A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales

Authors: Patricia Hernández-Ledesma, Walter G. Berendsohn, Thomas Borsch, Sabine Von Mering, Hossein Akhani, et. al.
Source: Willdenowia, 45(3) : 281-383
Published By: Botanic Garden and Botanical Museum Berlin (BGBM)
URL: https://doi.org/10.3372/wi.45.45301
A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales

Abstract


DOI: http://dx.doi.org/10.3372/wi.45.45301

The Caryophyllales constitute a major lineage of flowering plants with approximately 12,500 species in 39 families. A taxonomic backbone at the genus level is provided that reflects the current state of knowledge and accepts 749 genera for the order. A detailed review of the literature of the past two decades shows that enormous progress has been made in understanding overall phylogenetic relationships in Caryophyllales. The process of re-circumscribing families in order to be monophyletic appears to be largely complete and has led to the recognition of eight new families (Anacampserotaceae, Kewaceae, Limeaceae, Lophiocarpaceae, Macarthuriaceae, Microteaceae, Montiaceae and Talinaceae), while the phylogenetic evaluation of generic concepts is still well underway. As a result of this, the number of genera has increased by more than ten percent in comparison to the last complete treatments in the “families and genera of vascular plants” series. A checklist with all currently accepted genus names in Caryophyllales, as well as nomenclatural references, type names and synonymy is presented. Notes indicate how extensively the respective genera have been studied in a phylogenetic context. The most diverse families at the generic level are Cactaceae and Aizoaceae, but 28 families comprise only one to six genera. This synopsis represents a first step towards the aim of creating a global synthesis of the species diversity in the angiosperm order Caryophyllales integrating the work of numerous specialists around the world.

Additional key words: flowering plants, Caryophyllales network, checklist, phylogeny, taxon concept, genus, World Flora Online, EDIT Platform for Cybertaxonomy

General e-mail address for correspondence: caryophyllales@bgbm.org

1 Botanic Garden and Botanical Museum Berlin (BGBM), Freie Universität Berlin, Königin-Luise-Str. 6–8, 14195 Berlin, Germany.
2 Current address: Laboratorio de Genética Molecular y Ecología Evolutiva, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Campus Aeropuerto, Querétaro, Qto. 76140, Mexico.
3 Institut für Biologie, Systematische Botanik und Pflanzengeographie, Freie Universität Berlin, Altensteinstr. 6, 14195 Berlin, Germany.
4 Department of Plant Sciences, School of Biology, College of Science, University of Tehran, P.O. Box 14155-6455, Tehran, Iran.
5 Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Circuito exterior s.n., Ciudad Universitaria, Ap. postal 70-614, México D.F. 04510, Mexico.
6 Jardín Botánico de Villa Clara, Universidad Central “Marta Abreu” de Las Villas, Facultad de Ciencias Agropecuarias, Carretera de Camajuani km 5½, Santa Clara, Cuba.
7 Sukkulenten-Sammlung Zürich, Mythenquai 88, CH-8002 Zürich, Switzerland.
8 Department of Biological and Environmental Sciences, University of Gothenburg, Box 461, SE-40530 Göteborg, Sweden.
9 Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Circuito exterior s.n., Ciudad Universitaria, Ap. postal 70-614, México D.F. 04510, Mexico.

(Addresses continued on next page)
**Introduction**

**Background**

Recent years have yielded a wealth of new informatics tools and infrastructures to facilitate working with taxonomic data. Searching and accessing the necessary literature and type specimens has become much faster and easier, thus stimulating research in plant systematics. Modern monographic work synthesizes knowledge on a group of organisms and generates, manages, and publishes high quality data as needed for a variety of applications. To be biologically meaningful and to allow correct identification especially at the species level, the entities recognized such as species or genera should as much as possible reflect the latest understanding provided by phylogenetic and evolutionary approaches (Marhold & al. 2013; Borsch & al. 2015; Naciri & Linder 2015). In order to achieve this, an integration of the ever-increasing number of phylogenetic and evolutionary studies and the data generated by them with formal monographic work is imperative. This requires the research process to be organized in a way that explicitly links data on characters and specimens with evolutionary results and taxon concepts, and that allows for continuous updating to reflect the continuous generation of knowledge (Borsch & al. 2015). At the same time there is now an increased awareness for the need of a comprehensive assessment of the species diversity on our planet as a basis for conservation and sustainable use (Lughada & Miller 2009; Paton 2009; Hendry & al. 2010).

**The Caryophyllales Global Synthesis Initiative**

We have started a joint initiative entitled “Global synthesis of species diversity in the angiosperm order Caryophyllales”. The idea was to develop a practical model for integrative monographic work that is based on a sizable group of world-wide occurring organisms. Our approach is to develop a network and an internet portal based on a collaborative approach of institutions and individual researchers studying various aspects of the diversity and evolution of the Caryophyllales. Major partners will function as focal points with a long-term institutional commitment that ensures sustainability of the initiative. At the moment the core partnership consists of: the Instituto de Biología, Universidad Nacional Autónoma de México – UNAM (Mexico); the Instituto de Botánica Darwinion (Argentina); and the Botanic Garden and Botanical Museum Berlin – BGBM (Germany). The BGBM is committed to support the coordination of the initiative and will provide the biodiversity informatics infrastructure. Apart from aiming at satisfying the general scientific and applied need for quality data, we specifically envision the application of the Synthesis in the context of plant conservation. One of the immediate outputs of the Caryophyllales synthesis will be an up-to-date taxonomic backbone for the World Flora Online as called for by the Convention on Biological Diversity’s Conference of the Parties (2012). Considering the enormous progress on understanding and describing Caryophyllales diversity that has been made in the past two decades and will continue into the future, and also the need to have full coverage of the diversity for the users, the approach will entail a mechanism to integrate new results as they become available (Borsch & al. 2015) and therefore to present the best possible treatment for any given taxon. A comprehensive review and treatment at the generic level is an important step that will then be extended to the species level and be complemented by descriptive and other information.

**Caryophyllales as a model group**

Reasons for choosing Caryophyllales as model group are diverse. The group is one of the major lineages of angiosperms with about 12,500 species. It is strongly supported as monophyletic by several molecular phylogenetic studies (Savolainen & al. 2000; Soltis & al. 2000; Cuenoud & al. 2002; Hilu & al. 2003; Brockington & al. 2009; Schäferhoff & al. 2009; Qiu & al. 2010; Soltis & al. 2011; Crawley & Hilu 2012).

The Caryophyllales are of great ecological and evolutionary interest because they show multiple origins of specialized morphological, anatomical, and biochemical traits. The order for example comprises the highest diversity of species with C₄ photosynthesis after the grasses (Sage & al. 2011). Several lineages are highly specialized with adaptations to extreme habitats such as xeric conditions, salinity, or nitrogen-poor soils, and thus the group includes many succulent, halophytic, gypsophilous and...
carnivorous plants. The Caryophyllales are the order with the highest number of halophytes containing more than 21% of all halophytic species (Flowers & al. 2010) and with the evolutionary oldest halophyte lineages (e.g. Kadereit & al. 2012a). The anatomy of Caryophyllales is also interesting because there are many wood features that are difficult to interpret (e.g. successive cambia, vessel elements perforation plates, ray anatomy, and raylessness; Carlquist 2010). In several families, pollen has evolved complex architectures and ultrastructures, based on the tricolpate pollen of the eudicots (Skvarla & Nowicke 1976; Nowicke 1994) with several Amaranthaceae exhibiting strongly derived metacectate pollen with the highest number of apertures known in angiosperms (Borsch 1998; Borsch & Barthlott 1998). Caryophyllales are characterized by a unique phenomenon of petal loss (Borsch 1998; Borsch & Barthlott 1998).

Furthermore, the order is relevant in the context of the Global Strategy for Plant Conservation and CITES by including groups of plants with many endangered species (e.g. Hunt 1999), most importantly Cactaceae, Drosaceae and Nepenthaceae. Species of economic importance include cereals and green vegetables (e.g. amaranth, quinoa, spinach, sugar beet), ornamentals (e.g. many Cactaceae and Caryophyllaceae species, carnivorous groups), noxious weeds (e.g. Alternanthera philoxeroides (Mart.) Griseb., Amaranthus spinosus L. and Mirabilis and Opuntia species), and of medical importance (mainly allergens; e.g. Amaranthus retroflexus L., Atriplex species, Kali turgidum (Dumort.) Guertem.).

The rapidly increasing number of fully sequenced genomes (currently five: two Chenopodiaceae, two Amaranthaceae and one Caryophyllaceae; http://www.ncbi.nlm.nih.gov/genome) and transcriptomes (66 species of Caryophyllales are included in the 1KP initiative; https://sites.google.com/a/ualberta.ca/onekp/home) opens new exciting opportunities for evolutionary studies in this order.

Circumscription and phylogenetic relationships of Caryophyllales

Several pre-cladistic classification systems were proposed for the Caryophyllales (for a review until the 1990s see Cronquist & Thorne 1994). Rodman & al. (1984) were the first to evaluate the classification of Caryophyllales based on a cladistic analysis of morphological characters. They asserted the monophyly of the group and produced one of the first classifications based on a phylogenetic hypothesis (Table 1), even though this study was questioned with respect to its methodology and character selection (Gianassi & al. 1992). Subsequently, early molecular systematic studies (i.e. Rettig & al. 1992; Downie & Palmer 1994; Downie & al. 1997; Lledó & al. 1998) indicated the close relationship of the members of subclass Caryophyllidae (i.e. Caryophyllales, Plumbaginales and Polygonales sensu Cronquist 1981). Further studies (e.g. Albert & al. 1992; Chase & al. 1993) showed close phylogenetic relationships of Caryophyllidae with the carnivorous lineages Droseraceae and Nepenthaceae (Nepenthales sensu Cronquist 1981). Morton & al. (1997) found that the Madagascan Asteropeiaceae (Theales sensu Takhtajan 1987) and Physenaceae (described by Takhtajan 1985, but placed in Sapiidales) both belong to Caryophyllales. This placement of Asteropeiaceae was further supported by a morphological cladistic analysis (Luna & Ochotrena 2004). Other studies (e.g. Fay & al. 1997) clarified the placement of Rhabdodendraceae (Rosales sensu Cronquist 1981), Simmondsiaceae (previously placed in either Euphorbiaceae or Buxaceae; Tobe & al. 1992), Tamaricaceae and Frankeniaceae (Violales sensu Cronquist 1988). The suggested affinities of all these groups to Caryophyllales were examined by Nandi & al. (1998), with respect to the fit of morphological characters, who adopted the concept of “caryophyllids s.l.” for a clade including Caryophyllales sensu Cronquist (1981) plus most of the taxa mentioned above. Nandi & al. (1998) further showed that the Dioncophyllaceae (Theanae sensu Takhtajan 1987) and Ancistrocladaceae (Theales sensu Cronquist 1981) also belong to the carnivorous clade within the caryophyllids.

Based on a review of published molecular phylogenetic studies, the Angiosperm Phylogeny Group (APG 1998) considered 26 families to constitute the Caryophyllales with an expanded taxon concept. In this concept the order included all the families of the caryophyllids s.l. (Nandi & al. 1998) plus several family segregates such as Achatocarpaceae and Stegnospermataceae (segregated from Phytolaccaceae), Drosophyllaceae (segregated from Droseraceae) and Sarcobataceae (segregated from Chenopodiaceae). A molecular study by Savolainen & al. (2000) tested this circumscription and retrieved a well-supported clade. On their trees the authors annotated the families Halophytaceae (segregated from Chenopodiaceae) and Petiveriaceae (segregated from Phytolaccaceae).

Since then, further studies have improved the understanding of the phylogenetic relationships within...
the expanded Caryophyllales. The study by Cuénoud & al. (2002) based on 18S rDNA, rbcL, atpB, and partial matK sequences, was relevant in terms of its sampling, which included most of the families treated by Kubitzki & al. (1993) and Mabberley (1997), including Agdesti-daceae, Barbeariaceae and Gisekiaceae (segregated from Phytolaccaceae). Cuénoud & al. (2002) retrieved a well-supported Caryophyllales clade in most of their analyses, and one of their most relevant results was the detection of major subclades: the “core Caryophyllales” and “non-core Caryophyllales”. The core Caryophyllales included the traditionally recognized Caryophylalles (Cronquist 1981) and their segregated families; within this clade two subclades were retrieved, one is the “lower core Caryophyllales” including Achatocarpaceae, Aamaranthaceae s.l. (including Chenopodiaceae), Asteropoeiaceae and Caryophyllaceae, and the other is the “higher core Caryophyllales” including the rest of the traditional Caryophyllales and their segregated families. Within the “higher core Caryophyllales”, Cor-bichonia and Lophiocarpus (rbcL+matK analysis) were considered as separate lineages within Molluginaceae and Phyto- laccaceae, respectively. The “non-core Caryophyllales” clade also included two major subclades: one including Franken- iaceae, Plumbaginaceae, Polygonaceae and Tamaricaceae, and the other consisting of the carnivorous families Ancistrocladaceae, Dionc ophyllaceae, Draxonaceae and Nepenthaceae. The analysis of Cuénoud & al. (2002) resulted in inconclusive positions for Rhab- dodendraceae and Simmondsiaceae. In their combined tree, Rhabdodendraceae were recovered as sister to all Caryophylalles (100 % Bootstrap; BS), and Simmondsiaceae as sister to the core Caryophyllales (moderate BS), while in the analysis of matK (low BS), both taxa as sisters were recovered as sister to the core Caryophyllales.

The study by Hilu & al. (2003) based on matK also retrieved two moderately supported major clades: “Caryophyllales I” and “Caryophyllales II”, the former including the core Caryophyllales plus Simmondsiaceae and Rhabdodendraceae (expanded core Caryophylla- les). Within this clade two sister groups were recovered, “higher core I” and “higher core II”, one comprising Aizoaceae, Nyctaginaceae and relatives and the other Cactaceae, Portulacaceae, and relatives. The “Caryophyllales II” corresponded to the non-core Caryophylla- les of Cuénoud & al. (2002).

Schäferhoff & al. (2009) employed sequence data of the petD group II intron and matK and recovered the “caryophyllids” and “polygonids” as major clades with high confidence. The caryophyllids include the expanded core Caryophyllales, which in general correspond to the “Caryophyllales I” of Hilu & al. (2003). The polygonids correspond to the non-core Caryophyllales of Cuénoud & al. (2002) and Caryophyllales II of Hilu & al. (2003). Furthermore, Schäferhoff & al. (2009) described the Microteaceae (segregated from Phytophylaceae) with the sole genus Microtea, which they sampled for the first time in any molecular study. The study underscored the importance of a representative taxon sampling because Microtea was identified based on just two markers as an isolated lineage that together with the Simmondsiaceae is the successive sister to the rest of the caryophyllids.

Other recent authors mainly increased the number of characters analysed from the chloroplast. Brockington & al. (2009) using nine plastid genes from the single-copy region, the inverted repeat, and two nuclear genes, recovered the non-core Caryophyllales and core Caryophyllales clades with Rhabdodendraceae followed by Simmondsiaceae plus the clade Asteropoeiaceae–Physens- ceae as successive sisters of the rest of the core Caryophyllales. Within the core Caryophyllales, the authors designated the “globular inclusion” clade as the clade that corresponds to the “higher core Caryophyllales” of Cuénoud & al. (2002). Within this clade, they referred to the clade containing Cactaceae, Portulacaceae, and relatives as the “portulacaceous cohort” (an earlier-suggested name by Rodman & al. 1984, “cohort Portulacares”) and the lineage including Aizoaceae, Nyctaginaceae, and most parts of Physolaccaceae possessing raphides as the “raphide clade”. Soltis & al. (2011) used 17 genes (representing the three plant genomes) and came to results very similar to those of Schäferhoff & al. (2009) and Brockington & al. (2009).

