Evolutionary biology of Brunellia (Brunelliaceae, Oxalidales)

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GENERAL DISCUSSION AND CONCLUSIONS

Chapter 9

Much of the biological research carried out today furthers our knowledge of the relationships between the wide diversity of species. Observable attributes, or characters, the products of the evolutionary process, are used to establish these relationships. Therefore, the study of these characters is the most important activity of those working in systematics in their search for relationships among the diversity of species. Although each pool of characters identifies species or groups of species, not all of them are informative from the point of view of evolutionary relationships.

This phylogenetic study of 32 taxa and 45 morphological characters indicates that Brunellia is a monophyletic group (with 54 species). These species are grouped in five sections. Three of them, defined by evolutionary novelties (synapomorphies or autapomorphies) are Brunellia (26 species) widely distributed throughout the Andean region from Bolivia to Colombia and in Central America from Panama to Mexico, Simplicifoliae (24 species) has a narrower distribution than Sect. Brunellia, but with a wide diversification towards the northeast of the Colombian Andes, and Pauciflorae (1 species) with a restricted distribution in southern Ecuador. The remaining two sections also have a restricted distribution and are each defined by a unique combination of characters: Stuebelia (2 species) one species in southern Colombia and the second one in northeastern Peru, Ovalifoliae (1 species) in the northeastern Ecuador. Subsections and less inclusive groups were also recognized, some of them defined by synapomorphies or by a unique combination of characters. Unique combinations of characters, as was mentioned in the text (chapter 7), function as autapomorphies even though each contributing character is itself homoplasious. The hypothesis selected from the three MPTs obtained contains homoplasious characters arising no more than twice. Thus the information contained is less conflictive but at the same time has less power of explanation about the real evolution of the characters. Although Bradford (in prep.) criticizes the use of morphological characters in establishing the systematic position of Brunellia (due to the absence of information for many clades), in this case the kind of morphological data used is informative for defined groups of species and species as well. However, additional study is needed for the groups, B. cayambensis, B. rhoides, B. brunnea, and B. cutervensis due to their varying positions in the three MPTs. The appropriate outgroup
has been also criticized but as Bradford (in prep) stated Bruneliaceae is closely related to Cephalothaceae, Cunoniaceae, and Elaeocarpaceae (Oxalidales), thus the outgroup(s) could be selected from these taxa or any other taxon. The outgroup selection of this study was limited by the type of characters studied for Brunellia and not all the possible outgroups have been studied in depth with respect to the type of characters used in this research. After an unsuccessful attempt to obtain a phylogenetic hypothesis for Brunellia in 1993 (Orozco unpublished) owing to the lack of possible informative morphological characters, these are the first results about relationships within the genus.

Of all the characters used in the phylogenetic study of Brunellia, most research was carried out on what were considered as systems of characters, such as the leaf anatomy, typology of synflorescences, and floral and pollen morphology. Furthermore, some of these characters, such as floral morphology, had not been adequately defined in previous studies, and consequently, information resulting from their use was very contradictory, making this in depth intra-population study very important. The most outstanding result of this study was the finding of an asymmetric flower, the protandrous condition, and the apparent polyandry of some species, although the diplostemonous floral organ arrangement is the basic condition in Brunellia. The flower asymmetry is due to changes in sepal number influencing the apparent polyandry and possibly the carpel numbers as well. This apparent polyandry, due to extra-whorls of stamens resulting from sepal number variation within the species, was only found in a few species, for example, in the boliviana group. Apparent polyandry is less perceptible in the remaining species although it is seen in some individual flowers despite a clear underlying diplostemonous floral organ arrangement. The evolutionary novelties of floral reduction and increase in the number of floral parts define the sect. Simplicifoliae and the B. boliviana group.

Anatomical characters are useful for studying relationships above the species level. In Brunellia, the anatomical results contribute to establishing inter-family relationships as well as defining groups of species within the genus. It was made clear in this study that unifoliolate species had been wrongly considered as simple-leaved species in earlier studies. Nodal anatomy is a very important character for determining family relationships but further research is necessary to establish whether or not Brunellia has unilacunar or multilacunar nodes. Some of the anatomical leaf characters are evolutionary novelties at subsectional or infra-subsectional level. Among these characters, the presence of a hypodermis, the number of layers of palisade parenchyma, and some characteristics of the main vascular bundle of the central vein of the leaf are specially important in the unifoliolate species group, for example, Subsect. Simplicifoliae and Sect.
Pauciflorae. The presence of medullary bundles is also important at inter-family level as this character was only observed in B. foreroi and it is also present in some genera of Cunoniaceae, however, the homology of this character in the two families is doubtful. The presence of crypts in the abaxial foliar lamina of some species is a response to high altitude distribution, being the case in most species of the sect. Simplicifoliae. It seems that the presence of crypts is related to extreme environmental conditions as they have also reported also for some groups living in dry environments. Actinocytic stomata were present in most of the species examined but anomocytic stomata were only observed in B. cutervensis. As a result of a study of the indument that covers the foliar lamina of species of Brunellia, Orozco (1999) found it to be of informative value for defining groups and in some cases it correlates with other unique character combinations.

