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Molecular phylogeny of the *Acre* clade (Crassulaceae): Dealing with the lack of definitions for *Echeveria* and *Sedum*

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ABSTRACT

The phylogenetic relationships within many clades of the Crassulaceae are still uncertain, therefore in this study attention was focused on the "*Acre* clade", a group comprised of approximately 526 species in eight genera that include many Asian and Mediterranean species of *Sedum* and the majority of the American genera (*Echeveria*, *Graptopetalum*, *Lenophyllum*, *Pachyphytum*, *Villadia*, and *Thompsonella*). Parsimony and Bayesian analyses were conducted with 133 species based on nuclear (ETS, ITS) and chloroplast DNA regions (*rpS16*, *matK*). Our analyses retrieved four major clades within the *Acre* clade. Two of these were in a grade and corresponded to Asian species of *Sedum*, the rest corresponded to a European–Macaronesian group and to an American group. The American group included all taxa that were formerly placed in the Echeverioideae and the majority of the American Sedoideae. Our analyses support the monophyly of three genera – *Lenophyllum*, *Thompsonella*, and *Pachyphytum*; however, the relationships among *Echeveria*, *Sedum* and the various segregates of *Sedum* are largely unresolved. Our analyses represents the first broad phylogenetic framework for *Acre* clade, but further studies are necessary on the groups poorly represented here, such as the European and Asian species of *Sedum* and the Central and South American species of *Echeveria*.

1. Introduction

Crassulaceae with approximately 1400 species is one of the most important groups of succulents that are widely cultivated as ornamentals because their leaves are aggregated into colorful rosettes. Members of the family are typically leaf-succulent herbaceous plants with flowers that are usually pentamerous, actinomorphic, and with 4–5 unfused, dehiscent carpels. The family exhibits highly complex cytological and chromosomal variation (Uhl, 1956, 1961b, 1963, 1992b), in fact, Crassulaceae is probably the most cytologically complex angiosperm family. The highest base chromosome number known for any dicot ($n = 270$) belongs to *Graptopetalum suaveolens* (Kimnach, 1978). Furthermore, it has been demonstrated that many species easily hybridize in culture (Uhl, 1961b, 1963) and there is evidence of hybrids in nature (Uhl, 1961a; Bañares, 1990; 't Hart et al., 1993).

Although the distribution of Crassulaceae is nearly worldwide, most species are found in five centers of diversity: Mexico (ca. 330 spp.), the Mediterranean basin (ca. 100 spp.), Macaronesia (ca. 63 spp.), southern Africa (ca. 250 spp.) and eastern Asia (ca. 300 spp.) (Webb, 1964; Ohba, 1978; Thiede and Eggli, 2007; Mort et al., 2002). Species usually grow in arid to semi-arid rocky and mountainous environments (Mort and Mori, 2004).

While the position of Crassulaceae has been well established in Saxifragales (APG II, 2003; Fishbein and Soltis, 2004; Soltis et al., 2007), the phylogenetic relationships within many clades of the family still remain uncertain ('t Hart, 1995; 't Hart and Eggli, 1995; Mort et al., 2001). The largely followed classification of Berger (1930) recognized six subfamilies, three of which are in the New World: Echeverioideae, Sedoideae and Crassuloideae. However, based on recent evidence, Thorne and Reveal (2007) recognized only two subfamilies: Crassuloideae and Sempervivoideae, and Thiede and Eggli (2007) proposed the recognition of a third subfamily, Kalanchoideae, with a reduced concept of Sempervivoideae. Following this classification, Crassuloideae is mostly restricted to southern Africa (except for a small group of aquatic *Crassula* species that are distributed worldwide), Kal-

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anchoideae is distributed in Africa and southern Asia and Sempervivoideae is widely distributed in the northern hemisphere. The latter subfamily has the greatest diversity, with approximately 975 species (Thiede and Eggli, 2007). Sempervivoideae has been subdivided into five tribes and Sedeae is the largest of these tribes with 640 species. Within the Sedeae, two groups have been repeatedly recovered by phylogenetic studies: the *Acre* clade and the *Leucosedum* clade (van Ham and 't Hart, 1998; Mort et al., 2001). The *Acre* clade is comprised of almost 526 species in eight genera including many Asian and Mediterranean species of *Sedum*, and the majority of the American genera (i.e., *Echeveria*, *Graptopetalum*, *Lenophyllum*, *Pachyphytum*, *Villadia*, and *Thompsonella*; Table 1). The mountains of central and southern Mexico are the main center of diversity for the *Acre* clade. However, there are other American genera not placed within this clade such as *Dudleya*, *Sedella* and *Sedum* subgen. *Gormania*, which have been placed in the *Leucosedum* clade. Additionally, few species from North America, (i.e., *Hylotelephium telephioides* (Michaux) H. Ohba, *Rhodiola integrifolia* Raf., *R. rhodantha* (A. Gray) H. Jacobsen, and *R. rosea* L.), are placed in the *Hylotelephium* clade.

Previous phylogenetic analyses have found a number of unresolved relationships within the *Acre* clade and the generic delimitation of most of the genera has been controversial (van Ham et al., 1994; van Ham, 1995; van Ham and 't Hart, 1998; Mort et al., 2001; Acevedo-Rosas et al., 2004a,b; Mayuzumi and Ohba, 2004; Carrillo-Reyes et al., 2008). Some of the genera are difficult to define morphologically, resulting in a lack of taxonomic resolution (e.g., Moran, 1942).