Several phylogenetic studies have focused on the Port- tulacineae (= Cactinae/Portulacaceous cohort) (Applequist & Wallace 2001; Nyffeler 2007; Nyffeler & al. 2008; Ocampo & Columbus 2010). The most recent study by Nyffeler & Eggli (2010a) resulted in the disintegration of Portulacaceae, recognizing eight monophyletic families including the newly described Anacampserotaceae (segregated from Portulacaceae), the concept of Portulacaceae s.str. as a monotypic family, changes of the circumscription of some families (Didiereaceae), and the re-establishment and change of concept of others (Montiaceae and Talinaceae).

The family names Limeaceae and Lophiocarpaceae were published in 2005 (Hoogland & Reveal 2005) and 2008 (Doweld & Reveal 2008), respectively, based on phylogenetic data (e.g. Cuénoud & al. 2002) that were confirmed in later works (e.g. Schäferhoff & al. 2009; Brockington & al. 2009). In a similar way the Kewaceae were validated (Christenhusz & al. 2014) to accommo- date the second lineage of the biphyletic genus Hyper- telis that had been found outside of Molluginaceae s.str. (Schäferhoff & al. 2009; Brockington & al. 2011; Chris- tin & al. 2011) but in an isolated position sister to the raphide clade. The genus Macarthuria that was resolved in an isolated position as sister to the remainder of the core Caryophyllales (Brockington & al. 2011; Chris- tin & al. 2011) was accommodated in the new family Macarthuriaceae (Christenhusz & al. 2014).

In summary, our concept of Caryophyllales includes 39 families (Fig. 1; Table 1, 2). It is in line with the fami-
Fig. 1. Summary of the current knowledge on phylogenetic relationships in the Caryophyllales. Based on Cúenod & al. (2002), Brockington & al. (2009) and Schäferhoff & al. (2009). Branch widths shown as triangles indicate species richness in these clades. – = high support (95-100 BS/JK/PP), ‾ = medium support (75-94 BS/JK/PP), = low support (50-74 BS/JK/PP).
lies recognized by the APG III (2009) and Stevens (2001 onwards) but separates Agdestidaceae from Phytolaccaceae and Chenopodiaceae from Amaranthaceae and is updated by adding Kewaceae and Macarthuriaceae. In APG III (2009) Agdestis was included within Agdestidoideae (Phytolaccaceae) although its position as sister of Sarcobataceae obtained by Cuénoud & al. (2002) and Schäferhoff & al. (2009) supports the acceptance of the family described by Nakai (1942). APG III (2009) also recognized the Sarcobataceae. The Amaranthaceae are treated in a very wide sense in APG III (2009) including all Chenopodiaceae, merely reflecting that the two families form a monophyletic group (Cuénoud & al. 2002; Kadereit & al. 2003; Müller & Borsch 2005a), while the

Table 1. Circumscription of Caryophyllales in a phylogenetic context according to different authors. The names in bold represent changes in comparison to the previous concept. * = not at family level in APG; ** = different concept from APG III (2009) and Stevens (2001 onwards).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aizoaceae</strong></td>
<td>Aizoaceae Aizoaceae</td>
<td>Achatocarpaceae</td>
<td>Achatocarpaceae</td>
<td>Achatocarpaceae</td>
</tr>
<tr>
<td><strong>Amaranthaceae</strong></td>
<td>Amaranthaceae Amaranthaceae</td>
<td>Agdestidaceae*</td>
<td>Agdestidaceae*</td>
<td>Agdestidaceae*</td>
</tr>
<tr>
<td><strong>Ancistrocladaceae</strong></td>
<td>Ancistrocladaceae</td>
<td>Asteropeiaceae</td>
<td>Asteropeiaceae</td>
<td>Asteropeiaceae</td>
</tr>
<tr>
<td><strong>Barbenniaceae</strong></td>
<td>Basellaceae Basellace</td>
<td>Barbenniaceae</td>
<td>Barbenniaceae</td>
<td>Barbenniaceae</td>
</tr>
<tr>
<td><strong>Basellaceae</strong></td>
<td>Basellaceae</td>
<td>Basellaceae</td>
<td>Basellaceae</td>
<td>Basellaceae</td>
</tr>
<tr>
<td><strong>Cactaceae</strong></td>
<td>Cactaceae</td>
<td>Cactaceae</td>
<td>Cactaceae</td>
<td>Cactaceae</td>
</tr>
<tr>
<td><strong>Caryophyllaceae</strong></td>
<td>Caryophyllaceae</td>
<td>Caryophyllaceae</td>
<td>Caryophyllaceae</td>
<td>Caryophyllaceae</td>
</tr>
<tr>
<td><strong>Chenopodiaceae</strong></td>
<td>Chenopodiaceae</td>
<td>Chenopodiaceae</td>
<td>Chenopodiaceae**</td>
<td>Chenopodiaceae**</td>
</tr>
<tr>
<td><strong>Didiereaceae</strong></td>
<td>Didiereaceae</td>
<td>Didiereaceae</td>
<td>Didiereaceae</td>
<td>Didiereaceae</td>
</tr>
<tr>
<td><strong>Dioncophyllaceae</strong></td>
<td>Dioncophyllaceae</td>
<td>Dioncophyllaceae</td>
<td>Dioncophyllaceae</td>
<td>Dioncophyllaceae</td>
</tr>
<tr>
<td><strong>Droseraceae</strong></td>
<td>Droseraceae</td>
<td>Droseraceae</td>
<td>Droseraceae</td>
<td>Droseraceae</td>
</tr>
<tr>
<td><strong>Drosofyllaceae</strong></td>
<td>Drosofyllaceae</td>
<td>Drosofyllaceae</td>
<td>Drosofyllaceae</td>
<td>Drosofyllaceae</td>
</tr>
<tr>
<td><strong>Frankeniaceae</strong></td>
<td>Frankeniaceae</td>
<td>Frankeniaceae</td>
<td>Frankeniaceae</td>
<td>Frankeniaceae</td>
</tr>
<tr>
<td><strong>Gisekiaceae</strong></td>
<td>Gisekiaceae</td>
<td>Gisekiaceae</td>
<td>Gisekiaceae</td>
<td>Gisekiaceae</td>
</tr>
<tr>
<td><strong>Halophytaceae</strong></td>
<td>Halophytaceae</td>
<td>Halophytaceae</td>
<td>Halophytaceae</td>
<td>Halophytaceae</td>
</tr>
<tr>
<td><strong>Achatocarpaceae</strong></td>
<td>Molluginaceae</td>
<td>Molluginaceae</td>
<td>Molluginaceae</td>
<td>Molluginaceae</td>
</tr>
<tr>
<td><strong>Basellaceae</strong></td>
<td>Nepenthaceae</td>
<td>Nepenthaceae</td>
<td>Nepenthaceae</td>
<td>Nepenthaceae</td>
</tr>
<tr>
<td><strong>Cactaceae</strong></td>
<td>Nyctaginaceae</td>
<td>Nyctaginaceae</td>
<td>Nyctaginaceae</td>
<td>Nyctaginaceae</td>
</tr>
<tr>
<td><strong>Phytolaccaceae</strong></td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
</tr>
<tr>
<td><strong>Plumbaginaceae</strong></td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
</tr>
<tr>
<td><strong>Polygonaceae</strong></td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
</tr>
<tr>
<td><strong>Portulacaceae</strong></td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
</tr>
<tr>
<td><strong>Rhabdodendraceae</strong></td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
</tr>
<tr>
<td><strong>Simmondsiaceae</strong></td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
</tr>
<tr>
<td><strong>Steignospermataceae</strong></td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
</tr>
<tr>
<td><strong>Tamaricaceae</strong></td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
<td>Physenaceae</td>
</tr>
</tbody>
</table>
relationships of the major groups of Chenopodiaceae are still under debate. In this case, a merger resulting in a shift of family assignment for a major lineage of plants with many genera appearing in numerous studies in ecology, agriculture, and conservation had been promoted without robust phylogenetic data (see also respective family treatments).

For ease of recognition, we distinguish the two major Caryophyllales clades as caryophyllids and polygonids following Schäferhoff & al. (2009). The caryophyllids are the larger clade and include Simmondsiaceae and/or Rhabdodendraceae along with the core Caryophyllales (= Centrospermae). The polygonids include the “carnivorous clade” with Ancistrocladaceae, Dioncophyllaceae, Droseraceae, Drosophyllaceae and Nepenthaceae plus the Frankeniaceae + Tamaricaceae and Plumbaginaceae + Polygonaceae subclades (Fig. 1).

Rationale for a revised generic classification

More than twenty years have passed since the publication of the comprehensive treatment of the centrospermus families of Caryophyllales by several authors in “Families and genera of vascular plants” (Kubitzki & al. [eds.] 1993). There, 15 families are recognized in the order (Achatocarpaceae, Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Caryophyllaceae, Chenopodiaceae, Didiereaceae, Halophytaceae, Hectorellaceae, Molluginaceae, Nyctaginaceae, Physenaceae, Portulacaceae and Stegnospermaceae [= Stegnospermataceae]).

Ten years later the treatment was completed with the publication by Kubitzki & Bayer (2003), where the concept of “expanded Caryophyllales” was adopted, by now also treating Ancistrocladaceae, Asteropeiaceae, Dioncophyllaceae, Droseraceae, Drosophyllaceae, Frankeniaceae, Nepenthaceae, Physenaceae, Rhabdodendraceae, Simmondsiaceae, and Tamaricaceae. In addition to the treatments of these families, Cuénoud (2003) discussed the circumscription of the expanded Caryophyllales including Plumbaginaceae and Polygonaceae previously considered as separate orders by Kubitzki (1993b) and Brandbyge (1993), respectively. The two volumes edited by Kubitzki & al. (1993) and Kubitzki & Bayer (2003) represented the most inclusive generic treatment of the Caryophyllales with 675 genera in 27 families. In addition, there are even more comprehensive family-wide

Table 2. Comparison of the current treatment with the two volumes edited by Kubitzki & al. (1993) and Kubitzki & Bayer (2003) representing the so far most inclusive generic treatment of the Caryophyllales.

<table>
<thead>
<tr>
<th>Family</th>
<th>No. of genera (Kubitzki &amp; al. 1993; Kubitzki &amp; Bayer 2003)</th>
<th>No. of genera (present publication)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achatocarpaceae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Agdestidaceae</td>
<td>n.a.</td>
<td>1</td>
</tr>
<tr>
<td>Aizoaceae</td>
<td>127</td>
<td>125</td>
</tr>
<tr>
<td>Amaranthaceae</td>
<td>69</td>
<td>79</td>
</tr>
<tr>
<td>Anacampserotaceae</td>
<td>n.a.</td>
<td>3</td>
</tr>
<tr>
<td>Ancistrocladaceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Asteropeiaceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Barbeyiaceae</td>
<td>n.a.</td>
<td>1</td>
</tr>
<tr>
<td>Basellaceae</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Cactaceae</td>
<td>98</td>
<td>139</td>
</tr>
<tr>
<td>Caryophyllaceae</td>
<td>87</td>
<td>101</td>
</tr>
<tr>
<td>Chenopodiaceae</td>
<td>98</td>
<td>104</td>
</tr>
<tr>
<td>Didiereaceae</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Dioncophyllaceae</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Droseraceae</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Drosophyllaceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Frankeniaceae</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Gisekiaceae</td>
<td>n.a.</td>
<td>1</td>
</tr>
<tr>
<td>Halophytaceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Kewaceae</td>
<td>n.a.</td>
<td>1</td>
</tr>
<tr>
<td>Limeaceae</td>
<td>n.a.</td>
<td>1</td>
</tr>
<tr>
<td>Lophiocarpaceae</td>
<td>n.a.</td>
<td>2</td>
</tr>
<tr>
<td>Macarthuriaceae</td>
<td>n.a.</td>
<td>1</td>
</tr>
<tr>
<td>Microteaceae</td>
<td>n.a.</td>
<td>1</td>
</tr>
<tr>
<td>Molluginaceae</td>
<td>13</td>
<td>10</td>
</tr>
<tr>
<td>Montiaceae</td>
<td>n.a.</td>
<td>13</td>
</tr>
<tr>
<td>Nepenthaceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Nyctaginaceae</td>
<td>31</td>
<td>31</td>
</tr>
<tr>
<td>Physenaceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Phytolaccaceae</td>
<td>17</td>
<td>12</td>
</tr>
<tr>
<td>Plumbaginaceae</td>
<td>27</td>
<td>29</td>
</tr>
<tr>
<td>Polygonaceae</td>
<td>43</td>
<td>55</td>
</tr>
<tr>
<td>Portulacaceae</td>
<td>29</td>
<td>1</td>
</tr>
<tr>
<td>Rhabdodendraceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Sarcobataceae</td>
<td>n.a.</td>
<td>1</td>
</tr>
<tr>
<td>Simmondsiaceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Stegnospermataceae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Talinaceae</td>
<td>n.a.</td>
<td>3</td>
</tr>
<tr>
<td>Tamaricaceae</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>incertae sedis</td>
<td>5</td>
<td>1</td>
</tr>
</tbody>
</table>

Total          675     749
treatments including all genera and even species for the Aizoaceae (Hartmann & al. 2001a, b), Basellaceae (Eriksson 2007), Cactaceae (Hunt 2006) and Portulacaceae (Eggli 2002).


These and other molecular phylogenetic studies have resulted in the confirmation or rejection of monophyly in several taxa, and consequently in changes of their circumscription or status. Some of the re-established taxa are for example: Lymanbiasonia, Nyctiocereus (Cactaceae, Korotkova & al. 2010, Arias & al. 2005, respectively); Atocion, Eulianthe, Heliosperma (= Isoca), Viscaria (Caryophyllaceae, Oxelman & al. 2001); Lipandra, Oxybasis (Chenopodiaceae, Fuentes-Bazán & al. 2012b); and Afrobunichia (Polygonaceae, Sanchez & Kron 2009).

Taxa for which the circumscription had, or has, to be changed in order to accept them as monophyletic groups are for example: Arenaria (Caryophyllaceae, Harbaugh & al. 2010), Atocion (Caryophyllaceae, Frazier & al. 2009b), Atriplex (Polygonaceae, Schuster & al. 2011a, b), Austrocylindropuntia (Cactaceae, Ritz & al. 2012), Bassia (Chenopodiaceae, Kadereit & Freitag 2011), Beta (Chenopodiaceae, Kadereit & al. 2006b), Brunichia (Polygonaceae, Sanchez & Kron 2009), Chenopodium (Chenopodiaceae, Fuentes-Bazán & al. 2012b), Echinopsis (Cactaceae, Schlumberger & Renner 2012), Ferocactus (Cactaceae, Vázquez-Sánchez & al. 2013), Grayia (Chenopodiaceae, Zacharias & al. 2010), Hatiora (Cactaceae, Korotkova & al. 2011), Limoniastrum (Plumbaginaceae, Ledó & Crespo 2000), Lychnis (Caryophyllaceae, Oxelman & al. 2001; Popp & al. 2008), Mammillaria (Cactaceae, Bárcenas & al. 2011; Hernández-Hernández & al. 2011), Mesembryanthemum (Aizoaceae, Klak & al. 2007), Minuartia (Caryophyllaceae, Dillenberger & Kadereit 2014), Moehringia (Caryophyllaceae, Fior & Karis 2007), Opuntia (Cactaceae, Majure 2012), Pachycereus (Cactaceae, Arias & Terrazas 2009), Peniocereus (Cactaceae, Arias & al. 2005), Pfeiffera (Cactaceae, Korotkova & al. 2010), Polycarporn (Caryophyllaceae, Kool & al. 2007), Silene (Caryophyllaceae, Oxelman & al. 2001), Suada (Chenopodiaceae, Schütze & al. 2003), and Viscaria (Caryophyllaceae, Frazier & al. 2009b).

