A Historical Review of Adelgid Nomenclature

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ABSTRACT

Adelgids are known worldwide as pests of various conifers. Despite their pest status, the nomenclature of adelgids is in a state of disarray. Different classification schemes abound worldwide making information retrieval and communication among biologists, foresters, and taxonomists tedious and difficult. Historically, different adelgid workers have accepted either a two-genus or a multiple-genus system (or variations of each). Phylogenetic analyses of this small family of insects may help bring clarity to the situation.

KEYWORDS

Adelgids, Adelgidae, Hemiptera, taxonomy, nomenclature.

INTRODUCTION

Adelgids (Hemiptera: Sternorrhyncha: Adelgidae), the pine and spruce aphids, are small, soft-bodied insects that feed exclusively on coniferous plants using piercing-sucking mouthparts. Adelgids are primarily Holarctic in distribution (although found worldwide if counting exotic introductions), and 50 species have been described (Carter 1971 and Foottit and Richards 1993). According to Foottit and Richards (1993), the distribution of adelgids mirrors closely the distribution of spruce, a primary to exclusive host to many adelgids.

Adelgids are considered by many workers to be the most primitive members of the aphidoid group of insects (Ghosh 1983), having arisen in the Carboniferous when coniferous trees dominated the landscape. They are separated from aphids (in a strict sense) by the absence of cornicles, short antennal segments, reduced wing venation, a glandular body surface, and oviparity in both parthenogenetic and sexual forms (Carter 1971 and Ghosh 1983). Adelgids are differentiated from phylloxerans, their closest relatives, by a distinct chitinous ovipositor, separated CuA and CuP veins, four to five abdominal spiracles, antennae with three to five segments, and winged forms having three large sensoria at the tips of the antennae (Annand 1928 and Stoetzel 1998). In addition, phylloxerans are only found on deciduous hosts (Stoetzel 1998). Wingless forms of adelgids usually secrete a dense woolly mass from dorsal wax glands. This woolly mass surrounds the female and protects her and her eggs from various environmental elements. Like aphids, adelgids have extremely complex life

cycles involving different hosts (usually spruce) and alternation of sexual and parthenogenetic generations (Stoetzel 1998).

Numerous adelgid species, most notably the balsam woolly adelgid, *Adelges piceae* Ratzeburg, the hemlock woolly adelgid, *Adelges tsugae* Annand, and the pine woolly adelgid, *Pineus pini* Linnaeus, have attained pest status around the world. The two former species have become destructive pests in the United States causing widespread host mortality (McClure 1987 and Wallace and Hain 2000). As a result of these threats, numerous studies in recent years have examined the potential effectiveness of various adelgid natural enemies for use in biological control, particularly for the hemlock woolly adelgid (Cheah and McClure 1996 and 1998, Zilahi-Balogh et al. 2003).

Despite their importance as pests, there exists a great deal of instability and difference of opinion in adelgid nomenclature and taxonomy. Different workers around the world use various classification systems at all taxonomic levels, with the exception of the species group. Even the author and date of the family name is ambiguous. The continued use of different names for adelgids worldwide makes retrieval of information and communication among applied researchers and forest managers tedious.

Unfortunately, it is very difficult to regulate many of the different classification schemes via the International Code of Zoological Nomenclature (1999), as the choice of a scheme is largely based on "taxonomic license" and personal preference (Blackman and Eastop 1984). At its heart, the problem comes down to whether one agrees with the lumping of adelgid species into two genera or splitting them into more than two genera. Due to their importance as economic and ecological pests worldwide, universal acceptance of appropriate names for adelgids at all levels—species group, genus group, and family group—should have a high priority. Furthermore, before detailed searches and examinations of the effectiveness of potential natural enemies of pest adelgid species can take place, it is important to know the name of the adelgid they feed on.

This report reviews the two major published generic classifications of adelgids. It is important to understand the history of classification and why authors chose the names they did in order to make sense of what is happening today.

