

An up-to-date familial and suprafamilial classification of succulent plants

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Summary: We provide a short discussion of how the use of molecular data and sophisticated analytical methods has expanded our knowledge about the phylogenetic relationships among flowering plants and how this affects the familial and suprafamilial classification of succulents. A tree diagram illustrates the current hypothesis on their interrelationships and a table lists all 83 families that include succulent representatives (c.12,500 species from c.690 genera), together with information on taxonomic diversity (i.e. number of estimated species and genera) and architectural types of succulence. Furthermore, we briefly discuss some important recent modifications to the family classification of flowering plants and provide arguments for the proposed changes as far as succulents are concerned. In particular, we focus on the controversially discussed family classification of the monocotyledonous order Asparagales and provide arguments for a revised classification that considers the distinct variation patterns in this clade.

Zusammenfassung: In einer kurzen Diskussion zeigen wir auf, wie die Nutzung molekularer Daten und komplexer analytischer Methoden unsere Kenntnisse bezüglich der phylogenetischen Verwandtschaften innerhalb der Blütenpflanzen beeinflusst haben, und erklären, welche Auswirkungen das auf die Klassifikation der Sukkulente in Familien und übergeordnete Einheiten hat. Ein Baumdiagramm illustriert die aktuelle Hypothese der Verwandtschaften. Eine Tabelle listet alle 83 Pflanzenfamilien mit sukkulente Vertretern auf (c.12,500 Arten aus c.690 Gattungen), zusammen mit Angaben über die taxonomische Diversität (Schätzung der

Anzahl Arten und Gattungen) und die vorkommenden Sukkulenzformen. Schliesslich diskutieren wir kurz die wichtigsten neueren Ergänzungen der Klassifikation der Blütenpflanzen und beleuchten die Argumente für die vorgeschlagenen Veränderungen soweit Sukkulente betroffen sind. Insbesondere gehen wir auf die kontrovers diskutierte Familienklassifikation der einkeimblättrigen Ordnung Asparagales ein und unterbreiten Argumente für eine überarbeitete Klassifikation, welche die deutlichen Variationsmuster in diesem Clade berücksichtigt.

Introduction

The advent of molecular systematic methods in the 1980s and their subsequent widespread use has resulted in a burst of novel insights about the phylogenetic relationships among flowering plants (e.g. Savolainen *et al.*, 2000; Soltis *et al.*, 2007). These findings are now increasingly considered for updating current classification systems (APG, 1998, 2003, 2009). Furthermore, recently published manuals and textbooks on plant systematics introduce these modern phylogenetic systems to a broader audience (e.g., Simpson, 2006; Judd *et al.*, 2007; Mabberley, 2008).

In the past, plant classification was mainly based on morphological characters, supplemented by evidence from anatomy, cytology, or phytochemistry (e.g. Cronquist, 1981; Takhtajan, 1997). Now, the possibilities offered by molecular phylogenetic methods to directly analyze and compare parts of DNA sequences allow for the first time thorough verification of “traditional” classification systems on the basis of large

comparative datasets of completely independent and novel information gained directly from the individual genomes. The theory and methodology of phylogenetic systematics focuses on reconstructing phylogenetic relationships and to present them as hypotheses in the form of tree diagrams. Ranked hierarchical classification systems are then deduced from the branching pattern of the inferred tree diagram (e.g. Chase *et al.*, 2000). Phylogenetic classification systems are strictly genealogical and ideally recognize monophyletic taxa (conforming to clades of the phylogeny) of extant species only. Hence, they do not primarily mirror the *degree of divergence* (i.e. the amount of evolutionary change, be it in the form of differences in nucleotide sequences [but see Chase *et al.*, 2000: 688 for a statement to the contrary!], be it in the form of observable differences in morphology, anatomy, etc.) for assigning ranks at the different level in the Linnaean hierarchy – a strong contrast to tradition where the degree of observable morphological divergence strongly influenced decisions. An example from the world of succulents should help to clarify this point: the species of the former family Asclepiadaceae are clearly distinct because of their very elaborate floral architecture, though, phylogenetically they only represent an evolutionary lineage derived from *within* the broader diversity of the species included in Apocynaceae. In order to reflect this insight and to ensure a consistent classification of these taxa, Asclepiadaceae is nowadays included as part of Apocynaceae. Charles Darwin (1809–1882) stated in his famous publication *On The Origin of Species* that all classification “must be strictly genealogical” (Darwin, 1859: 420) in order to adequately represent the patterns of phylogenetic interrelationships (e.g. Ghiselin, 1969, 2004; but see Mayr, 1985, for a different interpretation and opinion). This challenge is now increasingly fulfilled with classification systems derived from molecular phylogenetic analyses.

At this point, we should clearly state that classification systems of organisms have a three-fold purpose: they should, at the same time, be an objective and universal representation of inferred phylogenetic relationships, a stable framework for the naming of organisms, as well as a practical tool consisting of easily identified and characterized entities (e.g. Thiele & Yeates, 2002; Stuessy, 2008). Newly gained knowledge from phylogenetic studies often calls for changes in the

classification and naming of organisms, which is a challenge to the goal of continuity and stability. Our suggestions for an updated classification of succulents considers this tension and aims at offering a compromise between well supported facts and the stability of long established classification systems as well as well-known names for rather small but more homogeneous families (e.g. Kubitzki, 1998). It should be kept in mind, however, that the short-term disruption to classificatory stability is balanced by the possibilities it offers towards a better understanding of the interrelationships among the recognized taxa for an appreciation of their evolution and diversification. The main question to ask before implementing any changes is thus the question about gains (or losses) of information connected to a newly proposed classification. Decisions about which clades in a phylogeny should receive a formal name should primarily be based on “(1) maximizing phylogenetic information and (2) support for monophyly” (Chase *et al.*, 2000: 687). Gains in phylogenetic information constitute excellent reasons for change. If such an information gain is minimal or lacking altogether, changes to existing classifications should be exerted with great care, because changes are always accompanied by some degree of disruption, especially when access to information in existing literature is considered.

During the past two decades, molecular phylogenetic studies have resolved numerous problematical and controversial cases in plant classification. In many cases, these studies provided strong support for relationships that were previously based largely on intuition. But in other cases they have shown that groups whose circumscription or affiliation went by unquestioned for a long time as “natural” taxa turn out to comprise lineages with distinctly different phylogenetic affinities. This results in new research questions and challenges to established classification systems. So far, the most profound impact of recent studies of flowering plant phylogeny has been at the rank of families and above. This is testified by the recognition of numerous new families (for succulents e.g. Anacampserotaceae, Montiaceae, and Talinaceae segregated from Portulacaceae; Nyffeler & Egli, 2010) as well as the disappearance of old favourites (e.g. Aloaceae to be included in Asphodelaceae [Dahlgren *et al.*, 1985; Smith & Wyk, 1991]; Asclepiadaceae to be included in

Apocynaceae [Endress *et al.*, 1997; Endress & Bruyns, 2000; Endress & Stevens, 2001]; Bombacaceae and Sterculiaceae included in Malvaceae [Baum *et al.*, 1998, Alverson *et al.*, 1999; Bayer *et al.*, 1999]). All of these cases are the result of improved knowledge of the genealogical interrelationships (= "topology" of the cladogram) between the taxa involved, and have helped to eliminate paraphyletic or polyphyletic taxa. These changes are thus in strong accord with both goals (i.e. maximizing phylogenetic information and increased monophyly) as formulated by Chase *et al.* (2000). Still, different opinions may persist about the ranking of family taxa (i.e. more broadly or more narrowly circumscribed families; Stuessy, 2008) despite a basic agreement about the phylogenetic relationships among the different lineages. Such a case is provided by the order Asparagales, whose family classification currently remains, in our opinion, "unsettled" (see discussion below).