In addition, molecular phylogenies also have resulted in the identification and description of new taxa at all levels, for example: Anacampserotacea (Nyffeler & Eggli 2010a), Microtectaceae (Schäferhoff & al. 2009), Didierioideae, Portulacarioideae (Didereae, Applique & Wallace 2003); Blossfeldiae (Cactaceae, Butterworth 2006); Caribaeae (Nycitaginaee, Douglas & Spellenberg 2010); Eremogoneae (Caryophyllaceae, Harbaugh & al. 2010); Gymnopodoeae, Leptogoneae (Polygonaceae, Burke & Schenck 2011); Chenopodi­astrum (Chenopodiaceae, Fuentes-Bazán & al. 2012b); and Surreya (Amaranthaceae, Masson & Kadereit 2013).

The new data also demonstrate that developing a classification system for the order is a dynamic process. An updated backbone at the generic level serves to present the current state of knowledge. We believe that this is an important step because many projects or researchers are specifically dealing with certain genera. Building upon a generic-level backbone will increase the efficiency of implementing the next steps towards a synopsis at species level. For example, Oxelman & al. (2013) keep a dynamically updated classification of Sileneae online. The long-term aim is to provide a portal where taxonomic, chorologic, nomenclatural, and phylogenetic information can be retrieved, along with literature, DNA sequences and images. This resource can be a valuable subproject for infragenERIC and species-level taxonomy, and also for various other biological research projects where there is a strong need for a solid taxonomy based on phylogenetic relationships in Sileneae (e.g. Bernasconi & al. 2009). Such initiatives will be strongly supported by the Caryophyllales network, also by providing a sustained informatics infrastructure and a joint concept for future monographic work (Borsch & al. 2015). The published treatment of the genera of Caryophyllales, produced directly from an EDIT-Platform database, will provide a stepping stone for further refinement, also to encourage further research and participation in the network. Members of the Caryophyllales network will be able to correct and add to the information presented as it
Fig. 4. A: Caryophyllaceae: *Dianthus androsaceus* (Boiss. & Heldr.) Hayek, Greece, Mt Taigetos, 14 Jul 2007, photo by N. Turland.  
– D: *Chenopodium vulvaria* L., Germany, Botanischer Garten der Universität Mainz, Aug 2015, photo by G. Kadereit.  
Revised generic classification of Caryophyllales

Methodology and content

The names of genera listed follows the rules of nomenclature (McNeill & al. 2012) and the family assignments adhere to APG III (2009) and Stevens (2001 onwards), if not noted otherwise. Notes are added to many genera providing information about the current state of knowledge in terms of monophyly or phylogenetic relationships. The data management is effected by means of the EDIT Platform for Cybertaxonomy software suite (Berendsohn 2010; Berendsohn & al. 2011). In a first step, data from Names in Current Use 3 (Greuter & al. 1993) were imported. Additions and corrections were then incorporated particularly from Bittrich 1993b–d; Bittrich & Kühn 1993; Brandhyge 1993; Carolin 1993; Endress & Bittrich 1993; Kubitzki 1993a, b; Kühn 1993; Rohwer 1993; Sperling & Bittrich 1993; Townsend 1993; Dickison 2003; Gaskin 2003; Kubitzki 2003a–e; Porembski 2003; Porembski & Barthlott 2003; France 2003, and for Aizoaceae and Cactaceae, corrections were incorporated from Hartmann (2001a, b) and Hunt (2006) respectively; if not noted otherwise. Data cited include the generic name, its author citation and its nomenclatural reference, the name of the type species, selected synonyms (including all names listed in NCU-3; Greuter & al. 1993), and later publications with their respective nomenclatural data.

Author names are abbreviated in conformity with Brummitt & Powell (1992) and its updates online; titles of serials in the nomenclatural reference citations are abbreviated in conformity with Bridson & al. (2004) and the titles of monographs are abbreviated in conformity with Stafleu & Cowan (1976–1988) and their successors, except that all components start with capital letters.

The name of the type species follows NCU-3 (Greuter & al. 1993); for genera not treated there, the names were obtained from reviewing protologues, Index Nominum Genericorum (ING; Farr & Zijlstra 1996+), Tropicos (undated), or The International Plant Names Index (IPNI 2004+). To denote the taxon concept followed in the present publication, a “sec.” (secundum, following, according to; Stearn 1992) reference is given (see, e.g., Berendsohn 1997; Franz & Cardona-Duque 2013). This is a bibliographic citation of a (recent) paper or work giving the circumscription of the taxon (by means of a description, synonymy and/or details of the relationship to other taxa). In some cases, this is further discussed in a note, particularly with reference to the authors mentioned in the previous paragraph and later publications. The text of the following section, Classification, consists of direct output from the EDIT-Platform database.

Fig. 7. A: Sarcobataceae: Sarcobatus vermiculatus (Hook.) Torr., Germany, Botanischer Garten Berlin, 29 Aug 2015, photo by N. Turland. – B: Tamaricaceae: Tamarix ramosissima Ledeb., Azerbaijan, Borsch & al. 5461 (B, BAK), photo by T. Borsch.
Classification

The families and genera are listed in alphabetical order, with a single incertae sedis genus at the very end of the list. Each accepted name is given in bold and includes the standardized information mentioned above. The homotypic and heterotypic synonyms are listed according to the conventions in *Willdenowia*. Many names are followed by notes as mentioned above.

**Achatocarpaceae** Heimerl sec. APG (2009).

A small family comprising two genera and 16 species occurring in tropical America, from southeastern United States to South America (Medina 2009). Traditionally, the family has been included in *Phytolaccaceae* s.l., but its position as an independent lineage has been well supported by several molecular phylogenetic studies (Hilu & al. 2003; Schäferhoff & al. 2009; Brockington & al. 2009, 2011), which also showed that the family is more closely related to the *Amaranthaceae/Chenopodiaceae* clade rather than to *Phytolaccaceae*. *Achatocarpaceae* are characterized by having unisexual flowers, the gynoeicum with two connate carpels, unilocular ovaries with two styles and a single ovule, berrylke fruits and pollen with obscure pores (Martínez-García 1985; Lipscomb 2003).


*Phaulothamnus* A. Gray in Proc. Amer. Acad. Arts 20: 293. 1885 sec. Bittrich (1993b). – Type: *Phaulothamnus spinescens* A. Gray – Fig. 2A.

**Agdestidaceae** Nakai sec. Cuénoud & al. (2002).

A monotypic family distributed from southern United States to Nicaragua (Rohwer 1993a), introduced and naturalized in Florida and the Antilles and cultivated as ornamentals in South America (Medina 2009). Traditionally, *Agdestis* was placed in *Phytolaccaceae*, subfamily *Agdestioideae* (e.g. Rohwer 1993a; Stevens 2001 onwards; Nienaber & Thieret 2003), but several molecular phylogenetic studies have shown that it represents a well-supported independent lineage (Cuénoud & al. 2002; Hilu & al. 2003; Schäferhoff & al. 2009). These studies also showed a close but only moderately supported relationship of the family with *Sarcobataceae*. *Agdestidaceae* are climbers and characterized by paniculate inflorescences, semi-inferior ovaries and cypsela crowned by winglike sepals (Nienaber & Thieret 2003).


Monotypic; southern United States, Mexico, and Central America.

**Aizoaceae** Martinov sec. APG (2009).

The *Aizoaceae* have a worldwide distribution throughout the tropics and subtropics (Hartmann 2001a, b). However, the centres of diversity are in the southwestern part of Africa (Bittrich 1986; Jürgens 1986; Hartmann 1991). Relatively few genera occur outside of southern Africa, mainly those from subfamilies *Aizoioideae*, *Sesuvioidae* and *Tetragonioidae*. In contrast, *Mesembryanthemoideae* and *Ruschioidae* are largely restricted to southern Africa with few species found outside of this area (e.g. *Mesembryanthemum crystallinum* L., *M. nodiflorum* L. and *Carpobrotus*, *Delosperma*, *Diaphyma* and *Sarcocozia* species) (Hartmann 2001a, b).

The family consists predominantly of succulent (mostly leaf succulent), annual to perennial herbs, subshrubs or shrubs, with undifferentiated perianth or biseriate with petals of staminal origin, with mostly hygrochastic loculical fruits.


≡ *Didade* E. Mey. ex Harv. & Sond., Fl. Cap. 2: 472. 1862, nom. nud.


The *Aloinopsis* clade includes several small genera (ranging from one to six species), i.e. *Aloinopsis*, *Melanthes*, *Nanathus*, *Pleiospilos*, *Prevodesma*, *Rabiea* and *Tangumu* (Khak & al. 2013). The group is found outside the winter-rainfall region of South Africa. The status and generic placement of numerous species in this group has been subject to many changes. For example, the monotypic *Prevodesma* has been included in five different genera by different taxonomic treatments. *Aloinopsis*, *Nanathus* and *Rabiea* are particularly poorly known in terms of species delimitation.


A monotypic genus, which is endemic to the Little Karoo, South Africa. The placement of this genus as
sister to Cylindrophyllum remains statistically poorly supported (Klak & al. 2013).

**Antimima** N. E. Br. in Gard. Chron., ser. 3, 87: 211. 1930. – Type: *Antimima dualis* (N. E. Br.) N. E. Br.

A large genus of 96 species, which has never been revised. Most species were previously placed in Ruschia, but separated from the latter based on fruit characters. Hartmann (2001a) recognized five subgenera within Antimima, but did not indicate which species belong to which subgenus. The molecular study by Klak & al. (2013) suggests that Antimima is not monophyletic in its current circumscription. A detailed morphological and molecular study is needed to establish generic boundaries within the Antimima clade, in which several other smaller genera such as Brausia, Hammeria, Smicrostigma and Zeukotropium take part (Klak & al. 2013).


There are four species included in Arenifera (Hartmann 2001a). Since this group was not sampled by Klak & al. (2013), its phylogenetic position within the tribe Ruschieae remains uncertain.


= *Roodia* N. E. Br. in Fl. Pl. South Africa 2: 78. 1922.


= *Bolusanthemum* Schwantes in Gartenwelt 32: 514. 1928.

**Braunia** Schwantes in Gartenwelt 32: 644. 1928. sec. Hartmann (2001a). – Type: *Braunia neli* Schwantes – Fig. 2D.


A monotypic genus, from the Worcester-Roberton Karoo (South Africa). Its sister relationship to Bijlia (two species) remains poorly supported (Klak & al. 2013).

**Calamophyllum** Schwantes in Z. Sukkulantenk. 3: 15, 28. 1927 sec. Hartmann (2001a). – Type: *Calamophyllum tereifolium* (Haw.) Schwantes

A mysterious genus including three species. These were described by Haworth between 1795 and 1812. However, for two of the names no types have been selected yet, whereas for the third a drawing by Duncansan serves as a lectotype (Hartmann 2001a). The distribution of the genus is uncertain.


= *Tischleria* Schwantes in Sukkulantenk. 4: 78. 1951.


**Cheiridopsis** N. E. Br. in Gard. Chron., ser. 3, 78: 433. 1925 sec. Hartmann (2001a). – Type: *Cheiridopsis tuberculata* (Mill.) N. E. Br. – Fig. 2C.

Cheiridopsis was found to be closely related to Ihlenfeldia and Odontophorus (Klak & al. 2013). In addition, one of the three subgenera of Cheiridopsis, C. subg. Odontophoroides, could be more closely related to Odontophorus than to the remainder of Cheiridopsis (Hartmann 2001b). Although Che­ridopsis and Odontophorus were revised at species level (Hartmann 1976; Hartmann & Dehn 1987), their generic limits need to be reinvestigated.


A monotypic genus; its only species was already known to Linnaeus as *Mesembryanthemum serratum* L. The area where it was previously recorded has been subject to extensive cultivation, so the species had been thought to be extinct. However, it was rediscovered in 2007 and is currently considered as critically endangered (Klak & Low 2007). The hypanthium found in the flowers suggests a close relationship with Erepsia, where this species had been included previously (as *E. serrata* (L.) L. Bolus).

= *Dorotheanthus* Schwantes in Möller’s Deutsche Gärtn.-Zeitung 42: 283. 1927.

= *Aethephyllum* N. E. Br. in Möller’s Deutsche Gärtn.-Zeit. 43: 400. 1928.

= *Pherolobus* N. E. Br. in Möller’s Deutsche Gärtn.-Zeitung 43: 400. 1928.


= *Derenbergia* Schwantes in Z. Sukkulentenk. 2: 137. 1925.

= *Ophthalomphyllum* Dinter & Schwantes in Möller’s Deutsche Gärtn.-Zeitung 42: 64. 1927.

= *Herreanthus* Schwantes in Gartenwelt 32: 514. 1928.

= *Berresfordia* L. Bolus, Notes Mesembryanthemum 2: 313. 1930.


The genus includes eight species and is endemic to the Eastern Cape, South Africa. Its phylogenetic position near *Delosperma* has been confirmed (Klak & al. 2013), but the genus lacks a taxonomic revision.


*Cylindrophyllum* includes five species (Hartmann 2001a), but lacks a taxonomic revision.


*Cyselea* includes three species (Hartmann 2011a) and is nested within *Sesuvium* (Bohley & al. 2015; Hassan & al. 2005; Thulin & al. 2012). Two of the species are endemic to Paraguay and Cuba, respectively (Hartmann 2011a).


A large genus of 142 species, which has never been revised. The study by Klak & al. (2013) suggests that *Delosperma* is not monophyletic in its current circumscription. A detailed morphological and molecular study is needed to establish generic boundaries within the *Delosperma* clade, in which several other smaller genera, including *Corpuscularia*, *Ectotropis*, *Fritia*, *Mestoklema* and *Trichidiadema* take part (Klak & al. 2013).


The phylogenetic position of this monotypic genus remains largely unresolved (Klak & al. 2013).


A large genus of 107 species, which has only partly been revised. With the exception of few misplaced species, the genus is thought to be monophyletic (Klak & al. 2003b; Klak & al. 2013). Hartmann (2007) recognized eight subgenera in *Drosanthemum* and also provided a key to the subgenera with a list of species included for each of them. Although also distribution maps were included for all eight subgenera, no vouchers were cited (Hartmann 2007), so that it remains uncertain on which material the maps were based. In addition, only one of the eight subgenera has so far been revised in part (Hartmann 2008). Since many species are threatened by agriculture or urban expansion, the genus is in urgent need of revision.


*Eberlanzia* includes eight species (Hartmann 2001a). However, the two species sampled by Klak & al. (2013) do not group together, suggesting that the genus is not monophyletic in its current circumscription.


= *Cylindrophyllum* Schwantes in Möller’s Deutsche Gärtn.-Zeitung 42: 283. 1927.