REVIEW OF CLASSIFICATION SCHEMES

Traditionally, there have been two classification schemes of adelgid genera used worldwide: the North American/Great Britain two-genus system and the German (and others) multiple-genus system. The formation of these two classifications is the result of each system focusing on different morphological characters from various life stages to distinguish taxa. The primary difference between them is that the two-genus system distinguishes genera primarily on the number of abdominal spiracles in adults while the German system relies on the morphology of the first instar nymphs of the sistens stage (Annand 1928). There have been modifications to both systems over time, but workers worldwide citing adelgid names have primarily used one of the former schemes.

Along with the different generic name systems, the use of adelgid family group names has varied. Workers have frequently created new family level classifications over time with few of them being accepted universally. Adelgid biologists today use interchangeably the superfamily names Adelgoidea (Dolling 1991), Phylloxeroidea (Heie 1980, 1987, and 1999; Heie and Pike 1992; Foottit and Richards 1993; and Maddison 1998), and Aphidoidea (Blackman and Eastop 1994 and Stoetzel 1998). The use of different superfamily names may add to the confusion in adelgid nomenclature, but most workers agree that placing adelgids in either Aphidoidea or Phylloxeroidea is acceptable: it is simply a question of preference.

Although workers have disagreed on what genus, tribe, subfamily, family, and superfamily to place adelgids in, they have for the most part agreed on the species names. For example, *Dreyfusia piceae* Ratzeburg, 1843, and *Adelges piceae* Ratzeburg, 1843, are two different generic names used by different workers for the same species.

GENERIC CLASSIFICATION SCHEMES

The first mention of adelgids was by the Dutch botanist Clusius in 1853 when he made observations on galls, although the genus *Chermes* was erected by Linnaeus (1756) (Annand 1928). The family group name Adelginae is attributed to Annand (1928). The first major taxonomic workers of adelgids were the Russian entomologist Cholodkovsky (1896) and the German entomologist Börner (1908), both of whom made valuable and independent contributions to adelgid biology in the discovery of alternate hosts and in taxonomy (Annand 1928 and Carter 1971).

One of the first major monographs on adelgid taxonomy was by Börner in 1908 (Annand 1928). Börner placed adelgids in the family Chermesiden and superfamily Aphidoidea. A major theme in this work was his disagreement with Cholodkovsky's definition of how taxonomic species should be separated. Börner believed that species should be separated by morphological differences rather than relying heavily on their biological differences. Subsequently, Börner synonymized many species (combined many species into one) based on morphological differences of the nymphal stages. He used chaetotaxy of head and thorax sclerites and gland features of 1st instar nymphs to differentiate adelgid genera (Shaposhnikov 1964).

Börner (1928) modified his existing classification by listing adelgids in the family Adelgidae. Heie (1980), although citing the year 1930, gives credit to Börner for the authorship of the family name Adelgidae from Börner's 1928 publication. Börner, along with his counterparts, stopped using the name Chermesidae (or variations thereof) at that time due to confusion with the use of a similar name for psyllids. Adelgidae, according to Börner, included the subfamilies Pineinae and Adelginae. Adelginae had two tribes: Dreyfusiini and Adelgini. Pineinae contained *Pineus* Shimer, 1867, and *Pineodes* Börner, 1926 (new genus). *Dreyfusia* Börner, 1908, and *Aphrastasia* Börner, 1909, were included in the tribe Dreyfusiini. The genera *Cholodkovskya* Börner, 1909; *Adelges* Vallot, 1836 (senior synonym of *Cnaphalodes* Macquart, 1843); *Gilletteella* Börner, 1928 (new genus); and *Sacchiphantes* Curtis, 1844, were included in the tribe Adelgini. Of noted absence was the genus *Chermes* Linnaeus,

1756, which Börner also stopped using, similar to the family name Chermesidae. He subsequently assigned the species in this former genus to new genera, current genera, and the reinstated genus *Sacchiphantes* (type species *Chermes abietis* L.)(Börner 1928). This work would provide the foundation for all subsequent adelgid classifications that followed the multiple-genus classification.