However, the advent of phylogenetic systematics on the basis of molecular data has not only changed the factual basis on which higher-level classifications are developed, but also the way this work is achieved. In past times, plant classification systems were often "one-man" efforts, and many famous classification systems are colloquially identified simply by the name of their author. Prominent examples are the systems proposed by Engler (1924), Cronquist (1981), or Takhtajan (1997). In contrast to these former systems *en vogue* until late in the last century, modern plant classification systems are the work of unprecedented collaborative efforts of many research teams from throughout the world. Recently, this resulted in the foundation of the Angiosperm Phylogeny Group (APG) project, a consortium of numerous molecular plant systematists that aims at a consensus for a phylogenetic classification for flowering plants at the ranks of family, order, and higher informal groups (APG, 1998, 2003, 2009). The participation of numerous specialists insures that relevant information from all fields of research is incorporated, that divergent phylogenetic hypotheses are weighed against each other, and that a balance is sought between splitting and lumping of traditional families and orders. This procedure generally contributes to a broader acceptance of a thoroughly revised classification system. It has proved especially fruitful because it rapidly promoted a stabilization of the names of orders in

current use, and it is our hope that in the near future the same will apply to the family classification.

Goals

Traditional succulent plant literature does not usually give much room to suprafamilial classification. However, the phylogenetic classification of families into higher taxa provides the all-important backbone towards an understanding of the evolution of plant diversity and plant group interrelationships. The past few years have witnessed an increasing acceptance of the updated familial and suprafamilial classification system of flowering plants as proposed by the Angiosperm Phylogeny Group (APG, 1998, 2003, 2009). In this paper, we present an updated system as outlined in the recent revised APG classification system (APG, 2009; Stevens, 2001 onwards) as far as succulents are concerned. However, in the case of the order Asparagales we clearly favour a narrow family concept that is less disruptive and more informative in comparison to the large and morphologically very heterogeneous families as proposed by APG III (APG, 2009; Chase *et al.*, 2009). However, for the purpose of comparison we provide a list of recognized succulent Asparagales families for both systems, our favoured version with a total of eight smaller but more homogeneous families, as well as the APG III (APG, 2009) version with only three large families.

The phylogenetic relationships among 60 major lineages classified at the rank of order (as derived from APG (2009)) are presented in the form of a summary tree (Figure 1; a few less well known lineages omitted). However, we are more conservative and recognize only clades (i.e. internal branches) in the tree topology that receive support from several different molecular phylogenetic analyses and the two most recent APG classification systems (APG, 2003, 2009). Overall, 32 orders contain succulent plants as recognized by us (marked in roman or bold in Figure 1). Our census, extended from Eggl (2007), shows a total of at least 12,500 succulent species from c.690 genera in 83 families. In addition, we provide a table of orders and accepted families with succulents following the sequential arrangement in the summary tree (Table 1). This list gives a complete overview of our current knowledge of succulent plant diversity and its higher-level classification. The moderate

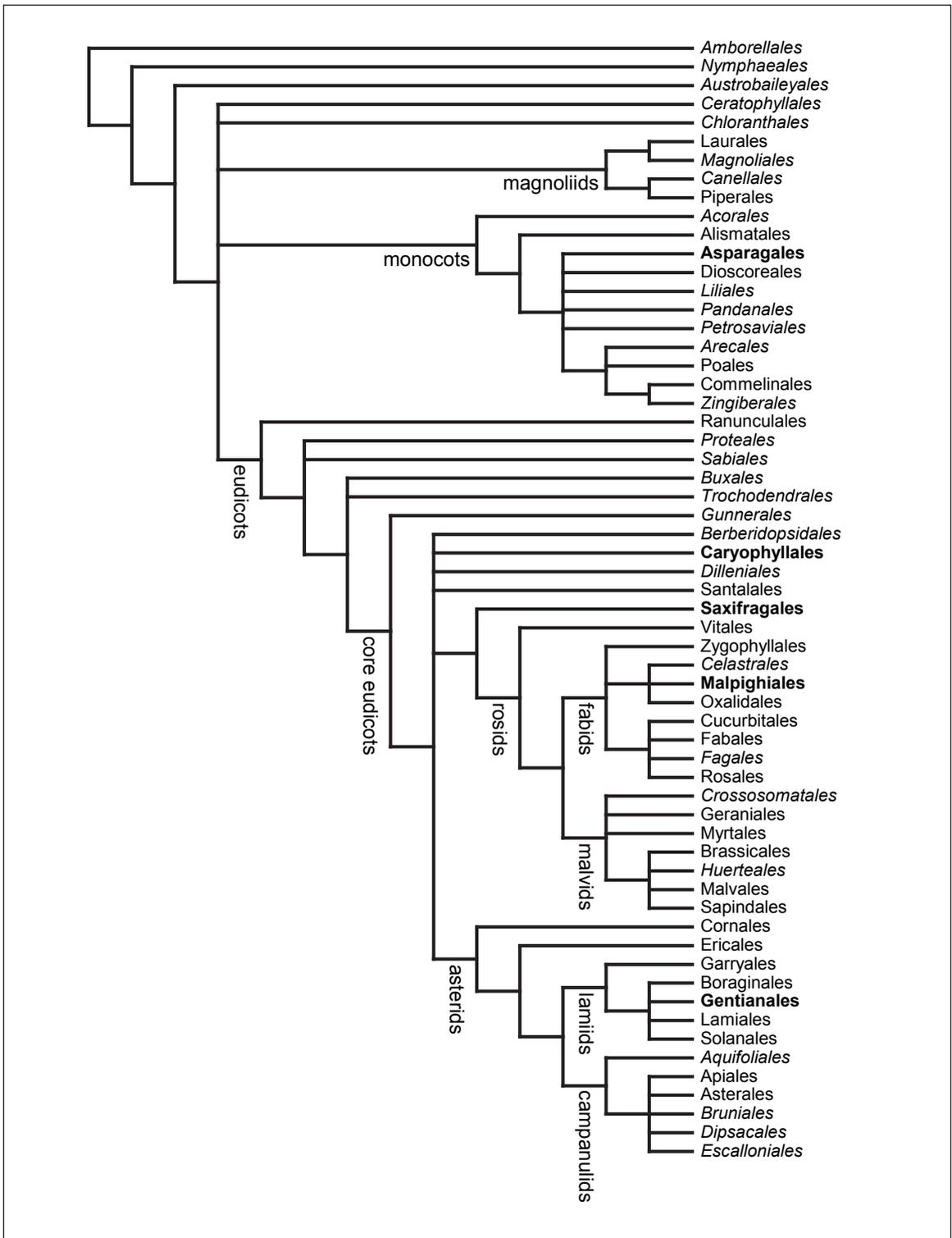


Figure 1. Summary phylogeny of inferred interrelationships among orders and some families of flowering plants. Orders with up to 500 species of succulents are in roman, those with more than 500 species of succulents are in bold, and those without succulents are in italics.

increase in the number of succulent species in comparison with Eggli (2007; 12,380 species) is explained by the continued uncertainties about the definition of “succulence” (see Eggli & Nyffeler, 2009) and its possible occurrence in many groups of plants not usually considered to exhibit succulence. The figure could become significantly higher once we have a better overview of succulence in families such as Piperaceae, Malvaceae s.l., Bromeliaceae, and especially Orchidaceae. The increase in the number of families with succulent plants (68 in Eggli, 2007) is due to the the dismemberment of Portulacaceae s.l. into smaller monophyletic units (Nyffeler & Eggli, 2010) as well as to the inclusion of a couple of families (marked with an asterisk in Table 1) that were hitherto not considered as embracing succulent species.