A monotypic genus, which is endemic to Namqua-lland. Relationships to other members in the Conophytum clade remain uncertain.


A small genus with five species endemic to the Cape region of South Africa. See further notes under Hartmannia.


A monotypic genus from Namqualand. See further notes under Cephalophyllum.


This bitopic genus was found to be closely related to Delosperma (Klak & al. 2013). See further remarks under Delosperma.


= Imitaria N. E. Br. in J. Bot. 65: 348. 1927.


The monotypic Muiria was placed in Gibbaeum, as G. hortenseae (N. E. Br.) Thiede & Klak, sec. Goldblatt & Manning (2000). The species was confirmed to be closely related to Gibbaeum, but its relationship to other species in the genus remains unresolved (Klak & al. 2013).


The genus is endemic to Australia.


A small genus consisting of only three species. The two species included in the molecular study by Klak & al. (2013) were not resolved as sisters. However, they were shown to group with other small genera such as Braunsia and Esterhuysenia in the Antimima clade (Klak & al. 2013).


Hereroa includes 27 species but lacks a taxonomic revision. The study by Klak & al. (2013) reveals Rhombophyllum (five species) and Bergeranthus (ten species) as its closest relatives. Denser sampling may in addition show that Hereroa is not monophyletic, with Rhombophyllum likely to be nested within it. On account of the close morphological resemblance between these genera, generic limits need to be critically reinvestigated.


The two species currently included in Ihlenfeldidia were previously included in Cheiridopsis. However,
the two species were moved each into their own genus and thought to be closely related to *Tanquana* (three species) and *Vanheerdia* (two species), based on characters of the fruits (Hartmann 1992). However Klak & al. (2013) confirmed the previous position of *Ihlenfeldtia* as a close relative of *Cheiridopsis*, which is supported by characteristics of the leaves (Hartmann 1992). See further notes under *Cheiridopsis*.


= *Drosanthemopsis* Rauschert in Taxon 31: 555. 1982. Although *Jacobsenia* currently includes only three species, they were shown not to be monophyletic (Klak & al. 2013).


*Lampranthus* is a large genus of 194 species, which has never been revised. A molecular study of the *Lampranthus* group identified a core of closely related species, which makes up the current genus (Klak & al. 2003a). Groups of species not closely related to *Lampranthus* s.str. were placed in other genera, with some placed in new genera (Klak 2005).


A monotypic genus, which was shown to be sister to *Dinteranthus* (Klak & al. 2013), where it had been placed previously. The two genera form a clade together with *Lithops* and *Schwantesia* (Klak & al. 2013).


*Lithops* is one of the best-known genera among collectors of succulents. Species and subspecies are largely distinguished by the colour and markings present on the flattened leaf tops. The genus was shown to be closely related to *Dinteranthus*, *Lapidaria* and *Schwantesia* by Klak & al. (2013). In view of the close morphological resemblance between the four genera in terms of fruit and floral characters, it needs to be reinvestigated whether all of the genera should be maintained.


= *Hymenocylus* Schwantes in Möller’s Deutsche Gärtn.-Zeitung 42: 27. 1927.

The genus includes 16 species, but lacks a taxonomic revision. Since the group is rather homogenous, further sampling is likely to confirm the monophyly of the genus with the species currently included.


A new infrageneric classification has been proposed by Klak & Bryuns (2013). A broad generic circumscription for Mesembryanthemum has been reaffirmed and Mesembryanthemum subdivided into five subgenera, with all five shown to be monophyletic. Two species were recently reinstated and shown to form part of subgenus Volkanthus, which is sister to the remainder of Mesembryanthemum (Klak & al. 2014). Thus, Mesembryanthemum currently includes 105 species.


See notes under Delosperma.


Monilaria Schwantes in Gartenwelt 33: 69. 1929 sec. Ihlenfeldt (2001e). – Type: Monilaria chrysoleuca (Schltr.) Schwantes


A small genus including only two species. See further remarks under Stomatum.


Octopoma has been recognized by several authors (Hartmann 2001b) and Klak & al. (2013). However, the two infrageneric groups distinguished on account of differences in fruit morphology (Hartmann 2001b) were not confirmed by Klak & al. (2013).


See remarks under Cheiridopsis.


Orthopterum, comprising two species, is closely al­lied to Faucaria (Klak & al. 2013), from which it mainly differs by the repeatedly opening and closing fruits (Hartmann 2001b).


A monotypic genus from Namaqualand, which was shown to be closely allied to Jordanella and to Raschia sandbergensis L. Bolus (Klak & al. 2013). However, relationships to other members of the xero­morphic winter-rainfall clade remain in many parts poorly resolved.


A small genus of only three species, which was shown to be closely allied to Rhinephyllum (Klak & al. 2013), where all three species were previously placed.


A small genus including only two species. It is closely allied to Schlechteranthus (Klak & al. 2013), which also only incorporates two species. As indicated by the molecular analysis by Klak & al. (2013), the generic limits need to be critically reinvestigated.


A large genus including 206 species, for which no taxonomic revision has been compiled. Dehn (1993) recognized nine subgenera, of which only one has been studied further, Ruschia subg. Spinosaee (Salm-Dyck) Dehn (Hartmann & Stuber 1993). However, it has since been established that Ruschia is not monophyletic in its current circumscription (Klak & al. 2013). The clade in which species of Ruschia s.str. are found is still poorly resolved, so that relationships of species groups of current Ruschia remain uncertain. In addition, much denser sampling is required to establish monophyly and relationships of the subgenera of Ruschia and their relationship to other members of the xeromorphic winter-rainfall clade (Klak & al. 2013).


A monotypic genus, which resolved within the Conophytum clade (Klak & al. 2013).


Monotypic. Saphesia is an insufficiently known genus that needs further study to clarify its identity (Klak & al. 2015).


The genus consists of only two species, which are endemic to Australia.


A small genus of two species, which is endemic to Namquadaland. See further remarks under Polymita.


≡ Schwantasia ruuedebuschi Dinter


A small genus with two species, which was placed in a clade with two species of the polyphyletic Ruschia (Klak & al. 2013). A comprehensive revision of Ruschia should therefore also address the generic delimitation of Scopeloga.


The genus includes about 15 species; the exact number, however, is unknown and a taxonomic treatment is needed. Sesuvium contains an African clade consisting of C₄ species and an American clade consisting of C₃ species and a C₃ Sesuvium clade (Bohley & al. 2015). Sesuvium portulacatum (L.) L., which belongs to the American clade, is found along tropical and subtropical coasts.


Skiatophyllum forms part of the tribe Apatesiaceae, which consists of only 11 species. The tribe is considered to be monophyletic (Ihlenfeldt & Gerbaulet 1990; Klak & al. 2003b; Klak & al. 2015). Skiatophyllum includes only three species, which are endemic to the south-western Cape region of South Africa (Klak & al. 2015). Based on a recent phylogenetic study, Klak & al. (2015) proposed that the monotypic Caryotophora Leistner should be considered part of Skiatophyllum. In addition, it was shown that the lec-
totype and protologue of *Mesembryanthemum flacci-dum* Jacq. did not correspond to the species currently associated with this name, which was described as *S. flaccidifolium* Klak (Klak & al. 2015). The type of the monotypic *Saphesia*, which is *M. flaccidum*, was found to be an insufficiently known species.

**Smicrostigma** N. E. Br. in Gard. Chron., ser. 3, 87: 72.


A monotypic genus, which was shown to be closely related to *Zeukotrophymum* (two species) and *Octoptoma* p.p. (Klak & al. 2013). All three taxa are endemic to the Little Karoo, South Africa. The overall similarity between these taxa suggests that a broader generic concept should be adopted for this group of species.

**Stayneria** L. Bolus in J. S. African Bot. 27: 47. 1960 sec. L. – **Type:** *Stayneria littlewoodii* L. Bolus

A monotypic genus, which was found to be closely allied to parts of the polyphyletic genus *Ruschia* (Klak & al. 2013).

**Stoeberia** Dinter & Schwantes in Z. Sukkulentenk. 3: 14, 17. 1927 sec. Hartmann (2001b). – **Type:** *Stoeberia beetzii* (Dinter) Dinter & Schwantes


Hartmann (2001b) treated *Ruschianthemum* as a distinct genus with *R. gigas* (Dinter) Friedrich as the only species. However, the species had already previously placed in *Stoeberia* because of strong similarities; it differs mostly in its fruit morphology, which has traditionally played an important role in delimiting genera in *Aizoaceae*. However, fruit characters have recently been shown to be far more homoplasious than previously expected (Klak & al. 2013), suggesting that fruit morphology on its own does not justify the recognition as a distinct genus.

**Stomatium** Schwantes in Z. Sukkulentenk. 2: 175. 1926 sec. Hartmann (2001b). – **Type:** *Stomatium suaveolens* Schwantes


*Stomatium* currently includes 39 species, but lacks a taxonomic revision. It was shown to be closely related to *Chasmatophyllum* (eight species), *Mossia* (one species), *Neohenricia* (two species), *Peerstia* (three species) and *Rhinephyllum* (11 species) by Klak & al. (2013). Both *Chasmatophyllum* and *Rhinephyllum* also lack a taxonomic revision. All of these genera occur outside the winter-rainfall region of South Africa. The group shares a similar floral morphology, i.e. yellow or more rarely cream-coloured petaloid staminodes, absence of filamentous staminodes and a concavely shaped ovary wall. Over the past decades species have been shifted between genera since generic boundaries are poorly circumscribed.


Based on differences in fruit morphology, Hartmann & Liede (1986) excluded three species from *Pleiospilos* and established a new genus for them, *Tanguana*. However, its previously recognized close relationship to *Pleiospilos* was confirmed by Klak & al. (2013), and is also corroborated by leaf-morphological characters (Hartmann & Liede 1986).

**Tetragonia** L., Sp. Pl. 1: 480. 1753 sec. Hartmann (2001b) = *Ludolfia* Adans., Fam. Pl. 2: 244. 1763 = *Tetragonocarpus* Hassk. in Flora 40: 99. 1857. – **Type:** *Tetragonia fruticosa* L. – **Fig. 2B.**


**Titanopsis** Schwantes in Z. Sukkulentenk. 2: 178. 1926 sec. Hartmann (2001b). – **Type:** *Titanopsis calcarea* (Marloth) Schwantes


The genus belongs to *Sesuvioideae* and comprises about 28 species in two monophyletic clades, *T.* subg. *Trianthema* and *T.* subg. *Papularia* (Bohley & al. 2015). The latter has been revised by Hartmann & al. (2011). Nearly all species are *C*₄ plants: an exception is the *C*₃ species *T. ceratosepala* Volkens & Irmsch.

**Tribulocarpus** S. Moore in J. Bot. 59: 228. 1921 sec. Thulin & al. (2012). – **Type:** *Tribulocarpus dimorphantha* (Pax) S. Moore

*Tribulocarpus* belongs to the *Sesuvioideae* (Klak & al. 2003; Thulin & al. 2012) and is sister to the remaining genera of the subfamily, i.e. *Sesuvium* (incl. *Cypselea*), *Trianthema* and *Zaleya*. It is the only genus in the *Sesuvioideae* that includes only *C*₃ species.


The genus includes 32 species and is divided into two subgenera (Hartmann & Niesler 2013). The latter study as well as earlier studies appear to be largely based on the types of *Trichodiadema* (Niesler 1997),
since very little additional material (none from a South African herbarium) is cited as the basis for their taxonomic conclusions. Distribution ranges for the recognized species remain uncertain due to the lack of cited vouchers. In addition, monophyly of the genus needs to be reinvestigated in view its having been found nested among species of Delosperma (Klak & al. 2013).


A monotypic genus from the cost of Namaqualand. Its phylogenetic position within the xeromorphic winter-rainfall clade remains unresolved (Klak & al. 2013).


= Rocauma Forssk., Fl. Aegypt.-Arab.: 71. 1775. The genus is monophasic and belongs to Sesuvio-ideae, where it is sister to Sesuvium (Bohley & al. 2015). Zaleya is a C₄ genus and distributed in eastern Africa, southern Asia and Australia. It contains seven species (Hartmann 2011b).


Amaranthaceae Juss. sec. Müller & Borsch (2005). Amaranthaceae belong to a clade together with Chenopodiaceae. Support for the monophyly of the “Amaranthaceae–Chenopodiaceae alliance” is found consistently in all molecular phylogenetic analyses (Manhart & Retting 1994; Downie & al. 1997; Cuénoud & al. 2002; Kadereit & al. 2003; Müller & Borsch 2005a; Schäferhoff & al. 2009; Brockington & al. 2009). The family circumscription of the Amaranthaceae in the sense of Schinz (1893) was upheld by Townsend (1993) and confirmed as monophyletic with high statistical confidence by Kadereit & al. (2003) and Müller & Borsch (2005a). Following this concept the Amaranthaceae predominantly occur in tropical and subtropical regions with most of the species diversity in the Neotropics, eastern and southern Africa and Australia (Müller & Borsch 2005a, b; Sánchez-del Pino & al. 2009). Subfamily Gomphrenoideae has been revealed as monophyletic and nested within the Amaranthoideae and is characterized by unilocular anthers (Sánchez-del Pino & al. 2009) and metareticulate pol-


The genus *Alternanthera* is well supported as monophyletic in the current circumscription and is characterized by the presence of capitate stigmas and in most species also distinct androecial appendages that alternate with the filaments. The previously recognized genera do not represent natural entities except *Mogiphanes*, which is nested within one of the two major subclades of *Alternanthera* (Sánchez-del Pino & al. 2012).


The genus, with its more than 75 currently recognized species, is monophyletic and constitutes a C2 lineage (Sage & al. 2007) within the otherwise completely C3 amaranthoid clade (Müller & Borsch 2005a, b). Correct generic assignment has to await a comprehensive analysis of the achyranthoid clade.


The genus is not monophyletic as currently circumscribed because its two species, *Calicorema capitata* and *C. squarrosa* (Schinz) Schinz, appear in two completely different lineages of the achyranthoid clade (Müller & Borsch 2005a, b). Correct generic assignment has to await a comprehensive analysis of the achyranthoid clade.


The genus is probably monophyletic considering phylogenetic trees of Müller & Borsch (2005b) and Sage & al. (2007).


**Celosiae. Dendroportulaca** (formerly placed in *Portulacaceae*) has been shown to be referable to *Deeringia* and the only species, *Dendroportulaca mirabilis* Eggli, has been transferred there (Applequist & Pratt 2005).


**Eriostylos** C. C. Towns. in Kew Bull. 46: 237. 1991

**Froelichia** Moench, Methodus: 50. 1794 sec. townsend


**Gomphrena** L., sp. Pl. 1: 224. 1753 sec. townsend

r. e. fr. in ark. Bot. 16(13): 3. 1921 sec. moench, methodus: 50. 1794 sec. townsend

**Froelichia** Hook. in Icon. Pl.: 251. 1840 sec. clem-


≡ **Guilleminea** illecebra Kunt.


see notes under *Gossypianthus*.

**Hebanthe** Mart., Beitr. Amaran. 96. 1825 sec. Borsch


The genus was resurrected based on its very distinctive flower and pollen morphology by Borsch & Pedersen (1997) and also appears to be monophyletic based on molecular phylogenetic analysis (Sánchez-del Pino & al. 2009; Borsch & Pedersen 2011).


