. in the sense of Gill (1935) has taxonomically challenged innumerable workers, resulting in a very extensive collection of synonyms and other nomenclatural combinations. It is a controversy of long standing. That it is not close to a resolution is shown by the fact that two major and contrasting approaches have been published within a couple of years of each other, each representing much meticulous work, one basically molecularly oriented but also building on earlier morphometric information (Nickrent 2012), the other with extensive morphometric data that cover 5 pages of tables and two geographic maps (Mathiasen & Kenaley 2015). The former study recognizes 13 subspecies within (but not limited to) the western United States. The latter one concerns only the three groups that are mostly limited to *Pinus ponderosa* Doug. ex Loud., *Larix occidentalis* Nutt., and *Tsuga heterophylla* (Raf.) Sarg., and are the most northerly representatives of the complex. The coastal plants of the Pacific Northwest, furthermore, have previously been further divided into *A. tsugense* (Rosend.) G. N. Jones subspecies *mertensianae* Hawksw. & Nickr. (Hawkswoth et al. 1992) and the taxonomically dubious *A. tsugense* subspecies *contortae* Wass & Math. (Wass & Mathiasen 2003).

I wish to start my comments with a disclaimer. It is not my purpose to claim that any one taxonomic solution to this baffling complex of plants is better than any other, even though I also will state my personal preference. Rather, my main purpose is to comment on the reliability of the mensural data that have in the past been gathered and are said to support both the positions in the two major recent papers.

I also hasten to say that I am not an expert in the intracacies of either molecular taxonomy or morphometric analysis, but I strongly suspect that the significant issues lie elsewhere. At this moment, I shall accept at face value the authentic nature of the techniques employed and the data gathered, and focus on some serious flaws in the claimed *significance* of mensural data.

First of all, a semantic issue that may appear to be a quibble. The words "morphometric" and "morphological" should not be used interchangeably, as Mathiasen and Kenaley do throughout. The former term refers to measurements, but the latter has a much broader meaning, including some things like branching patterns, flower position, leaf shape and position, and (in *Arceuthobium*) emergence patterns from hosts. The curious fan-shaped (flabellate) branching pattern of *A. campylopodum*, for example, is a gross *morphological* feature that is identical throughout the complex, and is also seen in *A*.

*vaginatum* (Willd.) Presl. This morphological feature is diametrically opposed to that of *A. americanum* Nutt., but comparisons with the smaller, highly reduced species are essentially impossible. Technically, I would maintain, in contrast to what Mathiasen and Kenaley write, that there are no strictly morphological differences in the elements of the *A. campylopodum* complex beyond possible mensural ones.

### Measurements

The idea that standardized measurements of internodes can be used to distinguish *Arceuthobium* taxa was first introduced in Hawksworth & Wiens' work on Mexican species (1965) and later refined more generally (1972, 1996). In the latter monograph, while admitting that shoot internodes may elongate for several years, these authors nevertheless defended the taxonomic utility of such measurements, narrowing the latter to the third internode of a shoot without providing a rationale for that particular choice. They stated that "The overall mature internode dimensions among various species differ so significantly that internodal elongation does not negate the usefulness of the character in these cases."

Since 1996, internodal length measurements have been employed for this purpose in Western North America (see Mathiasen & Kenaley 2015), and they form a major structural part of the taxonomic conclusions in the latter study. As mentioned above, Hawksworth & Wiens' early data are also said to support the very different conclusions reached by Nickrent (2012; see his Fig. 1). In all cases, the assumption clearly is that the third internode of a plant can reliably be utilized as a standard. This laudable goal of standardization is based on a patently false foundation. In fact, the idea was demonstrated to be untenable nearly 50 years ago in a major paper that has not, curiously, been cited in any of the above studies (Kuijt 1969) – a paper, ironically, that deals specifically with the very question at issue.

In that study, careful measurements were made of the lengths of internodes especially of a related species, *A. americanum*, a species showing a highly unusual sexual dimorphism in its inflorescences. The curious male inflorescnce unit is a one-flowered structure of a single internode, its two distal scale leaves in the following season subtending two more such units; this is repeated from year to year, although the initial situation is somewhat different. Thus, a continual forking results. The important point here is that the single inflorescence internode in each case elongates somewhat every successive year: it was demonstrated that a single such internode may increase its lenth by a factor of *ten or more* over a period of 5 years. (The female inflorescences undergo a separate, more modest internodal elongation in most species, separating the maturing fruits, but eventually are dropped). Since male inflorescences in *A. campylopodum* are very different in structure, no such age determination is possible in that species. However, it is quite clear that the phenomenon of yearly internodal elongation is also a fact in *A. campylopodum* and other large species. For one thing, the basal internodes of large, older plants are always much longer than those in their first flowering season, even if part of the same colony. "Seasonal extension of all internodes can be accepted as a fact in all large species of *Arceuthobium*" (Kuijt 1969).