General structure of the classification system

The modern classification of flowering plants departs from the traditional basic distinction between Dicotyledons (i.e. taxa with two cotyledons) and Monocotyledons (i.e. taxa with only one cotyledon) (Cronquist, 1981; Takhtajan, 1997). Molecular phylogenetic analyses of the past decade clearly showed that the Monocotyledons evolved from *within* the diversity of taxa with two cotyledons (i.e. group of Dicotyledons). The presence of only one cotyledon is a character state (condition) that is derived (i.e. apomorphic). As such it provides phylogenetic information insofar as all descendants of the common ancestor in which this character evolved form a monophyletic group (= clade, monophylum). However, the original (i.e. ancestral, primitive, or, plesiomorphic) character state of having two cotyledons does not convey phylogenetic information at this level in the phylogeny; the group so circumscribed (i.e. the traditional Dicotyledons) does not include the “derived” Monocotyledons. Therefore, contemporary classification systems of flowering plants recognize *monocots* based on their single cotyledon and *eudicots* based on their distinct pollen type (see Figure 1; Soltis *et al.*, 2005; Judd *et al.*, 2007). The pollen of the *eudicots* commonly have three longitudinal colpi (i.e. tricolpate pollen), although there are many deviations from this generalized structure. The “left-overs”, those with two cotyledons and monosulcate pollen, represent lineages that attach topologically basal in the phylogenetic tree of the

flowering plants and are often referred to as “primitive” flowering plants. The only succulent representatives of this paraphyletic group (= grade) are found in the family Piperaceae (pepper family, order Piperales), and possibly a weakly pachycaul succulent from the family Hernandiaceae (order Laurales). Both of these orders are part of the distinct supraordinal clade called *magnoliids*. All other succulents belong either to the *monocots* or the *eudicots*. Within the latter clade we find, again, a topologically basal grade and two major subclades of *core eudicots*, the *rosids* and the *asterids*. The five orders richest in succulent representatives (i.e. including families with more than 500 succulent species each) are found in the *monocots* (Asparagales), *rosids* (Malpighiales), *asterids* (Gentianales), and amongst the remaining unresolved lineages of *core eudicots* (Caryophyllales, Saxifragales).

The molecular investigations of the past two decades have provided a well-founded classification system with a fairly stable “backbone” in the form of the APG summary tree (APG, 2003, 2009; Figure 1). Several areas of incomplete knowledge about the interrelationships of orders remain, however, and are indicated conservatively with polytomies in the present tree topology. Future analyses with data from additional taxa and from additional molecular markers will, ultimately, fill these gaps and further refine our knowledge about the phylogenetic relationships among the multitude of flowering plants. A recent example where such studies have already contributed to better resolution relate to the position and circumscription of Icacinaceae, which were twice redefined and successively narrowed in circumscription (Karehed, 2001; Lens *et al.*, 2008). The same applies to the refined and improved knowledge about the relationships among the closest relatives of the family Cactaceae, requiring the recognition of several smaller families, including Anacampserotaceae, Portulacaceae s.s. (i.e., monotypic to only include *Portulaca*), and Talinaceae (Nyffeler & Eggli, 2010).

Notes on families with succulents

Table 1 presents a complete list of families with succulent representatives arranged according to the present, slightly modified (but still congruent) APG summary tree (APG, 2003, 2009; Figure 1). In particular, we depict and list orders in polytomies as well as families within orders in

alphabetical sequence rather than in a contrived phylogenetic sequence. For a number of families (marked with footnote numbers in Table 1), we provide a short discussion of the effects of changes in respect to the taxonomy used in current succulent plant literature and especially in the series of *Illustrated Handbooks of Succulent Plants* (Eggli, 2001, 2002, 2003; Hartmann, 2001, Albers & Meve, 2002; subsequently collectively abbreviated as *IHSP* in this paper). For several families, recent changes of the infrafamilial or generic classification are also briefly discussed in these notes. Finally, an alphabetical list of families with succulents traditionally recognized but now subsumed by APG (2003, 2009) under more broadly circumscribed taxa, is given in Appendix 1.

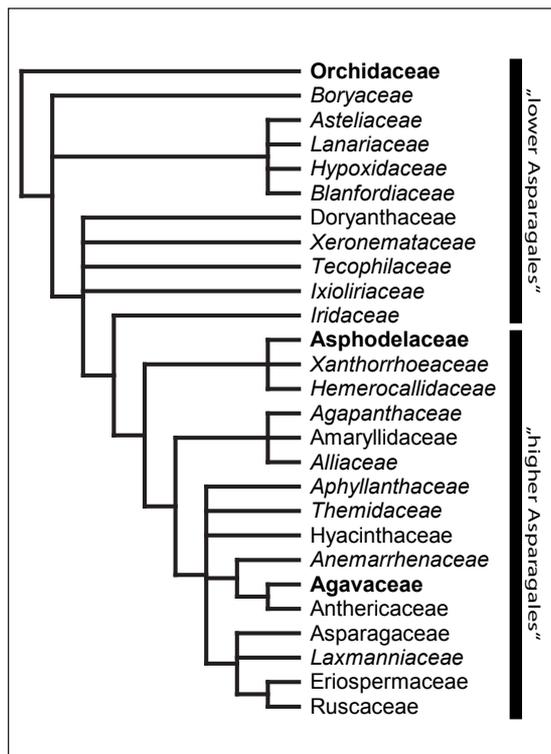


Figure 2. Summary phylogeny of the interrelationships among families of the order Asparagales as inferred by recent molecular phylogenetic studies. Our rather narrow taxonomic concept for this order results in recognizing 27 different families, of which nine families comprise succulents. Families with up to 100 species of succulents are in roman, those with more than 100 species of succulents are in bold, and those without succulents are in italics.

Introductory note on the families of Asparagales

Molecular phylogenetic studies of the past two decades confirmed that the broadly circumscribed family Liliaceae, in traditional classification systems basically including all Monocotyledons with actinomorphic showy flowers and syncarpous superior ovaries (e.g. Cronquist, 1981), is polyphyletic and should be disintegrated into a range of smaller families in line with suggestions made by Dahlgren and coauthors (Dahlgren *et al.*, 1985). In particular the basic distinction between taxa with superior versus inferior ovaries was found to be unjustified. In contrast, taxa characterized by nectaries in the septa of the ovaries as well as the formation of phytomelan and a syndrome of anatomical specialities in the seed coat (i.e. testa) are now grouped together to form the order Asparagales, while those characterized by nectaries at the base of filaments or tepals are now classified in the order Liliales (e.g. Judd *et al.*, 2007). Despite numerous recent efforts, the family classification of Asparagales remains controversial and as yet there is no broad acceptance for either a more conservative (i.e. few large families) or more progressive (i.e. many small families) approach. A series of studies during the past decade resolved molecular phylogenetic relationships among a broad sample of representatives of Asparagales (e.g. Chase *et al.*, 2000; Fay *et al.*, 2000; Bogler *et al.*, 2006; Givnish *et al.*, 2006; Pires *et al.*, 2006). All these studies are very much congruent with each other concerning topology and strong support for several terminal clades recognized as families as well as some internal relationships. The tree topology illustrated in Figure 2 is a summary tree of the relationships inferred by the individual primary studies listed above and is congruent to those summary trees published recently in various text books (e.g. Soltis *et al.*, 2005; Judd *et al.*, 2007). The large number of rather small and difficult-to-diagnose families in this order was a point of controversial discussion from the onset of the phylogenetically motivated classification systems (e.g. APG, 1998, 2003; Chase *et al.*, 2009). There is general agreement that the order Asparagales falls into a grade of so-called “lower Asparagales” (including Orchidaceae which probably is the sister-group to all other taxa of the order) on the one hand, and a well-supported clade of “higher Asparagales” on the other hand (Figure 2). In

earlier studies and in APG I (APG, 1998), almost 30 families were recognized for the order. Subsequently, it was repeatedly suggested to only recognize three major families for the “higher Asparagales” clade, reducing the number of recognized families in the whole order to 14 (APG, 2009; Chase *et al.*, 2009). Already the previous version of APG II (2003) proposed a lumpers’ approach and suggested to recognize three broadly circumscribed families Amarylloaceae, Asparagaceae, and Xanthorrhoeaceae, each of them representing a novel circumscription, plus 11 further families from the “lower Asparagales” grade. To address the concerns of those favouring the traditional fine-grained classification, APG II (2003) also provided “bracketed” families. APG III (2009) continued on this road but eliminated the “bracketed” families completely. The novel circumscription of the three families mentioned above causes a major disruption when compared to traditional classifications, and also affects how we classify succulent plant diversity. The magnitude of change is such that the information gain provided by the novel classification must be carefully evaluated and weighted against the disruption it causes (see discussion below for individual families).