Monotypic and known from a single historical specimen (Pedersen 2000). Affinities are unclear but a placement within the gomphrenoid clade of *Gomphrhnioideae* (Sánchez-del Pino & al. 2009) is certain, where it shares a pollen morphology similar to *Pfaffia*.


**Polycnemoideae. Hemichroa** consists of only one species; two further species have been segregated as *Surreya* (see there for details; Masson & Kadereit 2013). The succulent halophyte *H. pentandra* R. Br. is endemic to Australia. It is sister to *Surreya* (Masson & Kadereit 2013).


≡ *Dicraurus* Hook. f., Gen. Pl. 3(1): 42. 1880.

The genus is monophyletic (Sánchez-del Pino & al. 2009; Borsch, Flores Olivera, Zumaya & Müller, in review) with approximately 45 species all of which are characterized by *Irsine*-type pollen (Borsch 1998). The two species formerly classified as *Dicraurus* on the base of alternate and not opposite leaves are nested within the *Irsine* clade, confirming the merger by Henrickson & Sundberg (1986). Their dense indumentum with branched trichomes appears to be an adaptation to the dry habitats of northern Mexico.


**Polycnemoideae. Nitrophila** consists of four (to eight) species distributed in western North America and South America, and the genus represents a classical example of an amphitropical desert disjunction (Masson & Kadereit 2013). *Nitrophila* shows leaf anatomical adaptations to physiological drought.


The genus was resurrected by Pedersen (1997) under Trommsdorffia Mart., a later homonym of Trommsdorffia Bernh. (Compositae; Holub 1998). Pedersenia is well supported as monophyletic (Borsch & al. 2011).


= Blutaparon Raf., New Fl. 4: 45. 1838.
The genus name was lectotyfified by Standley (1917) using an Australian species, P. conicus R. Br. (= Gomphrena conica (R. Br.) Spreng.). Palmer (1998) accepted G. conica along with the other Australian species of Gomphrena and indicated that this is a rare species that grows in sandy soils close to coasts. Considering this, Philoxerus would have to be a synonym of Gomphrena. The problem is that Hooker (1880, Genera plantarum) kept the genus name Philoxerus separate from Gomphrena and, rather than using morphological characters, applied a genus concept for Philoxerus to comprise Gomphrena species of coastal habitats in America, Africa and Australia. This is practically upheld in the genus concept of Blutaparon Raf. (Townsend 1993), with four coastal species, although Townsend did not even cite the name Philoxerus. Mears (1982a, b) argued that Philoxerus had been used for the American coastal species, so he actually looked for a name that would define a genus of coastal species based on the American coastal plants originally described by Linnaeus as G. vermicularis. What Mears overlooked is that G. conica also appears to be a coastal plant (Palmer 1998), so that Bentham’s 1880 generic concept of a gomphrenoid genus of coastal plants under the name Philoxerus would actually have been correct with five and not four species. Strictly applying such a genus concept to formal nomenclature, Blutaparon is a synonym of Philoxerus. However, in the course of analysing evolutionary relationships it will have to be seen if the adaptation to coastal habitats correlates with other characters that could provide synapomorphies for circumscribing and maintaining a genus Philoxerus, and if these synapomorphies are shared by P. conicus and the other coastal species.

Pleuropetalum Hook. f. in London J. Bot. 5: 108. 1846 sec. Townsend (1993). – Type: Pleuropetalum darwinii Hook. f. – Fig. 2F.
Pleuropetalum is a member of Amaranthoideae. The genus is unusual in the family because of a higher stamen and carpel number (Eliasson 1988; Ronse De Craene & al. 1999).


Polycenemoeidae. The genus comprises six species distributed in Eurasia and northwestern Africa. It is sister to the rest of Polycenemoeidae (Masson & Kaderet 2013).


The genus is highly polyphyletic (Müller & Borsch 2005a, b). Correct generic assignment has to await a comprehensive analysis of the achyranthoid clade.

= Dipterantherum F. Muell. in South Sc. Record. 3: 281. 1883.
Pitolutus has been recovered as monophyletic in the current circumscription, with the species diversity the result of a rapid diversification in Australia (Hammer & al. 2015).


Polycnemoideae. The Australian Surreya comprises two species of subshrubs (Masson & Kadereit 2013).
A well-circumscribed monophyletic genus with two species that was long treated as part of a widely circumscribed genus Gomphrena Mart., but resurrected by Pedersen (1990) because of its morphological distinctness (gampetalous perianth, cauline leaves reduced to scales). Molecular phylogenetic analyses (Sage & al. 2007; Sánchez-del Pino & al. 2009) depicted Xerosiphon as an isolated lineage in the gomphroendae clade of subfamily Gomphrenoideae.
Anacampserotaceae Eggli & Nyffeler sec. APG (2009).
A family with three genera and around 36 species mainly distributed in the southern and eastern parts of Africa, but also found in North America, South America, and Australia (Nyffeler & Eggli 2010a). The species of this family are traditionally considered members of Portulaceae; however, molecular phylogenetic studies have shown that the traditional Portulaceae are not monophyletic (Hershkovitz & Zimmer 1997; Applequist & Wallace 2001; Nyffeler 2007; Nyffeleer & Eggli 2010a; Ocampo & Columbus 2010). Nyffeler & Eggli (2010a) proposed the segregation of the traditional Portulaceae into four families (Anacampserotaceae, Montiaceae, Portulacaceae and Talinaceae) based on morphological and molecular data. In this context, the Anacampserotaceae are recognized by their capsules with loculicidal dehiscence, endocarp valves forming a basket-like structure and seeds with testa layers separate from each other (Nyffeler & Eggli 2010a).
= Talinaria Brandegge in Zoe 5: 231. 1908.
Anacampseros with c. 34 herbaceous species distributed in Africa, Australia, North and South America, is the most diverse genus of Anacampserotaceae (Nyffeler & Eggli 2010a). Phylogenetic analyses recover this lineage as a derived monophyletic group with moderate statistical support (Nyffeler & Eggli 2010a).
Phylogenetic analyses recover the North American Talinus frutescens A. Gray, the only member of the genus, as the most basal member of Anacampserotaceae (Nyffeler & Eggli 2010a; Ocampo & Columbus 2010).
A monogeneric family comprising 18 species with a disjunct paleotropical distribution in western and central Africa and southeastern Asia (Rischer & al. 2005). The family includes only non-carnivorous plants characterized by having nuts, runinate endosperm and a gynoeceum partially inferior with a single ovule (Heubl & al. 2006).
Traditionally, the family was placed either in the order Theales (e.g. Thorne 1992) or Dilleniidae (e.g. Thorne 2000). However, the position of the family within Caryophyllales and its close relationship with the “partially carnivorous” Dioncophyllaceae (see there) was shown by the early molecular phylogenetic study of Nandi & al. (1998). These results were confirmed by subsequent studies (e.g. Meimberg & al. 2000; Cuénoud & al. 2002; Hilu & al. 2003; Brockington 2009, 2011; Schäferhoff & al. 2009; Renner & Specht 2011), which have also shown, with high support, that both Ancistrocladaceae and Dioncophyllaceae are part of the “carnivorous clade” of the Caryophyllales. Other studies focusing on the evolution of carnivory and relationships within this clade (e.g. Heubl & al. 2006; Renner & Specht 2011) suggest that the absence of carnivory in Ancistroclados hamatus (Vahl) Gilg can be explained as a complete secondary loss of this character.


Asteropeiaceae Takht. ex Reveal & Hoogland sec. APG (2009). A monogeneric family with eight species endemic to Madagascar (Kubitzki 2003). The genus was traditionally placed in Theales, either in its own family (e.g. Takhtajan 1987; Thorne 1992) or within Theaceae (e.g. Cronquist 1988). However, early molecular phylogenetic studies have shown the affinities of Asteropeiaceae within Caryophyllales and the close relationship with Physenaceae (e.g. Morton & al. 1997). These results were confirmed by subsequent studies (e.g. Cuénoud & al. 2002; Brockington 2009, 2011; Soltis & al. 2011). The clade Asteropeiaceae–Physenaceae is also well supported by wood-anatomical characters (e.g. Miller & Dickinson 1992; Dickson & Miller 1993; Carliqust 2006); some member species (with small circular alternate pits on vessels, vasicentric tracheids plus fibre tracheids, abaxial confluent diffuse parenchyma and predominantly uniseriate rays) have been proposed as synapomorphies to the family (e.g. Carliqust 2006).


Barbeuiaceae Nakai sec. APG (2009). A monotypic family restricted to Madagascar (Rohwer 1993). The family is characterized by ovaries consisting of two united carpels with two locules and by capsules (Rohwer 1993). Traditionally, the family was placed in Phytolaccaceae subfamily Barbeuioidae, but its position as an independent lineage has been supported by several molecular phylogenetic studies (Cuénoud & al. 2002; Hilu & al. 2003; Schäferhoff & al. 2009).


Basellaceae Raf. sec. APG (2009). Basellaceae are a small tropical and subtropical family native to the Americas, southeastern Africa, Madagascar and possibly Asia. The centre of diversity is in the Andes of northwestern South America, but the centre of origin may very well be in Africa. At present, four genera (Anredera, Basella, Tordonia, Ullucus) with a total of 19 species are recognized, most of them succulent vines occurring in dry habitats. Some species are cultivated, and one (Ullucus tuberosus Caldas) is an important high-Andean crop grown for its edible tubers.


= Siebena C. Presl in Isis (Okon) 21: 275. 1828, nom. nud.


A monophyletic group of species in Anredera corresponds to the previously recognized taxon Tandonia, but a formal recognition of Tandonia would make the remaining Anredera paraphyletic (Eriksson 2007).


= Gandola Raf., Sylva Tellur.: 60. 1838.

One species, B. paniculata Volkens, is morphologically deviating in Basella, and may be better placed in a genus of its own. A phylogenetic analysis based on morphological data gave inconclusive results regarding its placement (Eriksson 2007).


Cactaceae Juss. sec. APG (2009). Cactaceae comprise about 120 to 130 genera and some 1450 to 1870 species (Hunt 2006; Nyffeler & Eggli 2010b). Most species are highly modified perennial stem succulents which conserve water to survive temporary dry periods. Only some two dozen species of the genera Pereskia, Pereskiospis and Quiabentia have a shrubby or tree-like habit with more or less fleshy leaves. All species of the family bear characteristic spine clusters (i.e.
areoles), representing short shoots with leaves transformed into spines already at the stage of primordia. Some taxa are spineless and even lack areoles at maturity but all species bear areoles as seedlings. This characteristic is a true synapomorphy of the entire family. Cacti are native to the Americas, except for the widely distributed Rhipsalis baccifera (Sol.) Stearn that also occurs in tropical Africa, Madagascar, and on islands in the Indian Ocean. Several species from different lineages have been introduced worldwide as crop plants or ornamentals and have become naturalized, and are classified as invasive aliens in several areas, including Australia, southern Africa, and the Mediterranean. For a long time in the past, the classification in genera and suprageneric groups was based on form characteristics of vegetative and reproductive structures, culminating in the fine-grained classifications of Backeberg (1958–1962, 1966) or Buxbaum (1962) and Endler & Buxbaum (1974). Many of the highly modified structural features are associated with the succulent life strategy (e.g. Nyffeler & al. 2008), and hence provide particular challenges in the interpretation of a classification based on purported relationships. The consensus classification initiative as reported by Hunt & Taylor (1986) and subsequent papers helped to overcome the deviating systems (e.g. Nyffeler & al. 2010b), and therefore the transfer of Acanthocereus (Engelm. ex A. Berger) Britton & Rose (1938) to Astrophytum (Kunth) Borg in Conr. U. S. Natl. Herb. 12: 432. 1909 sec. Hunt (2006) = Cereus subsect. Acanthocereus Engelm. ex A. Berger in Rep. (Annual) Missouri Bot. Gard. 16: 77. 1905. – Type: Acanthocereus baxantiensis (Karw.) Borg = Monvillea Britton & Rose, Cactaceae 2: 21. 1920. Currently accepted as monotypic with A. tetragonus (L.) Britton & Rose (Hunt 2006), whereas all other names suggested in this genus are of uncertain application or were wrongly assigned to Acanthocereus. The molecular phylogenetic study of Arias & al. (2005) showed that Acanthocereus would need to be expanded to include Peniocereus subg. Pseudoacanthocereus Sánchez-Mej., but no new combinations have yet been published.


therefore segregated as a monotypic genus *Punotia* D. R. Hunt; see also there.  


= *Digitorebutia* Frič & Kreuz. ex Buining in Succulenta (Netherlands) 22. 1940.  

See notes under *Rebutia*.  

According to the molecular phylogenetic study of Mosti & al. (2011), *Aylostera* falls in two clades, *Aylostera* s.str. and *Mediolobivia* (incl. *Aylostera* speg.) (Frič ex Kreuz. & Buining) Mosti & Papini), which were recognized as subgenera by these authors. The genus is an excellent example for the notorious oversplitting prevalent in many cacti: Hunt (2006) (as *Rebutia* subg. *Rebutia*) accepted ten species, while Mosti & al. (2011) argued for 110 species.  


The genus contains only three species; two of them (*A. ritteri* and *A. hintonii* Glass & W. a. fitz maur.) have been found well supported as sisters to each other (Vázquez-Sánchez & al. 2013).  


The monotypic peculiar genus *Blossfeldia* is found as sister to the rest of the *Cactoideae* (Nyffeler 2002; Butterworth 2006).  


= *Seticereus* Backeb. in Kakt. And. Sukk. 1937: 37. 1937.  


*Borzicactus* is reinstated based on the results of Schlumberger & Renner (2012). Its circumscription has been the subject of some debate, as summarized by Bregman (1992). The exact delimitation of *Borzicactus* and the genera currently included or considered related to it is still unclear.  


Originally monotypic with *B. brasiliensis*. Majure & al. (2012) found good support for a sister-group relation of *Opuntia schickendantzii* F. A. C. Weber., and transferred this species to *Brasiliopuntia*.  


Monotypic; sampled by Korotkova & al. (2010) and resolved as sister to *Lymanbensonia*.  


= *Haseltonia* Backeb. in Blätt. Sukkulentenk. 1: 3. 1949.  


See under *Neobuxbaumia*.  


The broad circumscription of *Cleistocactus* as employed by Anderson (2001, 2005), and Hunt (2006) goes back to the *Cactaceae* consensus classification reported by Hunt & Taylor (1986), where the predominantly ornithophilous floral syndrome was used as a diagnostic character. Schlumberger & Renner (2012) found that *Cleistocactus* s.l. is polyphyletic — the monotypic *Cephalocleistocactus* was placed as sister to *Yungasocereus*, with *Cleistocactus* s.str. as sister to *Vatricania* next to *Weberbauerocereus*, and two terminals representing the former *Borzicactus* and *Loxanthocereus* were placed in the *Orocereus* clade, the former next to *Matucana* and the latter next to *Haageocereus*. Deciding whether *Cleistocactus* s.l. should be retained or split up is difficult, since sampling of the group and its possible sister taxa is still inadequate. The affiliation of *Loxanthocereus* with *Haageocereus* was seen earlier, and Nyffeler & Eggli (2010b) listed it as synonym of *Haageocereus*.