It can be seen immediately that this fact completely deprives third-internode measurements of their significance. Such internodes – all internodes – are not of the same length from year to year, or even within a single growing season. Significantly, in none of the above papers are the seasons or dates of measurements mentioned; in the Hawksworth & Wiens data reproduced by Nickrent (2012), neither sample sizes nor variances were mentioned. In fact, Mathiasen & Kenaley specifically write that in each collection the "dominant plant (largest plant)" was used for measurements, surely admitting bias in the light of the known internodal elongation that takes place.

A number of additional measurements were used by Mathiasen & Kenaley (2015). Several of these can be criticized on the same basis as internodal length (plant height, basal diameter, and others). Others are expressed even in 0.1 mm units, the accuracy of which is dubious. Nickrent (2012) already pointed out that staminate flower width appears to show very little variation.

But let us assume, for a moment, that the measurements in Mathiasen & Kenaley's paper are accurate, and even that the differences between their three groups are as consistent as stated there. The question at this point would be: do such differences necessitate the groups' recognition at either the specific or subspecific level? The answer surely is negative: this is where taxonomic judgment enters. There are innumerable instances in the taxonomic biological literature of complexes that defy an immovable hierarchic solution. The classical instance is that of the ring species (Rassenkreis) of gulls, *Larus spp.*, but several other such instances are known from the animal world. The first botanical instance of such a "ring species" was recently described by Cacho & Baum (2012). I am not implying that the situation in *A. campylopodum* is comparable; I am merely pointing out that population complexities exist that cannot be fully accommodated by a standard Linnean hierarchy. The many known botanical examples of hybrid swarms, sometimes even involving three species, might be cited as comparable situations.

Remarkably, the missing element in all cited papers is the possibility of infrataxon variation in host susceptibility and its possble bearings on the patterns observed in the field. Could the host species not influence morphometric data? Admittedly, the demonstration of such variation would be exceedingly difficult, but most students with field experience have seen suggestive evidence. It would by no means be extraordinary for such an effect to exist. The most convincing published example is seen in Fig. 10 of Kuijt (1955), where one spruce tree is very heavily infected and broomed while its close neighbor, with branches interlocking, is completely free of the parasite, *A. americanum*. We cannot deny the possibility that some populations of a conifer might be more, or less, susceptible than others to *A. campylopodum*, giving deceptive impressions in the field. The absence of data on this issue casts a shadow on the above taxonomic conclusions in *Arceuthobium*.

In Mathiasen & Kenaley paper (2015), it is stated that the authors purposely "did not include samples of plants collected from hosts other than principal hosts for each dwarf mistletoe because there is some evidence that plants are smaller on less susceptible hosts (Mathiasen & Daugherty 2009b)." I would argue that this is a procedural error, and shall illustrate my contention with an example. The plants that locally parasitize Larix occidentalis in the southern interior of British Columbia and those that commonly grow on Tsuga heterophylla in coastal regions constitute two of the three major groups in Mathiasen & Daugherty's contribution. It would be difficult, in the forested regions of the Province, to find two areas more ecologically unlike. Each group not uncommonly parasitizes *Pinus contorta* Dougl. ex Loud., on which it also can perpetuate itself (in at least some coastal locations, surely for many hundreds of years). The pivotal question is: can we distinguish plants in these two different occurrences on *P. contorta*? If the mistletoes concerned, when growing on the same host species, would show significant differences, a taxonomic decision might be more convincing. Several parallel questions could be raised in more southern areas, with other "principal hosts". That sort of comparison, in my opinion, would be more meaningful than comparing the plants on two different principal hosts; it would at least bypass, in the case mentioned, the potential host influences of L. occidentalis and T. heterophylla, even though significant environmental influences, and host variation within P. contorta, remain possible.

### **Color variation**

There is little doubt that coastal plants often tend to be greener than plants of the other two groups treated in Mathiasen & Daughtery (2015), even though some coastal plants are also distinctly yellow-green (Wass & Mathiasen 2003). Here also, the environment, including exposure to the sun, might exert some influence.

### CONCLUSIONS

1. Morphometric measurements of internodes in *Arceuthobium campylopodum* cannot support taxonomic conclusions, because the internodes continue to elongate in successive growing seasons.

2. The population complexities of *A. campylopodum* are such that no one infraspecific hierarchy may be acceptable. It is advisable to avoid infraspecific categories until the relevant variation patterns of both parasites and hosts are better known, as such categories tend to reflect a deceptive sense of accuracy.

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