Overall, we conclude that the novel arrangement of Asparagales families, first advocated by APG II (2003) and firmly proposed by APG III (2009), is not phylogenetically more informative than the traditional classification systems. The problems with the traditional fine-grained family classification of Asparagales (as identified by APG, 2009 and Chase *et al.*, 2009) are not that the entities recognized are para- or even polyphyletic, but mostly derive from the difficulties of how to interpret (and classify) a multitude of distinct lineages. The discussion is therefore not about the genealogy as such (i.e. how to treat paraphyletic grades, or to dismember polyphyletic taxa into their monophyletic components), but rather on where to “cut” the phylogeny to define branches to be recognized as families (i.e. “ranking”; Stuessy, 2008). As a consequence of these facts, the reasons for the radical lumpers’ approach as outlined by Chase *et al.* (2009) are not primarily a gain in information, but merely a gain in practicability, especially for teaching purposes. This is in accordance with the goal already formulated by Chase *et al.* (2000: 700) that “reducing the number of families recognized is desirable”, first on practical grounds, but

secondly also for maximizing information content of the system. We do not believe, however, that the information content of the system is enhanced by the lumpers’ approach, and we do not consider the “practical grounds” as a sufficiently firm argument for the proposed radical and disruptive change. Therefore, we opt for continuing the usage of the more traditional splitters’ classification of Asparagales. In the case of the very distinct genus *Eriospermum*, which all studies place as sister-group to the remaining taxa of the well supported clade recognized as Ruscaceae (Fay *et al.*, 2000; Rudall *et al.*, 2000; Bogler *et al.*, 2006; Pires *et al.*, 2006), we opt to exclude them from Ruscaceae and to recognize Eriospermaceae as a distinct monotypic family. This renders Ruscaceae much more homogeneous (for further discussion of characters see below), and in this recircumscribed classification Ruscaceae now include the traditionally recognized families Dracaenaceae and Nolinaceae (e.g. Rudall *et al.*, 2000; Givnish *et al.*, 2006). In contrast, *Aloe* and relatives are so firmly nested in the clade recognized as Asphodelaceae (e.g. Chase *et al.*, 2000; Pires *et al.*, 2006) that it is not feasible to recognize them as a separate family Aloaceae. Our suggestion for the classification of the diversity of succulent Asparagales families is congruent with the topologies published from molecular phylogenetic analyses and published phylogenetic classification systems (for references see above). Furthermore, our approach to recognize a larger number of families for the “higher Asparagales” largely parallels the approach to the grade of smaller families of the “lower Asparagales”. Finally, our line of argument is also congruent with our position of recognizing more finely grained but also more homogeneous families for Portulacineae of the order Caryophyllales (Nyffeler & Eggli, 2010). Conserving the traditional classification of the order Asparagales is not only phylogenetically completely acceptable, but furthermore keeps all links to previous literature and arrangement of families in herbaria intact. The option provided by Chase *et al.* (2009) to complement the lumpers’ families with subfamily names (see Table 2) is not a viable option in our eyes, and treating the families Amarylloaceae, Asparagaceae, and Xanthorrhoeaceae as superfamilies (as previously suggested for instance for the order Zingiberales by Kress [1990]) would be a much preferable option.

Table 1. Classification of families with succulent representatives as to order and informal supraordinal groups according to APG (2003, 2009). The sequence of the orders in the table corresponds to the tree topology given in Figure 1. Both orders in polytomies as well as families within orders are listed alphabetically. The total is 83 families with c.12,500 succulent species from c.690 genera.

Types of succulence: L = leaf succulence; S = stem succulence with green photosynthetic stems and no or short-lived leaves; PC = pachycauls & caudiciforms, i.e. non-green succulent stems with seasonally deciduous leaves as main photosynthetic organs; T = underground tubers; R = root succulence; codes given in descending order of importance of succulent type, codes included in parentheses when the type of succulence is of minor importance only. Families and orders with more than 500 species of succulents are printed in bold.

Abbreviations: s.l. = sensu lato = in the wide sense; s.s. = sensu stricto = in the narrow sense; * = family not covered in *IHSP*.

Code numbers after family names (1–31): refer to notes that follow.

Informal supraordinal group	Order	Family	Genera total / succulent	Species total / succulent	Types of succulence			
magnoliids	Laurales	Hernandiaceae (1)	4 / 1	60 / 1	PC?			
	Piperales	Piperaceae	5 / 1	3000–3600 / c.66	L, S, T/R			
monocots	Asparagales	Alismatales	Araceae	105 / 3	3400 / 3	L, T		
		Agavaceae s.l. (2)	14 / 6	400 / 312	L, (PC)			
		Amaryllidaceae s.s. (3)	59 / 6	850 / 13	L			
		Anthericaceae (2)	8–9 / 2	280 / c.2(?)	PC, R			
		Asparagaceae s.s. (4)	2 / 1	165–295 / c.3	R			
		Asphodelaceae s.l. (5)	15 / 8	785 / 613	L, T, (PC)			
		Doryanthaceae	1 / 1	2 / 2	(L)			
		Eriospermaceae (6)	1 / 1	102 / c.4	L, T			
		Hyacinthaceae	40–70 / c.9	770–1000 / c.46	L			
		Orchidaceae (7)	880 / c.52	21950 / c.2200?	L, S, R			
		Ruscaceae (6)	25 / 5–6	375 / 90	L, S			
		Dioscoreales	Dioscoreaceae	4 / 1	870 / c.20	T, PC		
		Poales	Bromeliaceae (8)	56 / 16	2885 / c.310	L		
			Poaceae * (9)	715 / 1	10550 / 1–2	L		
	Commelinales	Commelinaceae	40 / 7	625 / c.36	L, (R)			
eudicots	Ranunculales	Menispermaceae	71 / 5	450 / 10	PC/T			
		Caryophyllales	Aizoaceae	138 / 138	1882 / 1882	L, (S, R/T)		
core eudicots	Caryophyllales	Amaranthaceae s.l. (10)	174 / 1?	2050–2500 / 1?	(L?, S?)			
		Anacampserotaceae (11)	3 / 3	36 / 36	L, S, PC/T			
		Basellaceae	4 / 4	19 / 19	B, T			
		Cactaceae	127 / 127	1896 / 1896	S, (L, T)			
		Caryophyllaceae * (12)	86 / 3?	2200 / 3?	L?			
		Didiereaceae	7 / 7	19 / 19	S, (L, R)			
		Halophytaceae * (13)	1 / 1	1 / 1	L			
		Molluginaceae * (14)	13 / ?	c.120 / ?	L?			
		Montiaceae (11)	15 / 11	226 / 161	L, (S, PC)			
		Nyctaginaceae * (15)	30 / 4?	395 / 5?	(L?, R?)			
		Phytolaccaceae s.s. (16)	4 / 2?	31 / 4?	PC, (L?)			
		Portulacaceae s.s. (11)	1 / 1	116 / 116	L, S, PC, T, R			
		Talinaceae (11)	1–2 / 1–2	21 / 21	L, PC, T			
		Santalales	Loranthaceae (17)	68 / 1	950 / 1	L		
			Santalaceae * (17)	44 / 2	990 / 2	L, S		
		Saxifragales	Crassulaceae	34 / 34	1426 / 1420	L, PC, T		
			Saxifragaceae (18)	33 / 1	540 / 1	(L)		
		rosids	Vitales	Vitaceae	14 / 4	750–900 / 61	L, S, PC, T, R	
		rosids-fabids	Zygophyllales	Zygophyllaceae	22 / 4	240–284 / c.44	(L)	
				Malpighiales	Clusiaceae * (19)	27 / 1	1090 / 100?	(L)
				Euphorbiaceae s.s. (20)	218 / c.4(–9)	5735 / 878	S, L, PC, T, R	
				Passifloraceae	17 / 1	750 / c.50	S/PC, R	
				Phyllanthaceae (20)	55 / 1	1745 / 1	PC	
Oxalidales	Oxalidaceae			6 / 1	770 / c.12(–60?)	L, T, R		
Cucurbitales	Begoniaceae			2 / 1	1400 / c.9	L, PC, T		
	Cucurbitaceae			118 / 35	825 / c.87	L, PC, T, R, (S)		

Table 1 cont.