The most problematic and undoubtedly controversial taxon in the *Acre* clade is *Sedum*, the largest genus of the family, described by Linnaeus in 1753. At least 32 segregate genera have been published since then (Mort et al., 2001) and the most recent checklist of Crassulaceae includes 27 generic names as synonyms of *Sedum* ('t Hart and Bleij, 2003). Praeger (1921) recognized 10 sections within the genus and Berger (1930) recognized 22 of which ten are now known to be different genera or part of other groups (i.e., *Graptopetalum*, *Hasseanthus*, *Perrierosedum*, *Populisedum*, *Prometheum*, *Pseudorhodiola*, *Rhodiola*, *Sedella*, and *Telephium*; Sect. *Monanthella* is part of the *Leucosedum* clade and the status of Sect. *Telmissa* remains doubtful) (Eggli, 2003; Thiede and Eggli, 2007). The remaining 12 sections are part of the *Acre* clade, with the majority of species placed within *Sedum* sect. *Sedum* (e.g., Berger, 1930; Fu, 1965; 't Hart, 1991). Fröderström (1929–1935) proposed an alternative classification for *Sedum* based on geographic distribution and the type of fruit, proposing seven informally named groups. Fu (1965, 1974) described section *Filipes* and *Oreades*. Two another sections have been published, *Centripetalia* (Alexander, 1942) and *Craigia* (Clausen, 1943). Sections *Leptosedum* and *Dendrosedum* were merged under sect. *Fruticisedum* (Jacobsen, 1974; Uhl, 1980), and furthermore these sections together with *Pachysedum* were recognized as subgenus *Pachysedum* by Clausen (1943), who later also proposed the new subgenus *Sulcus* (Clausen, 1979).

Two subgenera are currently recognized: *Gormania* and *Sedum* ('t Hart and Bleij, 2003; Thiede and Eggli, 2007), the former was originally proposed as a separate genus by Britton (Britton and Rose, 1903). Subgenus *Gormania* has 110 species, which according to recent phylogenetic studies belong to the *Aeonium*, the *Sempervivum* and the *Leucosedum* clades (van Ham and 't Hart, 1998; Mort et al., 2001; Thiede and Eggli, 2007). Approximately 320 of the species ascribed to subgen. *Sedum* belong to the *Acre* clade (van Ham and 't Hart, 1998; Mort et al., 2001).

Among the American segregate genera of *Sedum* are *Sedastrum* and *Corynephyllum* (Rose in Britton and Rose, 1905), the first includes plants with numerous stems arising from dense basal rosettes and carpels with a concavity behind the scales, while the latter includes shrubby species with lateral inflorescences and flowers with a calyx larger than the corolla (Rose in Britton and Rose, 1905). While these genera are differentiated based on these morphological features, there is controversy over their recognition (Clausen, 1943; 't Hart and Bleij, 2003; Thiede and Eggli, 2007). By contrast, *Lenophyllum* (Britton and Rose, 1904), a small group from northeastern Mexico and southern USA with decussate leaves, thyrsoid inflorescences, and a putative base chromosome number of 11, has been clearly recognized as a separate genus from *Sedum* (Berger, 1930; Moran, 1994; Uhl, 1996; Thiede and Eggli, 2007). *Villadia* and *Altamiranoa*, two additional genera segregated from *Sedum*, have a broad distribution from the southern USA to South America. These taxa have alternate, small leaves, corollas that are fused basally, and thyrsoid and cymous inflorescences, respectively (Britton and Rose, 1903). Some authors include the species of *Altamiranoa* in *Sedum*, section *Fruticisedum* Berger (Moran, 1996; Thiede and 't Hart, 1999). *Lenophyllum*, *Villadia* and *Altamiranoa*, were initially placed within Berger's (1930) Echeverioideae, but were later transferred to

Table 1
Comparison of several classifications of the taxa comprising the *Acre* clade and *Sedum* subgen. *Gormania*.

Genus	Infrafamiliar classification				Number of species	Distribution	References
	Berger (1930)	Walther (1936)	't Hart (1995)	Thiede and Eggli (2007)			
Cremnophila Rose	Sedoideae/ Echeverioideae	Sedoideae/ Echeverioideae			2	S Mexico	Moran (1978)
Echeveria DC.	Echeverioideae	Echeverioideae			±145	From S USA to Argentina	Walther (1972), Kimnach (2003)
Graptopetalum	Sedoideae	Echeverioideae			19	From S USA to S Mexico	Acevedo-Rosas et al. (2004a,b)
Lenophyllum	Sedoideae	Sedoideae	Sedoideae	Sempervivoideae	7	SE USA and NE Mexico	Moran (1994)
Pachyphytum	Echeverioideae	Echeverioideae	Tribe Sedeae	Tribe Sedeae	17	C Mexico	Thiede and Eggli (2007)
Sedum subgen. *Sedum*	Sedoideae	Sedoideae	Subtribe Sedinae	*Acre* clade	±330	S USA, Mexico, S America, Eurasia and Asia	't Hart and Bleij (2003)
Villadia	Echeverioideae	Sedoideae			±25	S USA, Mexico, Guatemala, Peru	Thiede (2003)
Thompsonella	Echeverioideae (Sect. of *Echeveria*)	Echeverioideae			9	S Mexico	Moran (1992), Carrillo-Reyes et al. (2008)
Sedum subgen. *Gormania*	Sedoideae	Sedoideae	Sedoideae	Sempervivoideae	±110	N. America, Europa, East	't Hart and Bleij (2003)
			Tribe Sedeae Subtribe Sedinae	Tribe Sedeae *Leucosedum* clade		Africa	