A comparative study of inflorescences was used as another system of characters. This study was carried out according to Troll and Weberling’s typologic concept of synflorescence, making this information available for studying relationships. The position of the inflorescence in the vegetative system and its structure are informative characters for familial, intergeneric or even intrageneric relationships. A monotelic proliferating synflorescence was observed for the first time in Brunellia and in Spiraeanthemum and Acsmithia, two closely related genera of Cunoniaceae. This character is an evolutionary novelty shared by these taxa. Other inflorescence characters are also informative at sectional or subsectional level. The simpler monotelic proliferate synflorescence of triadic floriferous paraciadia, representing an evolutionary novelty or autapomorphy, is present in the Sect. Pauciflorae. For sections Brunellia and Simplicifoliae the degree of complexity of the floriferous paraciadia is also informative. The position in the synflorescence of a short paracladium is also an evolutionary novelty in the Subsect Propinquae. Congested and proliferate floriferous paraciadia are also important in infra-subsectional groups such as in B. congestiflora.

Pollen grain analysis provides greater knowledge of the exine sculpture variation than had previous studies. Interest in this character had been expressed by Cuatrecasas since 1970 with Marticorena’s work. Five categories of exine ornamentation were found in this study which had not previously been observed at all. From the point of view of establishing relationships the exine ornamentation is not much informative in the whole cladogram. The reason being that the exine ornamentation is variable at inter and intraspecific level. All species in the unifoliolate group having three leaflets per node share the evolutionary novelty of a modified reticulate ornamentation of the exine. Punctate exine is a plesiomorphic character while modified reticulate, striate reticulate and rugulate exine sculptures are considered apomorphies for
Although the latter two exine sculptures are apomorphies, these have a homoplasic behavior and are usually present in Sect. *Brunellia*. I consider TEM analysis as the most appropriate method for studying family relationships and it is expected to be informative at sectional level in *Brunellia* as well.

Current molecular research in Cunoniaceae (Bradford in prep.) shows that *Brunellia* (Brunelliaeae) is not a taxon of Cunoniaceae and must be considered as a separate family. This opinion is different to that of Hufford and Dickson (1992) who include *Brunellia* as a genus of Cunoniaceae. It is also different to that of Orozco (1997, chapter 2), who proposed that *Brunellia* and *Spiraeanthemum* and *Acsmithia* of Cunoniaceae, to be placed in a family different from Cunoniaceae. As Bradford (in prep.) found through molecular analysis. *Spiraeanthemum* and *Acsmithia* form a sister group apart from the rest of the taxa (of Cunoniaceae). Orozco (Chapter 2) observed the same group but including *Brunellia*. Orozco also considers that there is a lack of monophyly in Cunoniaceae due to the inclusion of *Eucryphia* and *Davidsonia*, each one previously placed in different families and also by the inclusion of *Spiraeanthemum* and *Acsmithia*. As a result of this research *Davidsonia* is also included for the first time in Cunoniaceae and the relationship of *Connarus* (Connaraceae) with Cunoniaceae and Brunelliaeae is made clear. These families are now included in the order Oxalidales (AGP 1998).

The relationship of Brunelliaeae with the Australian family Cephalothaceae and genera of Cunoniaceae from Australia and west Pacific Islands, including *Davidsonia* and *Eucryphia*, and also with South American genera of Cunoniaceae, indicates that at some time they shared a common evolutionary history. Southern South American land connections during the Tertiary with Australia and Antarctica support the supposed relationships of Brunelliaeae with the Australian groups (Cephalothaceae and some genera of Cunoniaceae). It is assumed that *Brunellia* has been present in the Andes at low altitudes since the Late Cretaceous. The high diversification of *Brunellia* is related to the ramification of the Colombian Andes during the Eocene and to their adaptation to high altitudes during the upheaval of the Andes which was completed in the Pliocene. The most important upheaval of the Andes over 3000m, 9-12 m.y., influenced the distribution range of species of *Brunellia*. Thirty four species are present in Colombia, 14 in Ecuador, 5 in Bolivia, 9 in Peru, 4 in Costa Rica and Venezuela, and 3 in Panama. Two species are present in other regions, *B. mexicana* in Mexico, El Salvador and Guatemala and *B. comocladifolia* in Cuba, Haiti, Jamaica, Puerto Rico, and the Dominican Republic.