Informal supraordinal group	Order	Family	Genera total / succulent	Species total / succulent	Types of Succulence
	Fabales	Fabaceae	730 / 5	19400 / 24	T, R?
	Rosales	Moraceae	37 / 2	c.1100 / 21	S/PC, T
		Urticaceae	54 / 5	2625 / 8	L, PC
rosids-malvids	Geraniales	Geraniaceae	5 / 2	835 / 155	PC, T, R, (L, S)
		Melanthaceae * (18)	5 / 1	19 / 1	L
	Myrtales	Melastomataceae	182 / 1	4570 / 1	L
	Brassicales	Brassicaceae	338 / 2	3700 / c.12	L
		Capparaceae	16 / 1	480 / c.1	(L)
		Caricaceae	6 / 6	35 / 35?	PC
		Moringaceae	1 / 1	13 / 13	PC, T
		Tropaeolaceae * (21)	1 / 1	95 / ?	T
	Malvales	Bixaceae (22)	3 / 2	20 / c.4	T
		Malvaceae s.l. (23)	243 / c.8	4300 / c.23	PC
	Sapindales	Anacardiaceae	70 / 2	600 / 6	PC
		Burseraceae	18 / 3	550–680 / c.23	PC
		Meliaceae	52 / 1	621 / 1	(PC)
		Sapindaceae s.l. (24)	135 / 1	1450 / 1	(PC)
asterids	Cornales	Loasaceae	20 / 1	330 / 1	T
	Ericales	Balsaminaceae	2 / 1	1000 / c.10	PC, T
		Ericaceae	126 / 1(-2?)	3995 / 1(-2?)	(L), T?
		Fouquieriaceae	1 / 1	11 / 11	PC
asterids-lamiids	Garryales	Icacinaeae s.s. (25)	24–34 / 1	150 / 2	PC/T
	Boraginales	Boraginaceae * (26)	148 / 1?	2740 / ?	(L?)
	Gentianales	Apocynaceae s.l. (27)	355 / c.74	3700 / 1151	L, S, PC, T, R
		Rubiaceae	563 / 8	10900 / 60	PC, L
	Lamiales	Bignoniaceae * (28)	104 / 1?	860 / 2?	T
		Gesneriaceae	147 / 9	3200 / 44(-89?)	L, T
		Lamiaceae	236 / c.7	7170 / c.104	L, PC, T, R
		Lentibulariaceae	3 / 1	320 / c.10	(L)
		Pedaliaceae	13 / 4	70 / 31	PC, T
		Plantaginaceae * (29)	90 / 1?	1700 / 1?	PC?
	Solanales	Convolvulaceae	55 / 3	1930 / c.20	PC, T
		Solanaceae s.l. (30)	102 / 1(-2?)	2510 / 30(-89)	L
asterids-campanulids	Apiales	Apiaceae	434 / 3?	3780 / 3?	PC, T/R
		Araliaceae	43 / 1	1450 / 5	PC
	Asterales	Asteraceae	1620 / c.14	23600 / 137	L, S, T, R
		Campanulaceae	84 / 1	2380 / 1-2	PC
		Goodeniaceae * (31)	11 / 1	400 / 2	L

Notes on selected families

The following notes refer to families that contain succulent species as listed in Table 1.

(1) **Hernandiaceae**: This small family is not usually considered to contain succulents, and is not included in *IHSP*. However, it appears that the pantropical and polymorphic species *Gyrocarpus americanus* has a pachycaul stem and thus some claim to succulence.

(2) **Agavaceae s.l., Anthericaceae**: The genera included in Agavaceae had a checkered classificatory history: in pre-1950 classifications, *Agave* and related genera with inferior ovaries were

placed in Amaryllidaceae, but *Yucca* and related genera with superior ovaries in Liliaceae. Agavaceae s.s. (i.e. as circumscribed in *IHSP*) embrace succulent to xeromorphic taxa from the New World; some authors at times also placed taxa from the traditional families Dracaenaceae and Nolinaceae here. Based on molecular phylogenies, the family has been expanded in recent years, but there is as yet no unanimous consensus about its circumscription. All recent phylogenies agree that Agavaceae s.l. include Hostaceae (= Funkiaceae, i.e. *Hosta* and some disparate small non-succulent groups, traditionally classified as Liliaceae) and the “Chlorogaloideae” (earlier placed in Hyacinthaceae, e.g.

Table 2. Family classification of succulent Asparaglaes in comparison: our present version, which favours narrow family circumscriptions is contrasted with the very broad family concepts proposed by APG III (2009). Subfamily names are listed according to Chase *et al.*, 2009.

Nyffeler & Eggli (this publication)	APG III (2009)	
(including synonyms)	Family	Subfamily
Agavaceae	Asparagaceae	Agavoideae
Amaryllidaceae	Amaryllidaceae	Amaryllidoideae
Anthericaceae	Asparagaceae	Agavoideae
Asparagaceae	Asparagaceae	Asparagoideae
Asphodelaceae (incl. Aloaceae)	Xanthorrhoeaceae	Asphodeloideae
Eriospermaceae	Asparagaceae	Nolinoideae
Hyacinthaceae	Asparagaceae	Scilloideae
Ruscaceae (incl. Dracaenaceae, Nolinaceae)	Asparagaceae	Nolinoideae

Camassia). There is no agreement, however, as to the treatment of Anthericaceae. While Stevens (2001 onwards), Graham *et al.* (2006), Pires *et al.* (2006), Givnish *et al.* (2006) and Judd *et al.* (2007) favour their inclusion into a further enlarged Agavaceae (“sensu latissimo”), Good-Avila *et al.* (2006), Bogler *et al.* (2006) and Smith *et al.* (2008) stress the lack of support for such an expanded circumscription and prefer to recognize Anthericaceae as sister-group to Agavaceae in a more traditional setup. This latter interpretation is here followed. However, there is no doubt that Agavaceae belong to the “higher core Asparagales”, together with Hyacinthaceae, Asparagaceae and Ruscaceae (see below, (6)) as well as further families without succulents. In a radical approach, all these families are treated as a much enlarged family Asparagaceae (APG 2003, 2009; Graham *et al.*, 2006), circumscribed by racemose inflorescences (in comparison with the umbellate inflorescences of the “lower core Asparagales”, but with numerous exceptions) (see below, (3)).

(3) Amaryllidaceae s.s.: In molecular phylogenies, Amaryllidaceae appear in sister-group position to the purely African family Agapanthaceae (no succulents), and could be united with that family as well as with the Alliaceae (no succulents) (APG, 2003; Janssen & Bremer, 2004). The resulting family, corresponding to the “lower core Asparagales”, is characterized by umbellate inflorescences. For nomenclatural reasons it would have to be called Alliaceae, but a proposal to conserve the name Amaryllidaceae is underway (Meerow *et al.*, 2007). Here, we follow

Judd *et al.* (2007) and accept the Amaryllidaceae in their traditional circumscription.