Annand (1928) described the biology and taxonomy of the North American adelgids. It was the first work to adopt the two-genus system using *Adelges* and *Pineus*. In his work, adelgids are listed in the subfamily Adelginae (formerly Chermesinae) of the superfamily Aphidoidea and family Phylloxeridae. Annand likely placed adelgids in the phylloxeran family due to their close physical resemblance and similar biology (Carter 1971). Annand believed that the genus *Pineus* should stand by itself, similar to Börner. However, Annand combined the remaining current genera in Börner's classification into the genus *Adelges*. *Adelges* Vallot, 1936, is the oldest name of all adelgid genera and therefore has priority in zoological nomenclature (Article 23.1, International Code for Zoological Nomenclature 1999). Annand used the number of spiracles on the adult female abdomen (five pairs in *Adelges*, four pairs in *Pineus*) to distinguish the two genera. He stated that *Pineus* was likely derived from *Adelges* citing the greater number of abdominal spiracles in *Adelges* as evidence of a primitive character (Annand 1928).

Annand believed Börner had separated genera based on species-level characters resulting, in his opinion, in the reduction of genus to a rank equivalent to species. He also thought that the genus was an artificial group often based on subjective characters but at the same time a valid phylogenetic entity existing in nature and having definable characters that separated it from other such groups. According to Annand, by creating numerous genera for a similar number of species, Börner had lessened the practical value of the genus group taxon and its significance in elucidating evolutionary relationships (Annand 1928). Furthermore, Annand determined that some of Börner's characters were not applicable to all adelgid life stages. For example, Börner based the genus *Cnaphalodes* on the fused cephalic and prothoracic plates and the absence of glands in the first instar nymph of the sistens generation. However, these characters are not relevant to the progrediens stage. Annand believed generic characters should be based on adult characteristics and rarely nymphal characters. He largely based his "lumping" of adelgids into two genera, *Adelges* and *Pineus*, on these beliefs.

FURTHER CLASSIFICATIONS

Following the publications of these two major workers, most taxonomic works on adelgids did not follow Annand's recent work (Silvestri 1939, Börner 1944, Börner and Heinze 1957, Heinze 1961, Shaposhnikov 1964, and Steffan 1968). Most workers followed Börner's classification or a variation of his scheme. The reason for this is unclear; it could have been due to workers not knowing about his work, not accepting it, or thinking it was only applicable to North American genera.

In 1965, the confusion associated with *Chermes* and higher-level uses of the name was put to rest by the International Commission for Zoological Nomenclature. According to a ruling by the Commission (International Commission for Zoological Nomenclature, Opinion 731, 1955), the generic name *Chermes* Linnaeus, 1758, and the family group name *Chermides* Fallen, 1814, were declared invalid due to the confusion associated with their dual use with psyllid insects. This would make any subsequent use of these names in the literature invalid. Apparently, adelgid workers like Annand and Börner realized the confusion long before the Commission did—both stopped using these names in their 1928 works. Nevertheless, many other adelgid workers did not (Silvestri 1939 and Bodenheimer and Swirski 1957).

Carter's manuscript (1971) on the conifer woolly aphids in Britain was the first to recognize and use the two-genus system of classifying adelgids since Annand (1928). Carter placed the Adelgidae in the superfamily Aphidoidea as Börner did. Like Annand, Carter believed adelgids should be placed into either *Pineus* or *Adelges* based on the number of abdominal spiracles of the adult. Carter subsequently reduced in rank all of Börner's genera to subgenera within *Adelges* and *Pineus* and used characters from the antennae (shape, length, and characteristics of the sensoria) and abdominal spiracles of the winged forms to help distinguish adelgid genera.

A few other aphidoid taxonomists have supported Annand and Carter's classification for a number of reasons (Ilharco and van Harten 1987 and Blackman and Eastop 1994). They believed that the separation of Adelgidae by Börner into numerous genera was based on very slight differences (i.e., differences more appropriate for species) and that splitting of taxa into numerous lower groups created greater confusion. Foottit and Richards (1993) provided descriptions and a key for Canadian adelgids, using the two-genus system of *Adelges* and *Pineus*. They stated that, although current European classifications may have merit, they preferred the two-genus system of North America and Great Britain. They said to apply the European system to the North American adelgids "would require extensive revision."