Plastid and nuclear ITS data so far provided inconclusive results for the placement of *Consolea* and its separation from *Opuntia*. *Consolea* was found to be imbedded in *Opuntia* by Griffith & Porter (2009) based on combined nuclear and plastid data. The plastid and nuclear data of Majure & al. (2012) supported the monophyly but were incongruent regarding the placement of *Consolea*: while plastid data resolved *Consolea* outside of *Opuntia* (BS=53%), nuclear ITS data resolve *Consolea* within *Opuntia* (BS=75%), yet both these placements receive only weak support. Support for a placement outside of *Opuntia* increased to 81% BS when only diploids were included in a combined nuclear and plastid analysis. Majure & al. (2012) pointed out that evolution in *Opuntia* and allies involves hybridization and allopolyploidization and that *Consolea* might be of allopolyploid origin, as indicated by the incongruent plastid and nuclear trees. Nevertheless, Majure & al. (2012) argued for recognizing *Consolea* as a genus distinct from *Opuntia* because of good support for its monophyly, the placement by combined plastid and nuclear data outside of *Opuntia* and unique morphological characteristics.


Recent floristic treatment by Hoffmann & Walter (2005).


Found as highly polyphyletic by Bárcenas & al. (2011), and as nested in *Mammillaria*. One core *Coryphantha* clade was resolved but only weakly supported as monophyletic (0.65 PP from Bayesian Inference). Vázquez-Sánchez & al. (2013) likewise found *Coryphantha* as polyphyletic, but not nested in *Mammillaria*; however, far fewer species were sampled therein. One maximally supported group was found that also contains *Neolloydia matehualensis* Backeb., while other *Coryphantha* species were found close to *Echinomastus* and *Escobaria*. As in the whole mammillloid clade, support for the relevant nodes is still weak and generic limits of *Coryphantha* need further evaluation. See also notes under *Mammillaria* and *Neolloydia*. Recent traditional monograph by Dicht & Lüthy (2003).


Monotypic; segregated from *Coryphantha* based on the results of Vázquez-Sánchez & al. (2013).


Griffith & Porter (2009) found no support for a monophyletic *Cumulopuntia*, but it was also not contradicted. *Cumulopuntia* was then confirmed as monophyletic by Ritz & al. (2012). *Cumulopuntia* falls in two clades in the molecular phylogeny, one consisting of *C. sphaerica* (C. F. Först.) E. F. An-
derson and related taxa from the W Andean slopes of Chile and Peru, characterized by forming dwarf shrubs with easily detachable stem segments, and another consisting of Cumulopuntia s.str., characterized by growth in often dense cushions, with firmly attached stem segments (Griffith & Porter 2009; Ritz & al. 2012). For the C. sphaerica clade, the generic name Sphaeropuntia was recently published, but its circumscription is not yet fully resolved, and it this thus better treated as synonym for the time being.


Griffith & Porter (2009) found no support for a monophyletic Cylindropuntia based on combined nuclear and plastid markers, while Bárěnas & al. (2011) found a monophyletic Cylindropuntia with high to maximal support based on plastid data only.


= *Aporocactus* Lem. in Ill. Hort. 7: misc. 67. 1860.


= *Chiapasia* Britton & Rose, Cactaceae 4: 203. 1923.

= *Nopalxochia* Britton & Rose, Cactaceae 4: 204. 1923.


= *Emorycactus* Doweld in Succulenta (Netherlands) 75: 270. 1996.


= *Kroenleinia* Lodé in Cact. Avent. Int. 102: 25. 2014. *Echinocactus* turns out to be paraphyletic in recent molecular studies (Bárěnas & al. 2011; Hernández-Hernández & al. 2011; Vázquez-Sánchez & al. 2013), with *E. grusonii* Hildm. resolved in a separate clade from the remaining four species, yet with only low support (Vázquez-Sánchez & al. 2013) or in a polytomy (Bárěnas & al. 2011). Vázquez-Sánchez & al. (2013) re-circumscribed *Echinocactus* to include only four species, excluding *E. grusonii* and also *E. polycephalus* Engelm. & J. M. Bigelow but did not suggest new generic assignment for these species. The generic name *Kroenleinia* was recently erected for *E. grusonii*, but it may be premature to accept this monotypic genus in view of the numerous unresolved or poorly supported topologies in the group.


*Echinocereus* was studied in detail and found as monophyletic by Sánchez & al. (2014) but excluding *E. pensilis* J. A. Purpus, which was resolved distant from *Echinocereus* and as sister to the *Stenocereus* group. Because *E. pensilis* had been regressed as a monotypic genus *Morangaya*, its reinstatement was suggested by Sánchez & al. (2014).


= *Chamaecereus* Britton & Rose, Cactaceae 3: 48. 1922.

= *Lobivia* Britton & Rose, Cactaceae 3: 49. 1922.


= *Setiechinopsis* (Backeb.) de Haas in Succulenta (Netherlands) 22: 9. 1940.

= *Acanthobivia* Backeb. in Cactaceae (Berlin) 1941(2): 76. 1942.

= *Pseudolobivia* (Backeb.) Backeb. in Cactaceae (Berlin) 1941: 76. 1942.

= *Reicheocactus* Backeb. in Cactaceae (Berlin) 1941(2): 76. 1942.


= *Leucocestele* Backeb. in Kakt. And. Sukk. 4: 1. 1953.

The present wide circumscription of *Echinopsis* goes back to the mid-1970s. First indications that this broad *Echinopsis* is polyphyletic were found by Lendel & al. (2006) and Ritz & al. (2007), and Schlump-
berger & Renner (2012) in their deeply sampled study indeed found vast polyphyly and paraphyly throughout most of the subtribe Trichocereinae. Species of Echinopsis were scattered over eight different clades and interspersed with species of Acanthocalycium, Arthroacereus, Borzicactus, Cephaloeleistocactus, Cleistocactus, Denmoza, Espostoa, Haageocereus, Harrisia, Matucana, Mili, Oreocereus, Oroya, Pygmaeeocereus, Rauchocereus, Samaipaticereus, Weberbauerocereus and Yangasocereus, all of which are part of a highly supported clade (100% BS). To transform their results into a formal classification of monophyletic genera is no easy task. It would entail either to further broaden an already very heterogeneous genus by including the genera mentioned above or to accept about a dozen segregates (valid generic names are at hand). Nevertheless, maintaining Echinopsis (sensu Hunt 2006) is rather not an option, as it is clearly polyphyletic and should be split up. The necessary new combinations are already available (Schlumpberger 2012); a fully revised generic circumscription is still to be published.


The number of species is in dispute, and the recent work of Donati & Zanovello (2011) recognizes about half a dozen species. So far only \textit{E. micromeris} sampled in a phylogenetic study (Vázquez-Sánchez & al. 2013), and found in an isolated position within the tribe Cactaeae.


The diminutive \textit{Eriosyce laui} Lüthy from northern Chile has been found to differ morphologically from the remaining taxa of \textit{Eriosyce} s.l. by Nyffeler & Eggli (1997), and was subsequently segregated as the monotypic genus \textit{Rimacactus}. As long as this segregation is not backed up by molecular data, it appears premature to accept the genus. Recent treatments by Kattermann (1994) and Hoffmann & Walter (2005; Chile).


Recent monograph by Gibson (1988a).


Vázquez-Sánchez & al. (2013) found \textit{Ferocactus} in its current circumscription to be vastly polyphyletic, and the same is true for \textit{F. sect. Bisnaga}. The \textit{Ferocactus} clade found by Vázquez-Sánchez & al. (2013) also includes the genera \textit{Glandulicactus}, \textit{Leuchtenbergia}, \textit{Stenocactus} and \textit{Thelocactus}, corroborating the results of a much less dense sampling by Hernández-Hernández & al. (2011). The \textit{Ferocactus} clade is morphologically characterized by pericarps with scales and ribbed stems, and Vázquez-Sánchez & al. (2013) suggested expanding \textit{Ferocactus} to embrace the genera just mentioned as the best taxonomic solution to make \textit{Ferocactus} monophyletic, yet \textit{Leuchtenbergia} is the oldest name of this assemblage and would have priority, unless the name \textit{Ferocactus} is conserved.


Monotypic; sampled by Vázquez-Sánchez & al. (2013) and resolved as sister to Aztekium.


See notes under Ferocactus.


= Corynopuntia F. M. Knuth, Kaktus ABC: 114, 410. 1936.


= Marenopuntia Backeb. in Desert Pl. Life 22: 27. 1950. *Corynopuntia* was included in *Grusonia* s.l. (Wallace & Dickie 2002; Anderson 2001, 2005; Nyyfeler & Eggl 2010b), then accepted as separate genus by Hunt (2006). Griffith & Porter (2009) argued for recognizing *Corynopuntia* as a distinct genus, and *Grusonia* as monotypic, although support for the monophyly of *Corynopuntia* was only 67% BS in their study. Their data also suggest that *Micropuntia* could be recognized as a separate genus. Bárcenas & al. (2011) did not find support for treating *Corynopuntia* separately from *Grusonia*, and in addition found no support for a monophyletic *Corynopuntia*; therefore, the circumscription of *Corynopuntia* still needs to be clarified.


Found as monophyletic at first by Ritz & al. (2007), then studied in more detail and confirmed as monophyletic by Meregalli & al. (2010). Demaio & al. (2011) conducted the most detailed phylogenetic study by sampling almost the whole genus and again confirmed the monophyly of *Gymnocalycium* with maximal support. Recent illustrated synopsis by Charles (2009).


Recent monograph by Calderón & al. (2007).


= Estevesia P. J. Braun in Kakteen And. Sukk. 60(3): 64. 2009.

*Harrisia* was confirmed as monophyletic by Franck (2012), with a revised infrageneric classification published shortly after (Franck & al. 2013a). The recently described genus *Estevesia* P. J. Braun was not included in any molecular study so far. It was provisionally placed in the synonymy of *Harrisia* by Nyyfeler & Eggl (2010b). For synopsis see Franck (2012); further phylogenetic studies see Franck & al. (2013b).


The circumscription of *Hatiorea* has been clarified recently. *Hatiorea* including *Rhipsalidopsis* as adopted by Barthlott (1987), Barthlott & Hunt (1993), Barthlott & Taylor (1995), Hunt (2006) and Nyyfeler & Eggl (2010b) was found to be polyphylectic (Calvente & al. 2011; Korotkova & al. 2011). *Hatiorea* should therefore be restricted to species with cylindrical stems, terete pericarps, and small yellow-orange or magenta flowers, corresponding to *Hatiorea* in the traditional sense. Accordingly, *Rhipsalidopsis* in its traditional circumscription should again be accepted at generic rank.


*Hylocereus* is morphologically very similar to *Selencereus*, and available phylogenetic studies as well as morphological and anatomical data so far suggest that the two genera could be merged (Hernández-Hernández & al. 2011; Bárcenas & al. 2011, Gómez-Hinostroza & al. 2014), but they still need to be studied more extensively before firm conclusions on their circumscription are possible.


In the second half of the 20th century, Lemaireocereus was referred to as a synonym of Pachycereus (see there) by Buxbaum (1961), Bravo-Hollis (1978), and Gibson & Horak (1978), based on similar floral morphology. Phylogenies based on molecular (Arias & al. 2003) and structural data (Arias & Terrazas 2006) consistently have revealed that Lemaireocereus is an early-diversified lineage within Pachycereinae. Lemaireocereus should be restricted to species with rounded ribs, terminal flowers with long hairs and bristles, fruit with irregular dehiscence, and red pulp (Arias & Terrazas 2009; Arias & al. 2012).


Several considerably different generic concepts have been suggested for Lepismium in the past 80 years. It was either recognized as monotypic for L. cruciforme (Vell.) Miq., e.g. by Britton & Rose (1923) or included into Rhipsalis (Schumann 1899; Vaupel 1925, 1926). Barthlott (1987) and Barthlott & Taylor (1995) redefined Lepismium based on the mesotonic branching as the main diagnostic character, but this circumscription was found to be polyphyletic by Nyffeler (2002) and Korotkova & al. (2010). Consequently, some of its species were transferred to Lymanbensonia and Pfeiffera by Korotkova & al. (2010). Recent monograph by Barthlott & Taylor (1995).


See notes under Ferocactus.


Segregated from Pereskia to include the northern clade; see note under Pereskia.


Lophocereus (including L. gatesi and L. schottii) was strongly recognized as a separate genus, restricted to the Sonoran Desert, by e.g. Lindsay (1963) and Bravo-Hollis (1978). Comparative studies carried out by Gibson & Horak (1978) showed that those species share morphological and anatomical characteristics with Pachycereus marginatus (DC.) Britton & Rose. However, other taxonomists preferred to include this genus and others (e.g. Backbergia, Lemaireocereus, Marginocereus, Mitroceereus, Pierocereus) in a broader genus Pachycereus (Barthlott & Hunt 1993; Hunt 2006). Phylogenetic studies based on structural (anatomy + morphology) and molecular data confirm that Lophocereus is monophyletic including three species (L. marginatus (DC.) S. Arias & Terrazas as sister to the remaining species). The genus represents a lineage within the subtribe Pachycereinae, but is not directly related to Pachycereus s.str. or Backbergia (see there; Hartmann S. & al. 2001, 2002; Arias & al. 2003; Arias & Terrazas 2006). A proposal to recognize this genus newly circumscribed (now going also beyond the Sonoran Desert) was conducted by Arias & al. (2012). Lophocereus now includes taxa characterized by cylindrical stems with basal branching, an apical fertile zone with areoles, and spines larger than those of the sterile zone, and two or more flowers per areole. The flowering zone is conspicuously modified in all three species (L. marginatus (DC.) S. Arias & Terrazas 2009; Arias & al. 2012). Structural changes in the fertile zone exist between several genera of Pachycereinae, including cephalium (e.g. Backbergia and Cephalocereus species), pseudocephalium (e.g. Lophocereus and Neobuxbaumia species) and intermediate forms. However, those structures are highly homoplastic and occur within several genera.


Butterworth & al. (2002) found L. williamsii as sister to Obregonia and L. diffusa (Croizat) Bravo as sister to Acharagma, yet both with only moderate support. In contrast, Lophophora williamsii and L. dif-
fusa were resolved as sisters with moderate support in the study of Vázquez-Sánchez et al. (2013), who also found high support for the sister relationship of Lophophora and Obregonia, justifying generic rank for both.


≡ Acanthorhalsis Kimmach in Cact. Succ. J. (Los Angeles) 55: 177. 1983, nom. illeg. Segregated from Acanthorhalsis (Kimmach 1984), but otherwise either assigned to Lepismium (Barthlott 1987; Barthlott & Taylor 1995; Anderson 2001, 2005) or to Pfeiffera (Hunt 2006). The molecular phylogenetic study of Korotkova & al. (2010) unexpectedly found the three species now assigned to Lymanbensonia to represent a highly supported isolated clade distant from either Lepismium or Pfeiffera. As this new clade contained the nomenclatural type of Lymanbensonia, this generic name was reinstated.


≡ Bartschella Britton & Rose, Cactaceae 4: 57. 1923.


≡ Mamillopsis Britton & Rose, Cactaceae 4: 19. 1923.

≡ Phelosperma Britton & Rose, Cactaceae 4: 60. 1923.

≡ Solisia Britton & Rose, Cactaceae 4: 64. 1923.

≡ Chilita Orcutt in Cactography 2. 1926.

≡ Porfuria Boed. in Z. Sukkulentenk. 2. 1926.


≡ Oehmea Buxb. in Sukkulentenk. 7: 17. 1951.