(4) Asparagaceae s.s.: In traditional classification systems, Asparagaceae consisted mainly of the large genus *Asparagus* (incl. *Myrsiphyllum* in contemporary circumscriptions, contrasting the treatment in *IHSP*), to which the monotypic non-succulent genus *Hemiphylacus* (previously included in Asphodelaceae) was more recently added. APG (2003, 2009) suggests an alternative to this narrow circumscription by expanding Asparagaceae to include all “higher core Asparagales” with racemose inflorescences (see above, (2), and below, (6)). Here again, we follow Judd *et al.* (2007) and accept Asparagaceae in sister-group position to Ruscaceae.

(5) Asphodelaceae s.l. (incl. Aloaceae): In traditional classifications, the genera of Asphodelaceae were placed in Liliaceae. Between about 1950 and 2000, *Aloe* and its close relatives (i.e. subtribe Aloineae of the former Liliaceae) were treated as a distinct family Aloaceae. This was a conveniently circumscribed monophyletic taxon from the point of view of succulent plant diversity, but molecular phylogenetic studies revealed that keeping Aloaceae separate from Asphodelaceae s.s. results in a paraphyletic arrangement. Consequently, there is fair agreement that Aloaceae should be subsumed (as subfamily Alooideae) under Asphodelaceae (Graham *et al.*, 2006, Givnish *et al.*, 2006). This is the position followed by Judd *et al.* (2007) and here, in contrast to the *IHSP* treatment. APG (2003, 2009) goes one step further in the

rationalization of Asparagales, and alternatively suggests treating Asphodelaceae together with Hemerocallidaceae (no succulents) as part of an expanded family Xanthorrhoeaceae s.l.

(6) Eriospermaceae, Ruscaceae (incl. Dracaenaceae, Nolinaceae): According to recent molecular phylogenies, the families Dracaenaceae, Eriospermaceae, Nolinaceae and Ruscaceae s.s. (plus Convallariaceae, no succulents) form a monophyletic group. Therefore, several authors suggested uniting them under the name Ruscaceae (or sometimes Convallariaceae, but Ruscaceae is correct for nomenclatural reasons) as part of the core Asparagales (Rudall *et al.*, 2000; Bogler *et al.*, 2006; Graham *et al.*, 2006; Givnish *et al.*, 2006). Ruscaceae s.l. diagnostically show articulated pedicels (Graham *et al.*, 2006) and fruits in the form of juicy or dry berries (Givnish *et al.*, 2006), and seeds lacking phytomelan (Rudall *et al.*, 2000). Asparagaceae s.s. are similar in flowers and berry fruits but have seeds with phytomelan, and can conveniently be accepted as sister family to Ruscaceae. APG (2003, 2009) suggests an even more radical approach by subsuming the whole group in Asparagaceae.

Dracaenaceae, Nolinaceae and Ruscaceae s.s. share a predominance of drought-adapted fibrous scleric leaves (or phylloclades in the case of Ruscaceae s.s.), smallish to insignificant white or pale-coloured flowers and juicy (Dracaenaceae, Ruscaceae) or dry (Nolinaceae) berries. However, the Eriospermaceae with their tuberous corms, herbaceous growth, capsular fruits and very different seeds (hairy-woolly, with oily perisperm) do not “fit” into such an expanded concept of Ruscaceae. We therefore propose acceptance of Eriospermaceae as basal sister of an expanded Ruscaceae that includes Convallariaceae, Dracaenaceae and Nolinaceae. In the more distant past, Dracaenaceae were classified as Liliaceae or Agavaceae. The members of Nolinaceae were often and up to quite recently classified as Agavaceae (e.g. Rowley, 1987).

(7) Orchidaceae: Even though Orchids are not usually covered by works on succulent plants (including *IHSP*), their claim to succulence is undisputed. Water storage can be in the leaves (hypodermis or mesophyll, depending on species), stems (pseudobulbs) or roots. Roots of orchids are

frequently distinctly thickish, but their role in storing water needs further research. At least in some taxa, water storage in the roots appears to occur in mucilage-filled supra-endodermal spaces (Figueroa *et al.*, 2008). Estimates of the number of succulent species of Orchids are difficult to determine, in line with the general disagreement about the total number of species for the family (18,000–35,000, Pires *et al.*, 2006). The figure of 2,200 succulents (Eggli, 2007) is merely a first guess, and the actual number could easily be twice as high.

(8) Bromeliaceae: Bromeliads, like Orchids, are not usually covered by succulent plant literature (including *IHSP*). Slightly to distinctly succulent leaves are, however, commonly encountered. Water storage occurs in the mesophyll (usually devoid of chlorophyll) (Horres & Zizka, 1995) with multiple layers of collapsible water-storage parenchyma cells (Benzing, 2000: 65). The degree of succulence found for Bromeliads is comparable to values found for many undisputed succulents such as *Graptopetalum bellum* or *Aloe pearsonii* (Horres & Zizka, 1995).

(9) Poaceae: Grasses were hitherto not considered to include succulent representatives (and consequently are not treated in *IHSP*), but already Smith *et al.* (1997) listed the genus *Dregeochloa* as having succulent leaves. This was recently corroborated by Jaarsveld (2009).

(10) Amaranthaceae s.l. (incl. Chenopodiaceae): Amaranthaceae and Chenopodiaceae were traditionally considered as two separate families, but their close relationship was recognized for a long time. Apart from gross morphology and similarities in flower architecture, the two families share a unique type of sieve-element plastids that lack central crystalloids (Behnke, 1976a: 42, 47). In *IHSP*, a single taxon of Amaranthaceae s.s. is covered (*Arthraerva leubnitziae*), whose succulence is, however, rather doubtful considering its anatomy (Carlquist, 2003; Dinter & Hass, 2008). Amongst former Chenopodiaceae, both stem succulence and leaf succulence is frequent, although often associated with halophytic traits. At least xero-halophytic taxa have a well-founded claim to succulence. Stem succulence is either cortical (with an outer palisade-like layer, and a central water-storage parenchyma; Fahn & Cutler,

1992), or derived from sheathing leaf bases (“false” stem succulence) (Kadereit *et al.*, 2006). Weakly expressed leaf succulence is common, and in terete leaves (e.g. *Salsola* species), water storage occurs in a central parenchymatic mesophyll largely devoid of chlorophyll (Volkens, 1887; Ku *et al.*, 1981; Gibson, 1996: 113).

(11) Anacampserotaceae, Montiaceae, Portulacaceae s.s., Talinaceae: Portulacaceae in their traditional wide circumscription have been the focus of considerable recent research, which culminated in a complete dismantling of the family by Nyffeler & Egli (2010; see also Nyffeler, 2007). On this basis, we now recognize Anacampserotaceae, Montiaceae, Portulacaceae s.s. and Talinaceae as segregate families, a change already accepted by APG (2009). Together with the transfer of *Ceraria*, *Portulacaria* and *Calypstrotheca* to Didiereaceae (Applequist & Wallace, 2001, 2003), the new arrangement of the families of suborder Portulacineae now reflects our current understanding of the phylogeny of this clade.