USE OF NAMES TODAY

Unfortunately, classification of adelgids above the species level has become a question of preference (Blackman and Eastop 1984). There has been little consistency in the adelgid nomenclature; recent and past publications on adelgid biology and taxonomic publications have used the various higher-level classification systems interchangeably. Most European authors have used, and continue to use, Börner's generic classification (Eichhorn 1989, Alles 1994, Roversi and Binazzi 1996, Dragan 1999, and Sato 1999). Eichhorn (1968 and 1969), however, used the genus name *Adelges* in various publications. Nonetheless, Carter's and Annand's generic classification is followed by many aphid biologists today (Blackman and Eastop 1984 and 1994, Heie 1999), by most adelgid applied biologists in the New World (McClure 1987, Cheah and McClure 1996 and 1998, Soria et al. 1996, Wallace and Hain 2000, and Zilahi-Balogh et al. 2003; also see this proceedings), and some in the Old World (Szklarzewicz et al. 2000).

DISCUSSION: CAN THERE BE STABILITY IN THIS SYSTEM?

The use of different classification systems at the generic level in the family Adelgidae continues to present day. It has become a problem of personal taxonomic license; just because someone publishes synonymies of certain taxa, it doesn't mean that everyone will follow it. Comparing figures and descriptions of 1st instar nymphs shows that the species entities that each system describe are the same (Annand 1928, Shaposhnikov 1964, and Carter 1971), as discussed previously in this paper. *Dreyfusia piceae* Ratzeburg in Börner's work is the same species as *Adelges piceae* Ratzeburg in Annand's work. Where the classifications disagree is how they should be classified at the generic level.

Consistent classification of adelgids has most likely been hampered by the inherent difficulty in describing the morphological variation in the group and the complexity of their life cycle. Misidentifications of adelgid species are very common in the literature. Researchers at first may have encountered only one stage of the life cycle and named it as a new species unaware of the other life stages. It is therefore important to thoroughly document the biology of the adelgid species in question before assigning it a new name. Furthermore, different adelgid species use the same host at the same time of year, making it even more of a challenge to distinguish species (Annand 1928). As pointed out by many authors (Annand 1928, Carter 1971, and Foottit and Richards 1993) different adelgid workers have historically disagreed on what are the informative generic characters for the family. Instability is also a problem in this family because the ratio of workers to adelgid species is so high (Foottit and Richards 1993). Therefore the number of opinions created via taxonomic license is substantial.

Unfortunately, the confusion in adelgid classification is not unique to this family. People around the world tend to study the taxa unique or endemic to their region, often creating a different classification than their peers around the world. These differences are likely due to poor communication among workers and poor means of information retrieval in isolated areas. Often, workers will also tend to focus on species level problems while ignoring higher level classification. The need for rigorous phylogenetic analyses which sample taxa from all regions and that take into account the worldwide fauna is very important in standardizing a classification that most workers will follow.

With the recent revolution in molecular phylogenetic techniques, it is now possible to collect and use two kinds of data in phylogenetic analyses: molecular and morphological. The only way to determine which and how many genera the 50 species should group into is by performing a rigorous phylogenetic analysis, preferably using both types of data collection, on all adelgid species. Morphological analyses should include characters from immatures and all stages and body regions of the adults. Species that cluster together at the tips of a phylogenetic tree are thereby taken as the most closely related. For example, if all the species in *Adelges* and *Pineus* clustered into two separate natural (monophyletic) groups respectively, it would support Annand and Carter's reasoning that Adelgidae should be split into two natural entities. If each of Börner's genera, with their respective species, clustered separately within the analysis, it would lend support Börner's multiple genus system. If however, two species within *Dreyfusia* were to fall out on opposite ends of the tree, it would be evidence that *Dreyfusia* was not a natural group.

It is important for this systematic research on Adelgidae to continue. Numerous pest adelgids threaten the well-being of forest ecosystems around the world. In order for taxonomists, applied adelgid biologists, and forest managers to communicate, formulate management plans, and attempt to solve these problems, they should all be using the same names.

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