Mammillaria is the largest genus within Cactaceae, and numerous suggestions for infrageneric entities have been proposed, often then segregated as different genera; the different taxonomic concepts were summarized by Butterworth & Wallace (2004). Although several phylogenetic studies dealing with the genus and allies have been published, there are still many uncertainties that result from insufficient phylogenetic resolution and support. Mammillaria was studied in detail using data from the plastid rpl16 intron and psbA-trnH intergenic spacer by Butterworth & Wallace (2004), who sampled c. 4/5 of the accepted species, and Bárcenas & al. (2011) for trnKmatK compiled an even more extensive sampling. Mammillaria was also included in the phylogenetic studies of the tribe Cacteae by Butterworth & al. (2002) and Vázquez-Sánchez & al. (2013), though with much fewer species sampled. The first sequence data already hinted at a non-monophyly of Mammillaria (Butterworth & al. 2002), yet without support. The results of Butterworth & Wallace (2004), based on a detailed sampling, again suggested polyphyly of Mammillaria. The genera Coryphantha, Escobaria, Mammillloydia, Neolloydia, Ortegocactus and Pelecyphora were found nested in a maximally supported Mammillaria s.l. clade. Bárcenas & al. (2011) did not find sufficient support for a monophyletic Mammillaria, and Coryphantha (likewise polyphyletic), Escobaria and Ortegocactus were nested in different Mammillaria clades. Vázquez-Sánchez & al. (2013) found that Coryphantha and Mammillaria could be separate clades, yet Mammillaria was supported as monophyletic only in the parsimony tree (61% BS/78% JK), but not found as monophyletic by Bayesian Inference. A clade of Coryphantha incl. Neolloydia was maximally supported in the parsimony and Bayesian trees, but C. macromeris (Engelm.) Lem. fell outside that clade, suggesting that Coryphantha is likewise polyphyletic. Escobaria was found polyphyletic as well (Vázquez-Sánchez & al. 2013), but only few species have been sampled. The results of Vázquez-Sánchez & al. (2013) also provided some insights into generic limits in the whole assemblage, as well as taxonomic changes by segregating Cochemiea from Mammillaria, and Cumaria from Coryphantha. Mammillloydia was found nested in Mammillaria (Butterworth & al. 2002; Butterworth & Wallace 2004; Bárcenas & al. 2011; Vázquez-Sánchez & al. 2013), and
all authors argue *Mammilloydia* should therefore no longer be recognized at generic rank. The *Mammillaria* assemblage therefore remains one of the Cactaceae groups that need further detailed study. Some nodes were so far only weakly supported, and final conclusions regarding the monophyly and generic limits of *Mammillara* must await a more extensive sampling, especially for Coryphantha and Escobaria; only then will firm taxonomic and nomenclatural conclusions be possible.


Recent monograph by Taylor (1991); recent floristic treatment by Taylor & Zappi (2004). Cactus species are divided into several groups that need further detailed study. Some authors agree that the monotypic *Melocactus miquelii* is not contradicted by the currently available data.


= **Rooksbya** (Backeb.) Backeb., Cactaceae Handb. Kakteen. Pereskioideae Opuntioideae 4: 2015. 1960. Phylogenetic studies so far resolved *Neobuxbaumia* as closely related to *Cephalocereus* and *Pseudomitrocereus* (Arias & al. 2003; Arias & Terrazas 2006; Hernández-Hernández & al. 2011). However, these studies did not specifically focus on *Neobuxbaumia*, and its generic limits are therefore not yet firmly established. Arias & al. (2003) found *Neobuxbaumia* in a weakly supported polytomy with *Cephalocereus* and *Pachycereus fulviceps* (F. A. C. Weber ex Schumann) D. R. Hunt (= *Pseudomitrocereus*) as sister to both. The two *Cephalocereus* species were well supported as sister to each other, but could not be separated from *Neobuxbaumia* in any tree (Arias & al. 2003). Bár- cesas & al. (2011) and Hernández-Hernández & al. (2011) found *Neobuxbaumia* to be polyphyletic but the relevant nodes were weakly supported, therefore a monophyletic *Neobuxbaumia* is neither confirmed nor contradicted by the currently available data.


Found to be polyphyletic by Vázquez-Sánchez & al. (2013), with the type species sister to the rest of the mammillloid clade, but support <50%, while *N. mahuensis* Backeb. was nested in *Coryphantha* with maximal support.


= **Neocardenasia** Backeb. in Blätt. Sukkulentenk. 1: 2. 1949.


Monotypic; segregated from *Peniocereus* by Arias & al. (2005) because *N. serpentinus* was resolved distant from the *Peniocereus* clade.


See notes under *Lophophora*.

**Opuntia** Mill. in Gard. Dict. Abr., ed. 4: [974]. 1754 sec. Majure & al. (2012). – Type: *Opuntia vulgaris* Mill. – Fig. 3C.

= **Nopalea** Salm-Dyck, Cact. Hort. Dyck. (1849): 63-64, 233. 1850. *Opuntia* is the second-largest genus of the family Cactaceae. As in all species-rich Cactaceae groups, numerous different generic concepts with a varying number of segregate genera have been suggested for *Opuntia*. Both extensive splitting (e.g. Backebberg 1966) or lumping into a broadly defined *Opuntia* were put forward (Rowley 1958; Benson 1982). The first phylogenetic study by Wallace & Dickie (2002) based on the rpl16 intron found *Opuntia* in the broad sense to be polyphyletic. For the revised generic classification they presented based on their data, they argued for splitting *Opuntia*, because otherwise further genera (e.g. *Pereskioidea*, *Pterocactus*) were also nested within *Opuntia* and merging those would make *Opuntia* a
highly heterogeneous assemblage. Therefore, Wallace & Dickie suggested reinstating the earlier-proposed *Opuntia* segregates Austrocylindropuntia, Brasiliopun- tia, Consolea, Corynopuntia, Camulopuntia, Cylindropuntia, Grusonia, Maihueneiosps, Miquelopun- tia, Nopalea, Tephrocactus, and Tumilla. *Opuntia* s.str. was thus restricted to the taxa with flattened stems and reticulate pollen. This concept was entirely adapted by Hunt (2006), and largely by Nyffeler & Eggli (2010b), Griffith & Porter (2009), using data from plastid trnL-F and nuclear ITS, found *Opuntia* in this restricted sense to additionally include *Con- solea* and *Nopalea*, the clade including all these genera received 100% support, and both *Consolea* and *Nopalea* were also as monophyletic with 100%. The tree resolution, however, did not allow an immediate conclusion on the delimitation of these genera. *Nopalea* used to be separated from *Opuntia* s.str. because it differs primarily in its hummingbird-syndrome flowers. Nevertheless, it was repeatedly found to be nested in *Opuntia* (Wallace & Gibson 2002; Griffith & Porter 2009; Bárcenas & al. 2011; Hernández-Hernández & al. 2011; Majure & al. 2012) and is therefore no longer maintained as separate genus. The relationship of *Consolea* to *Opuntia* has remained more difficult to resolve, but available data suggest it is not part of *Opuntia* (see also notes under *Conso- lea*).


**Ortegocactus** Alexander in Cact. Succ. J. (Los Angeles) 33: 39. 1961 sec. Vázquez-Sánchez & al. (2013). – Type: *Ortegocactus macdougallii* Alexander Merging *Ortegocactus* into *Mammillaria* was proposed by Hunt & Taylor (1990) and Barthlott & Hunt (1993). The sole species, *O. macdougallii*, was first sampled by Butterworth & Wallace (2004) and found nested in *Mammillaria*, so the authors argued future transfer to *Mammillaria* may be justified, but must await further clarification of generic limits in this group. Vázquez-Sánchez & al. (2013) found *O. mac- dougallii* not nested in *Mammillaria*, but in a weakly supported polytomy in the mammillloid clade, suggesting maintaining it as a separate genus for the time being.


Phylogenetic studies based on morphological and molecular data show consistently that *Pachycereus* s.str. is a monophyletic group with five species (Arias & al. 2003; Arias & Terrazas 2006, 2009; Arias & al. 2012). Other species previously considered in *Pachycereus* (Buxbaum 1961; Gibson & Horak 1978; Anderson 2001; Hunt 2006; Nyffeler & Eggli 2010b) have been transferred to *Lemaireo- cereus*, *Lophocereus*, and *Pseudomitrocereus*. More inclusive and robust new evidence may corroborate or refute the current delimitation of these last genera. *Pachycereus* s.str. includes tree-like species, interareolar grooves on the stems, abundant trichomes on the flower, and flexible spines on the fruit. The genera *Backebergia* and *Pterocereus* (both monotypic) remain inconclusive on molecular data available (Arias & al. 2003; Hernández-Hernández 2011); therefore their recognition as separate genera remains premature. Recent monograph by Arias & Terrazas (2009).


**Pereskia** Mill. in Gard. Dict. Abr., ed. 4: [1026]. 1754 sec. Hunt (2006). – Type: *Pereskia aculeata* Mill. – Fig. 3D. = *Pereskia sect. Rhodocactus* A. Berger, Kakteen: 43. 1929 = *Rhodocactus* (A. Berger) F. M. Knuth, Nye Kaktsusbog: 102. 1930. *Pereskia* has been repeatedly found to be paraphyletic by Nyffeler (2002), Edwards & al. (2005), and Butterworth & Edwards (2008). The genus forms a grade at the base of the *Cactaceae*, with a northern clade including Mesoamerican and Caribbean pereskias as the first branching group followed by a southern clade, with mainly the Andean pereskias, which also include the nomenclatural type of *Pereskia* (Butterworth & Wallace 2005; Edwards & al. 2005). No nomenclatural changes to reflect the paraphyly of *Pereskia* were proposed by Edwards & al. (2005), who preferred their results to be tested with additional genes before suggesting a new classification for *Pereskia*. Also, no generic name was readily available for the northern *Pereskia* clade – the type of the earlier-proposed segregate *Rhodocactus* was in the southern clade together with the type of *Pereskia* itself. *Pereskia* was accepted as polyphylectic to reflect its morphological differences to the rest of the *Cactaceae*. Both *Pereskia* clades have characters that are interpreted as ancestral within *Cactaceae*, such as a woody stem, the presence of true leaves, a flower morphology that differs from the rest of the *Cactaceae* and *C3* photosynthesis. Only recently, the northern pereskias were segregated as *Leuenbergeria*, yet this segregation also received criticism because the two clades are hard to distinguish morphologically (http://www.mobot.org/MOBOT/research/Edge/apr13/april13lit.shtml; Hunt 2013). Seeking a compromise between molecular phylogenetic hypotheses and nomenclatural stability, Rowley (2013) suggested a subgenus *Leuenbergeria* (note the different spelling!) for the northern *Pereskia* clade. Monograph by Leuenberger (1986).


Recent monograph by Gibson (1988b).


Monotypic; *Pseudomitrocereus fulviceps* was previously included in *Pachycereus* or *Cephalocereus*, later elevated to generic rank as *Mitrocereus* (Backeb. 1942) and later *Pseudomitrocereus* (Bravo & Buchbaum, in Buxbaum 1961). Arias & al. (2003) found *P. fulviceps* to be unrelated to *Pachycereus* and instead as sister sister to a clade of *Cephalocereus* and *Neobuxbauma*. Therefore, *Pseudomitrocereus* was reinstated by Arias & al. (2012). *Pseudomitrocereus* is characterized by having distinct fertile stem parts, flowers completely covered with trichomes, and thick axial tissue (pericarpel and receptacle; Buxbaum 1961). Its inclusion in *Pachycereus* was supported by non-informative attributes (e.g. growth form), shared by other members of *Pachycereinae* (or *Echinocereinae* sensu Nyffeler & Eggli 2010b).

However, it is part of the clade “*Cephalocereus*” according to Arias & al. (2003), composed by *Cephalocereus*, *Neobuxbauma*, and *Pseudomitrocereus*. The species of this clade share the presence of prismatic crystals in the epidermis, inner stamens and nectarial chamber, while the fruit is dehiscent and the pulp is white (Arias & Terrazas 2006).


Recent monographs by Kimnach (1993) and Bauer (2003).


The sole species of this recently segregated genus, *Punotia lagopus*, was formerly placed in *Austrocyldropuntia*, but was recovered as sister to the remaining species of *Austrocyldropuntia* and *Cumulopuntia* by Ritz & al. (2012). It differs from *Austrocyldropuntia* in several characters, especially its growth form as flat, extensive cushions.


Suggested as synonym of *Haugeocereus* by Nyffeler & Eggli (2010b).


= *Lodia* Mosco & Zanovello in Bradleya 18: 44. 2000. Traditionally included in *Turbinicarpus* (see there); separated from it by Vázquez-Sánchez & al. (2013) after *Turbinicarpus* was found to be polyphyletic by them and previously also by Bárceanas & al. (2011). Recent monograph by Lüthy (2003).


The circumscription of *Rebutia* s.l. vs a suite of proposed segregates (including *Aylostera*, *Digitorebutia*, *Mediobovia*, *Sulcorebutia* and *Weingartia*) has been the subject of continued debate in the past 30 years. The wide circumscription (including these taxa) was adopted by Anderson & al. (2001) and Hunt (2006), but not by Anderson (2005), who recognized *Sulcorebutia* and *Weingartia*. The broad concept goes back to the consensus *Cactaceae* classification as summarized by Hunt & Taylor (1986), and some participants of the discussions at that time even argued that *Rebutia* sensu latissimo should be placed in the synonymy of an even more expanded *Echinopsis*. Recent molecular phylogenetic studies showed, however, that *Rebutia* does not belong in the *Echinopsis* clade (Ritz & al. 2007; Mosti & al. 2011; Schlumpberger & Renner 2012), and that the genus in this broad concept is an untenable polyphyletic assemblage, as first noted by Lendel & al. (2006). In
the molecular phylogeny of Ritz & al. (2007), three independent clades with taxa of Rebutia s.l. are found, namely “Rebutia I” (including the segregates Aylostera, Digitorubutia and Mediolumbvia), “Rebutia II” (conforming to Rebutia s.str.) and Weingartia (incl. Cinthia and Sulcorebutia). While Rebutia s.str. is placed as sister to Browningia, Aylostera is placed in a clade with Cereus and Stetsonia (Ritz & al. 2007; Mosti & al. 2011). Therefore it appears reasonable to abandon the concept of Rebutia s.l., to restrict Rebutia to the “true” rebutias, and to accept both Aylostera as well as Weingartia as separate genera. Most of the necessary new combinations have been published for Aylostera (Monti & al. 2011) and Weingartia (Hentzschel & Augustin 2008).

As explained under Hatiora, the inclusion of Rhipsalidopsis in Hatiora is not supported by recent molecular phylogenies. Calvete & al. (2011) found the two traditional Rhipsalidopsis species (R. gaertneri (Regel) Moran, R. rosea) are sister to Schlumbergera, but with moderate support. Korotkova & al. (2011), however, found Hatiora s.str., Rhipsalidopsis and Schlumbergera to form a grade, and even though support for this topology is also moderate, support for the monophyly of the three genera is maximal: therefore, Rhipsalidopsis (Easter cacti) is best kept as a clade with Schlumbergera and Euphorbia; but with moderate support. Korotkova & al. (2011). Recent annotated checklist by Barthlott & Taylor (1995, as Hatiora subg. Rhipsalidopsis (Britton & Rose) Barthlott).