*Brunellia* is widely distributed in lower and upper montane rain forest, usually between 1500 and
3400 m above sea level. Only one species, *B. hygrothermica*, is frequently found at altitudes lower than 1000 m, except for one collection of *B. comocladiolophia* that was recorded at less than 500 m. The distribution of *B. hygrothermica* ties in with the possible scenario of the ancient distribution of *Brunelia* at lower altitudes before the upheaval of the Andes. With the exception of two collections of *B. ecuadorensis* and *B. tomentosa* (both species from sect. *Simplicifoliae*), *Brunelia* is not found higher than 3500 m. Species of the Sect. *Brunelia* are very often distributed between 1000 and 3000 m, while the most frequent altitudinal range for sections *Ovalifoliae*, *Pauciflorae*, *Simplicifoliae*, and *Stuebelia* is between 2000 and 3400 m.

In an early cladogenesis of *Brunelia* an altitudinal range between 2000-3000 m is observed. Species of Sect. *Simplicifoliae* reach the highest altitudes. In this section, at latest cladogenesis level, altitudinal reversals were observed in the cladogram and these reversals are attributed to glacial and interglacial periods. It could mean that the most recently speciation process is found in *Simplicifoliae*.

There is little fossil evidence regarding which groups in *Brunelia* are primitive or derived. To establish this, it is necessary to find historical relationships between geographic areas, in the same way that phylogenetic study provides this information among the species. Biogeographical hypotheses about ancestral areas and vicariance events associated with speciation are necessary to make any assumption on primitive taxa and areas. Any attempt, therefore, implies assumption that speciation events of the relationship patterns can only be explained by dispersal biogeography. However, under dispersal biogeography any explanation can be possible, and by consequence, the scenario can neither be corroborated or refuted. As is mentioned in the text, it is necessary to know the phylogenies of other groups with a similar distribution in the Andes to obtain a working historical biogeographic hypothesis that can be corroborated or refuted.

*Brunelia* is considered to have been present in the Andes since the Middle and Late Cretaceous. This consideration is based on the scenario resulted by the current distribution of *Brunelia* and the geological formation of the Andes. The Gondwanan origin of *Brunelia* is also assumed based on the ancient geomorphology of the continents, and its relationships with groups of Australian and West Pacific distribution such as *Cephalothaceae*, *Spiraeanthemum* and *Acsmithia* (Cunoniaceae). A diversification area instead of center of origin and speciation area were defined for *Brunelia*. Diversification area is an area in which species of different morphological lineages co-occur. This area is localized between 3° North and 7° South (from the Macizo Colombiano (in southern Colombia) to northern Peru). In this area species of the
five sections recognized in Brunellia are present. Speciation area is here defined by the presence of highest number of species of any morphological lineage. Colombia is the country with widest speciation. For Sect. Brunellia Western. West of the Central and East of Eastern Cordilleras is the area of most speciation, whereas the Macizo Colombiano and northern Central and Eastern Cordilleras is the area of highest speciation for Sect. Simplicifoliae. According to the cladogram, Sects. Simplicifoliae and Brunellia have a later cladogenesis compared with the early cladogenesis of Sects. Ovalifoliae, Pauciflorae, and Stuebelia.

According to information from collections of Brunellia, flowers and fruits are produced practically throughout the whole year, for example in those species which have been intensively collected such as B. comocladiifolia, B. sibundoya and B. colombiana. For the remaining species fruiting and flowering is not present during the whole year, however, these data could be due more to the absence of collections than to biological behavior. Thus, taking as reference the data of those species collected widely, the production of flowers or fruits throughout the year must be a consequence of the reproduction system in Brunellia. The protandrous condition of Brunellia assuring cross fertilization (between female and bisexual individuals) may well be the reason for continuous periods of flowering and fruiting. The flowering and fruiting period decreases in the dry season for species of sections Simplicifoliae and Brunellia, on the contrary for the rest of sections the data indicate flowering and fruiting periods in months of little rain. However, collections of these sections are scarcer, thus this information could change with additional collections. The most productive period for both flowering and fruiting, at least for sects. Brunellia and Simplicifoliae was seen between September and November. In October (rainy season) 18 of 51 species of Brunellia are flowering.