The problematic circumscription of Portulacaceae in the traditional wide sense was known for a considerable time. The genera now segregated as Montiaceae were first recognized as a distinct clade (called “Western American Portulacaceae”) separate from the remainder of the family both on morphological (Carolin, 1987; Hershkovitz, 1991b, 1993a) and molecular grounds (Hershkovitz & Zimmer, 1997, 2000). One of the major problems associated with the traditional wide circumscription of Portulacaceae is that the families Basellaceae, Didiereaceae, and most notably Cactaceae, are nested within Portulacaceae, rendering the latter paraphyletic (Applequist & Wallace, 2001, 2003; Applequist *et al.*, 2006; Nyffeler, 2007). The past circumscription of Portulacaceae was predominantly based on the presence of two “sepals”, five “petals”, and capsular fruits – but excluding those taxa either with a scandent or viny habit (Basellaceae) or a spiny and cactus-like growth-form (Didiereaceae) (Nyffeler & Egli, 2010, with discussion of the morphological nature of the floral envelope). In addition, Applequist *et al.* (2006) and Wagstaff & Hennion (2007) showed that the non-succulent Hectorellaceae are also nested within traditional Portulacaceae as part of the clade now recognized as Montiaceae.

In the classification proposed by Nyffeler &

Egli (2010), Anacampserotaceae embrace the two monotypic genera *Grahamia* and *Talinopsis*, plus *Anacampseros* (incl. *Talinaria*, *Xenia* and *Avonia*). Talinaceae are restricted to *Talinum* (incl. *Talinella*) and perhaps also include *Amphipetalum*, and Portulacaceae s.s. are restricted to *Portulaca*. All remaining former genera of Portulacaceae (except those now referred to Didiereaceae) form the family Montiaceae.

(12) Caryophyllaceae: This family is not usually considered to include succulent taxa, and the family is not treated in *IHSP*. However, the shrubby species *Polycarpaea nivea* (NW Africa, Canary Islands) and *Gymnocarpos salsoides* (Canary Islands) (Kunkel & Kunkel, 1978) as well as *Dicheranthus plocamoides* (Canary Islands) all show weakly expressed leaf succulence.

(13) Halophytaceae: This family – inadvertently omitted from *IHSP* – embraces the single taxon *Halophytum ameghinoi*. This is a monoecious succulent-leaved annual with condensed spike-like inflorescences, and is of widespread occurrence in the Argentinian monte vegetation. Its claim to succulence appears to be undisputed, and even though a certain preference for saline soils is notable, the taxon cannot really be considered as a pure halophyte.

(14) Molluginaceae: Like Caryophyllaceae, Molluginaceae are not usually considered to include succulent taxa, and the family is absent from *IHSP*. Slightly fleshy leaves are mentioned for the genera *Corbichonia*, *Glinus*, *Hypertelis* and *Mollugo* (Endress & Bittrich, 1993), but it is questionable whether this really represents true succulence. Also some taxa of *Limeum* have distinctly thickened, somewhat succulent leaves (Egli, pers. obs.). *Corbichonia* is most probably best classified into the small family Lophiocarpaceae, while *Limeum* should be segregated as Limeaceae (Schäferhoff *et al.*, 2009). More research is necessary to disentangle these genera of the formerly widely circumscribed Molluginaceae.

(15) Nyctaginaceae: Another family not usually considered to include succulent taxa, and thus not covered by *IHSP*. However, at least a couple of species of *Abronia* and *Commicarpus* have

weakly succulent leaves (Bittrich & Kühn, 1993), and Wilson (1972) reports succulent tuberous roots in two species of *Abronia*. While the tuberous roots of *Mirabilis jalapa* do not appear overly succulent at first sight, their tissue is described as highly parenchymatic (Carlquist, 2004). The roots of *M. expansa* (“Mauka”, traditional local food crop from the South American Andes) are also noted to be “fleshy” in the literature.

(16) Phytolaccaceae s.s.: The traditional wide circumscription of the family (e.g. Rohwer, 1993) is questioned by several molecular phylogenetic studies (Rettig *et al.*, 1992; Brown & Varadarajan, 1985; Cuénoud *et al.*, 2002; Schäferhoff *et al.*, 2009), and Phytolaccaceae are now restricted to just Phytolacchoideae of the formerly widely circumscribed family, with all other elements recognized as several small families (all without succulents). APG (2009), on the other hand, points out that this fine-grained division of the traditional Phytolaccaceae is premature and requires further investigations.

(17) Loranthaceae, Santalaceae (incl. Viscaceae): *IHSP* covered one species of *Tapinanthus* (Loranthaceae) and one species of *Viscum* (Santalaceae, in *IHSP* treated as Viscaceae). Whether these are truly succulent plants is open to debate, especially also with regard to the widespread occurrence of coriaceous, thickish leaves in many other hemiparasitic taxa of the two families.

(18) Saxifragaceae, Melianthaceae: Many discordant elements that were traditionally included in Saxifragaceae s.l. in the recent past have been found to belong to completely unrelated taxa (e.g. *Parnassia* now recognized as Parnassiaceae in Celastrales) (Soltis, 2006). Another such element is the monotypic Chilean genus *Tetilla*, which was covered in *IHSP* as belonging to Saxifragaceae, but which is now classified within an extended family Melianthaceae (Linder, 2006) or, alternatively, in Francoaceae. This re-arrangement is notable since Saxifragaceae belong to the order Saxifragales, while Melianthaceae are placed in Geraniales.

Succulence in Saxifragaceae as circumscribed by Soltis (2006) appears to be restricted to a single species of *Saxifraga* (*S. tolmiei*, W North

America, with thickened fleshy leaves).

(19) Clusiaceae: Another family (alternative family name Guttiferae) not usually considered as having succulent representatives, and therefore not covered in *IHSP*. Many species of *Clusia* do, however, clearly present perennial leathery and succulent leaves. Water is stored in the adaxial hypodermis (2- to several-layered) and the spongy mesophyll tissue (Lüttge, 2007). Clusiaceae are notable amongst succulents in so far as they appear to represent the only clade where leaf-succulence is combined with the tree growth form.

(20) Euphorbiaceae, Phyllanthaceae: Phyllanthaceae were traditionally included in Euphorbiaceae s.l. (as subfamily Phyllanthoideae, e.g. in *IHSP*), but differ consistently in carpels with 2 (rather than 1) ovules (Wurdack *et al.*, 2004) and turn out to be rather distantly related to Euphorbiaceae s.s. (Wurdack *et al.*, 2004, 2005; Tokuko & Tobe, 2006; Tokuko, 2007). Other differences are the lack of laticifers and latex, and seeds without arils.

Within Euphorbiaceae s.s., recent research suggests considerable re-alignments of genera with succulent representatives: all recent molecular phylogenies show the genus *Euphorbia* in its traditional circumscription to be grossly paraphyletic relative to several segregates. Wurdack *et al.* (2005) conclude that all cyathia-forming taxa should be united with *Euphorbia*, and both Bruyns *et al.* (2006) and Park & Jansen (2007) underline the fact that the “succulent” genera *Elaeophorbia*, *Endadenium*, *Monadenium* and *Synadenium* form a monophyletic clade that is firmly placed within *Euphorbia* subgen. *Euphorbia*. Likewise, *Pedilanthus* (Steinmann, 2002; Park & Jansen, 2007) and *Cubanthus* (Steinmann *et al.*, 2007) should also be included in *Euphorbia* s.l. The alternative to the sinking of all these well-established segregates (each conforming to a more or less monophyletic clade) would be to break up *Euphorbia* s.l. into numerous small and difficult-to-diagnose genera.

(21) Tropaeolaceae: This monogeneric family is not usually considered as having succulent species, and is not covered by *IHSP*. Several taxa of *Tropaeolum* have underground tubers that are derived either from rhizomes, underground axillary shoots, or from the hypocotyl, with or

without participation of the primary root (after Bayer & Appel, 2002). The tubers of *T. tuberosum* (“Mashua”, “Añu”, a traditional root crop from the South American Andes) have a water content of 87% (Sperling & King, 1990), and the plants appear to qualify as succulents.

(22) Bixaceae: In traditional classifications, Bixaceae was a monogeneric strictly neotropical family (Poppendieck 2002), but the close relationship with Cochlospermaceae, now subsumed in this family, was known for a long time.

(23) Malvaceae s.l.: The concept of Malvaceae has considerably changed on the basis of several recent morpho-anatomical (Judd & Manchester, 1997) and molecular phylogenetic studies (Alverson *et al.*, 1999; Bayer *et al.*, 1999), and there is consensus that the traditionally but arbitrarily circumscribed separate families Bombacaceae (c.250 species), Sterculiaceae (c.1,000 species) and Tiliaceae (c.400 species) are firmly intertwined with Malvaceae s.s. (c.1,500 species). This expanded Malvaceae has been found to be monophyletic. The close relationship was already apparent in earlier classifications, where a number of genera and suprageneric taxa were differently placed by different authorities (Alverson *et al.*, 1999; their table 1). Within Malvaceae s.l., succulents are classified in subfamilies Bombacoideae and Sterculioideae.

(24) Sapindaceae s.l.: According to contemporary classifications, the Sapindaceae, which in their traditional narrow circumscription were a tropical and subtropical family, now also include the temperate families Aceraceae and Hippocastanaceae (Judd *et al.*, 2007).

(25) Icacinaceae: In its traditional circumscription, this family was found to be widely polyphyletic, and this was one of the reasons why the family could not be easily placed within the APG framework (APG, 2003). Icacinaceae s.s. appear to share relationships with the order Garryales, and the other discordant elements (no succulents included) have been found to belong either to the order Aquifoliales (Cardiopteridaceae, Stemonuraceae) or Apiales (Pennantiaceae) on molecular and morphological grounds (Karehed, 2001). According to Lens *et al.* (2008), the resulting restricted Icacinaceae are still not monophyletic but are composed of two clades, of which one is

probably closely related to Garryales, while the “*Icacina* group” (i.e. Icacinaceae *sensu strictissimo*; here belongs *Pyrenacantha* as the only genus with succulent taxa) probably takes a sister-group position to a clade that includes Gentianales, Lamiales, and Solanales as part of the *asterids*. Consequently, APG (2009) list the family at the base of the whole lamiid clade.

(26) Boraginaceae: A family not normally considered to include succulent taxa, and thus not covered by *IHSP*. There are, however, a couple of taxa of *Heliotropium* with weakly expressed leaf succulence, probably influenced by saline habitat conditions. More research is necessary to establish their claim to succulence.

(27) Apocynaceae s.l.: In traditional classification systems, Apocynaceae s.s. (conforming to the subfamilies Rauvolfioideae and Apocynoideae below) were contrasted with Asclepiadaceae. The main difference was that Apocynaceae s.s. have free pollen, and Asclepiadaceae have pollen united into complex pollinaria. The Periplocoideae, either treated as a subfamily of Asclepiadaceae, or accepted as segregate family Periplocaceae, are somewhat intermediate and have agglutinated pollen placed openly on a flat-tish carrier. This traditional classification into three separate families is, however, not tenable according to all recent molecular phylogenies because Asclepiadaceae in the traditional circumscription is not a monophyletic clade due to the fact that Periplocoideae are derived from within Apocynoideae (Judd *et al.*, 2007). The broadened concept of Apocynaceae s.l. is widely accepted today (e.g., Endress & Stevens, 2001; Endress, 2002; Endress *et al.*, 2007). Endress *et al.* (2007) recognize five subfamilies: Rauvolfioideae (here belongs *Plumeria*), Apocynoideae (= Apocynaceae s.s.), Periplocoideae (as traditionally circumscribed), Secamonoideae (no succulents), and Asclepiadoideae (= Asclepiadaceae s.s.).

At the generic level, the classification of the family in general, and that of the Stapeliads (Asclepiadoideae – Ceropegieae) in particular, continues to be riddled with problems and uncertainties: *Brachystelma* has been found to be nested within *Ceropegia* in a recent study (Meve & Liede-Schumann, 2007), and all stem-succulent Stapeliads are nested in a highly derived position in *Ceropegia* (Meve & Liede, 2002; Meve & Liede-Schumann, 2007). Floral characters

(especially the architecture of the corona) have been widely used as important indicators of relationship, and were repeatedly employed to justify the topology of classifications. Evidence is growing, however, that floral architectures in general, and coronal structures in particular, are plastic and “evolutionary labile” (Wanntorp *et al.*, 2006 for *Hoya*; Krings *et al.*, 2008 for *Matelea* with a “dazzling array of floral variation”). Molecular studies indicate a rapid radiation for the core *Ceropegieae* (here belong all “Stapeliads”) with a very low rate of molecular divergence (Meve & Liede, 2002). The Stapeliads have been found to consist of a number of reasonably well-supported clades, but their topology remains largely unresolved (Meve & Liede, 2002). Meve & Liede (2002) also suggest major rearrangements in the “*Caralluma* complex” that deviate considerably from the treatment of *Caralluma* s.l. in *IHSP*. The circumscription of the widespread genus *Cynanchum* continues to be a challenge, and the inclusion of *Folotsia*, *Karimbolea*, *Platykeleba* and *Sarcostemma* by Liede & Meve (2001) and Liede & Täuber (2002) was regarded as premature by Rapini *et al.* (2003), but is now gaining acceptance (Goyder, 2008).

(28) Bignoniaceae: A family largely consisting of trees or lianas, not usually considered to include succulent taxa, and therefore not included in *IHSP*. Several taxa of *Argylia* do, however, have fleshy underground tubers, though their claim to succulence remains unverified.

(29) Plantaginaceae: Several recent molecular studies revealed that the traditional concept of Scrophulariaceae cannot be maintained because of vast paraphyly (Olmstead *et al.*, 2001), and the bulk of the former “scrophs” have been transferred to a completely recircumscribed Plantaginaceae and an expanded Orobanchaceae. None of these families is regarded as embracing succulents, but it appears that at least one species of Plantaginaceae, *Lophospermum* (*Asarina*) *rubescens*, has a moderately succulent underground caudex. The taxon remained untreated in *IHSP*.

(30) Solanaceae s.l.: The previously separate monogeneric family Nolanaceae has been found to be firmly derived from within Solanaceae subfamily Solanoideae. Solanaceae are incredibly variable as to fruit morphology; while the characteristic schizocarpic fruits of *Nolana* with their nutlet-like mericarps are unusual, all other characters are fully compatible with a placement in Solanaceae (Knapp, 2002). Within subfamily Solanoideae, *Nolana* is classified as monotypic tribe Nolaneae. According to Dillon *et al.* (2007), 89 species can be distinguished (versus 30 species treated in *IHSP*).

In addition to *Nolana*, succulence (in the form of fleshy leaves) also occurs in a couple of species of *Lycium* (also Solanoideae), which was not covered by *IHSP*.

(31) Goodeniaceae: This family is not usually considered to include succulent taxa, and is absent from *IHSP*. Some species of *Scaevola* (e.g. *S. plumieri* from the Indo-Atlantic region, *S. sericea* from the Indo-Pacific region) show distinctly fleshy leaves and have some claim to succulence, although they are at least facultative halophytes and their usual occurrence is along beaches and the sea-shore.

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Appendix 1. List of families with succulent representatives (and their assignment to orders), traditionally recognized and accepted in *IHSP*, but now according to APG (2003, 2009) subsumed under more broadly circumscribed taxa.

Family	Order	Accepted family
Aloaceae	Asparagales	→ Asphodelaceae
Asclepiadaceae	Gentianales	→ Apocynaceae
Bombacaceae	Malvales	→ Malvaceae
Chenopodiaceae	Caryophyllales	→ Amaranthaceae
Cochlospermaceae	Malvales	→ Bixaceae
Dracaenaceae	Asparagales	→ Rusceae
Hectorellaceae	Caryophyllales	→ Montiaceae
Nolanaceae	Solanales	→ Solanaceae
Nolinaceae	Asparagales	→ Rusceae
Sterculiaceae	Malpighiales	→ Malvaceae
Viscaceae	Santalales	→ Santalaceae