The circumscription of Rhipsalis – one of the oldest genera of the family – has changed repeatedly over time, and often Hatiora, Lepismium and Pseudorhipsalis, all now accepted at generic rank, were variously subsumed under Rhipsalis. The morphology-based circumscription of Rhipsalis by Barthlott & Taylor (1995) has been entirely confirmed as monophyletic with maximal support in the molecular phylogenetic study of Korotkova & al. (2011); the same result was shown by Calvente & al. (2011b), though with a less comprehensive sampling. Rhipsalis is notable since R. baccifera (Sol.) Stearn is the only species of the family that naturally occurs outside the New World. Recent annotated checklist by Barthlott & Taylor (1995).

This monotypic genus has been found in a polyclomy with Brasiliopuntia + Tacinga and Opuntia s.str. (i.e. the platypuntioids) by Griffith & Porter (2009). The study of Majure & al. (2012) confirmed that Salmiopuntia is not part of Opuntia s.str.


= Zygocactus K. Schum., Fl. Bras. 4: 223. 1890.
Schlumbergera (Christmas cacti) is one of the best-known and one of the morphologically best-defined Cactaceae genera, recognizable by its flattened stems and bright pink zygomorphic flowers. Its monophyly was confirmed by the molecular phylogenetic analysis of Calvente & al. (2010) and Korotkova & al. (2011). Recent annotated checklist by Barthlott & Taylor (1995).

= Echinomastus Britton & Rose, Cactaceae 3: 147. 1922.
= Toumeya Britton & Rose, Cactaceae 3: 91. 1922, nom. illeg.
= Ancistrocactus Britton & Rose, Cactaceae 4: 3. 1923.
= Coloradoa Boissee. & C. Davidson in Colorado Cact. 54. 1941.
Confirmed as monophyletic by Butterworth & al. (2002) and Vázquez-Sánchez & al. (2013). The generic status and limits of Echinomastus need further evaluation because it was found to be polyphyletic by Vázquez-Sánchez & al. (2013). Revisions/monographs by Heil & Porter (1994) and Hochstätter (2005).


See notes under Ferocactus.


=Grisocereus Guiggi in Cactology 3(Suppl.): 1. 2012.


Recent treatments by Gibson (1991) and Arreola-Nava & Terrazas (2003).


Confirmed as monophyletic by Vázquez-Sánchez & al. (2013).


=Deamia Britton & Rose, Cactaceae 2: 212. 1920.


Tephrocactus was confirmed as monophyletic by Ritz & al. (2012). Recent monographs by Kiesling (1984) and Gilmer & Thomas (1998).


=Hamatocactus Britton & Rose, Cactaceae 3: 104. 1922.


See notes under Ferocactus.


Turbinicarpus has been found to be polyphyletic in the molecular studies of Bárcenas & al. (2011) and Hernández-Hernández & al. (2011). The most comprehensively sampled dataset of Vázquez-Sánchez & al. (2013) showed Turbinicarpus to fall into three separate clades. Turbinicarpus was re-circumscribed restricted to 11 species, while species with a tuberous root connected to the body with a long, thin neck are now segregated as Rapicactus based on these results. Two further species (T. horripilus (Lem.) V. John & Říha and T. pseudomacrochele (Backeb.) Buxb. & Backeb.) are outside the main Turbinicarpus clade (incl. Gymnocactus) and a new generic name would be needed for them. Recent treatments by Lüthy (2002) and Lüthy & Moser (2002).


Vatricania Backeb. in Cact. Succ. J. (Los Angeles) 22: 154. 1950 sec. Schlumberger & Renner (2012). – Type: Vatricania guentheri (Kupper) Backeb. Included in Espostoa s.l. by modern lexicographic treatments such as Anderson (2001, 2005) and Hunt (2006), the genus was found to be distant from the Espostoa in the Cleistocactus s.str. clade by Schlumberger & Renner (2012). Consequently, the monotypic Vatricania was suggested to be reinstated.


Recent monograph by Arakaki (2003).


Cintia Knüxe & Říha in Kaktusy (Brno) 31: 37. 1995.


Weingartia and Sulcorebutia used to be merged in Rebutia, e.g. by Barthlott & Hunt (1993), Anderson (2001), and Hunt (2006), but were recognized by Anderson (2005). The Rebutia s.l. assemblage was found highly polyphyletic by Ritz & al. (2007), and was shown to be separated into three well-supported clades. One of these clades comprises species of Cintia, Sulcorebutia and Weingartia and includes the nomenclatural type of Weingartia. Ritz & al. (2007) suggested that all three could be merged into a single genus, for which Weingartia is the oldest name.


A family of chiefly opposite-leaved herbs comprising about 100 genera and 3000 species. The family is widely distributed in north-temperate, montane and alpine areas with a centre of diversity in the eastern Mediterranean and Irano-Turanian regions, while presence in the tropics and the southern hemisphere is limited and mostly at higher elevations (Bittrich 1993c; Rabeler & Hartman 2005a). Several taxa (especially species of Dianthus, Gypsophila and Silene) are important in the horticultural trade, while others (e.g. Stellaria media (L.) Vill.) have become widely known weedy taxa. The number of genera included here is over 10% higher than most recent estimates (Bittrich 1993c; Rabeler & Hartman 2005a; Harbaugh & al. 2010), reflecting the results of recent molecular studies on large genera (especially Minuartia; Dillenberger & Kadereit 2014) as well as retention of several genera (e.g. Myosoton, Velezia and Xerotia) that may eventually disappear. The family is monophyletic as circumscribed by Bittrich (1993c), although the “traditional” division into three subfamilies (Bittrich 1993c; Pax & Hoffmann 1934) based on stipule, petal, sepal and fruit features does not provide monophyletic groups and should be replaced with the tribe-based scheme presented by Harbaugh & al. (2010) and confirmed by subsequent studies (e.g. Greenberg & Donoghue 2011).


Consists of about 60 cushion-forming subshrubby species of the subalpine steppe region in central to southwestern Asia (Bittrich 1993b; Ghaffari 2004). Pirani & al. (2014) showed that the genus is paraphyletic in this circumscription with Allochrusa, Diaphanoptera p.p., Ochotonophila and Scleranthopsis nested within it.


Monotypic genus; southwestern United States and Mexico. Hartman (2005a) noted that seed and flower characters suggest a close relationship to Scopolo­phia. Greenberg & Donoghue (2011) showed a similar result from molecular data.


Two to three species, probably native in the Mediterranean region, but widely spread as agricultural weeds and/or ornamentals. Several phylogenetic studies (Oxelman & Lidén 1995; Oxelman & al. 1997; Fior & al. 2006; Greenberg & Donoghue 2011) strongly support Agrostemma as a sister group to the rest of the tribe Sileneae.


Comprises seven species from southwestern Asia that are probably nested in Acanthophyllum (Pirani & al. 2014).


Four species in the eastern Mediterranean region east to Armenia. Closely related to Gypsophilea, but not yet sampled for DNA.

Arenaria L., Sp. Pl. 1: 423. 1753 sec. Sadeghian & al. (2015). – Type: Arenaria serpyllifolia L. – Fig. 3E.

Spergularastrum Michlx., Fl. Bor.-Amer. 1: 275. 1803.


About 160 species, in north-temperate areas, the Mediterranean, and Andean South America. Harbaugh & al. (2010), Greenberg & Donoghue (2011) and most recently Sadeghian & al. (2015) have sampled Are-
naria and, between their results, have removed about one-half of the species into four segregate genera not aligning in the same tribe as Arenaria. Sadeghian & al. (2015) found that four of the five remaining subgenera that McNeill (1962) recognized form Arenaria s.str., with the placement of A. subg. Dicranilla (Fenzl) F. N. Williams still unknown. While a few of the infrageneric groups recognized by McNeill (1962) are confirmed by molecular results (e.g. A. subg. Leiosperma McNeill, A. sect. Plinthine (Rchb.) McNeill), most are not.


Recently revised byFrajman & al. (2013), who recognized six, mostly European species. Well supported as monophyletic by several unlinked DNA sequence regions, and also as sister to Viscaria (Frajman & al. 2009b; see under Viscaria).

**Bolanthus** (Ser.) Rchb., Deut. Bot. Herb.-Buch: 205. 1841 sec. Bittrich (1993c) = *Saponaria* sect. Bolanthus Ser. in Candolle, Prodr. 1: 366. 1824. – Type: *Bolanthus hirsutus* (Labill.) Barkoudah – Fig. 3F. About 15 species in the eastern Mediterranean region, especially Greece and Turkey (Koç & Hamzaoğlu 2015). Closely related to Acanthophyllum and Gypsophila, but not yet sampled for DNA.


Monotypic; Himalayas, SE Asia. Likely near Arenaria and Moehringia; one rbcL sequence exists (Saslis-Lagoudakis & al. 2012), but has not been included in a phylogeny including these genera.


About 20 species in the Mediterranean region. Greenberg & Donoghue (2011) showed Bufonia as sister to the remainder of Sagineae (except for Drypis), while Dillenberger & Kadereit (2014) found it was an unsupported sister to a clade containing Minuartia s.str. and Mcneillia.


Monotypic; Mexico. Listed as a “doubtful genus” in the Caryophyllaceae by Bittrich (1993c).


Six species found from western North America south to Chile. Sosa & al. (2006) found Cardionema and Scopulophila clustered with Cerdia. Greenberg & Donoghue (2011) showed Cardionema belonging to a poorly resolved group of genera in the tribe Polygonaceae.


Includes 100 or, more likely, close to 200 north-temperate species, especially diverse in the eastern Mediterranean. The genus is in need of monographic study. The most recent infrageneric classification is presented by Schischkin (1936); even with corrected nomenclature and inclusion of extra-Russian taxa, it is not likely to be representative of relationships in the genus. Greenberg & Donoghue (2011) included 39 species of Cerastium in their study and found several interesting points. Cerastium subg. Dichodon (Bartl. ex Rchb.) Boiss. should be treated as a genus, Dichodon (see there), being a sister to Holosteam. As in Dianthus, resolution of the species was very poor, most species falling into either a polytomy of 11 species or one of 23. They also found Cerastium formed a clade within Stellaria. These genera are considered quite distinct by nearly all workers, so this must be investigated further.


Monotypic; endemic to Mexico. Placement within the Polygonaceae is probable (near Cardiomena and Scopulophila?), but Sosa & al. (2006) suggested that further study is needed. In a broader survey using a different voucher, Greenberg & Donoghue (2011) found Cerdia clustering near Drymaria.


Monotypic; western Mediterranean. Probably a close relative of Paronychia, but as yet not sampled for molecular phylogenetic analysis.


Originally including only *C. sedoides* found in mountains of Europe, but Dillenberger & Kadereit (2014) proposed expanding it to 19 species of Eurasia and western North America; Mosyakin suggests 23 to account for some additional eastern European taxa not yet transferred to Cherleria (S. Mosyakin, unpubl. data). Formerly included (with Pseudocherleria) in Minuartia sect. Spectabiles (Fenzl) Hayek, Dillenberger & Kadereit (2014) found the two groups segregated into different clades far from Minuartia s.str., proposing the recognition of both Cherleria and Pseudocherleria.


Comprises 20 species of cushion plants most diverse
in the southern hemisphere. The genus is monophyletic and a sister to *Sagina*.


Two species; deserts from NW India to NE Africa. Likely a member of *Polycarpaceae*, but the one available ITS sequence has not been included in a broader survey.


About 11 species. Harbaugh & al. (2010) and Greenberg & Donoghue (2011) both confirmed placement (with *Telephium*) in tribe *Corrigioleae*, near the base of *Caryophyllaceae*.


Monotypic; mountains of Greece and Turkey. Closely related to *Saponaria*, but not yet sampled for DNA.


Monotypic; Iran. Listed as a “doubtful genus” in the Caryophyllaceae.

**Dianthus** L., Sp. Pl. 1: 409. 1753 sec. Bittrich (1993c). – Type: *Dianthus caryophyllus* L. – Fig. 4A

With about 300 species, *Dianthus* is the second largest genus in the Caryophyllaceae. *Dianthus* is most diverse in southeastern Europe and southwestern Asia. No recent monographic work has been undertaken; the most comprehensive infrageneric classification is presented in Pax & Hoffmann (1934). Although Greenberg & Donoghue (2011) included 37 species in their analysis, virtually no resolution was found; 26 species formed a polytomy. May include Velezia (see there).


A genus of six species according to Schiman-Czeika (1988), but recent molecular phylogenetic analyses indicate polyphyly, with some species nested in *Acanthophyllum* (Pirani & al. 2014).


Monotypic; Canary Islands. A member of the *Polycarpaceae*, clustering with *Pteranthus* (Greenberg & Donoghue 2011).


Five species of the Arctic, central Europe, and Iran. Treated as *Cerastium* subg. *Dichodon* (Bartl. ex Rechb.) Boiss. in most recent works. Greenberg & Donoghue (2011) found that the two sampled species of *Dichodon* formed a clade sister to *Holostea*, and together formed a clade sister to *Cerastium + Moenchia*.


A genus of four or five Himalayan species. Most recently treated as a subgenus of *Arenaria* (McNeill 1962). Sadeghian & al. (2015) suggested the genus be again recognized after finding that the one sampled species clustered near *Eremogone*, either as a sister to *Silene* or between *Eremogone* and *Silene*. They also noted that the result reported by Greenberg & Donoghue (2011), showing *Arenaria przewalskii* Maxim. clustering with members of *Lepiodytis* and *Pseudostellaria*, suggests that *Dolophragma* may be polyphyletic.


About 30 species, all but two found only in the New World. Little is known about relationships within *Drymaria*. Duke’s (1962) preliminary revision, in which he described but did not validly publish 17 series, is the only recent comprehensive study. Greenberg & Donoghue (2011) included all four sampled taxa and show a poorly resolved, possibly polyphyletic genus.


Monotypic; eastern Mediterranean. Formerly placed in an isolated position within the Caryophylloideae. Molecular studies, including Harbaugh & al. (2010), Greenberg & Donoghue (2011) and Dillenberger & Kaderete (2014), place *Drypis* as sister to all other sampled taxa in tribe *Saginae*.


= *Brewerina* A. Gray in Proc. Amer. Acad. Arts 8: 620. 1873.

About 90 species, most diverse in eastern Asia and western North America. Harbaugh & al. (2010) confirmed the wide separation from *Arenaria* that Fior & al. (2006) reported. Broad sampling is still needed to resolve infrageneric relationships; existing information (Sadeghian & al. 2015) is not consistent with the extant classification (McNeill 1962) erected for these taxa in two subgenera under *Arenaria*.

Two western Mediterranean annual species, well supported as not belonging to the core Silene/Lythrum group (Oxelman & Lidén 1995; Oxelman & al. 1997; Oxelman & al. 2001).


Five species found in high mountains of Europe. Dillenberger & Kadereit (2014) found *Facchinia* to be both distant from *Minuartia* s.str. and a sister to the clade containing *Colobanthus* and *Sagina*.


Ten species, occurring from the Canary Islands east to Mongolia. Oxelman & al. (2002) found an expanded *Gymnocarpus* was monophyletic and sister to part of *Paronychia*.


About 50 species, most of them narrowly distributed endemics. *Herniaria* remains largely unsampled for DNA (four species in Greenberg & Donoghue 2011) and is likely to be closely related to *Paronychia* subg. *Anoplonychia* (Fenzl) Rchb.; see Oxelman & al. (2002) and Greenberg & Donoghue (2011).

**Holosteum** L., Sp. Pl. 1: 88. 1753 sec. Bittrich (1993c). – Type: *Holosteum umbellatum* L. Three to four species of temperate Eurasia. While Harbaugh & al. (2010) found that *Holosteum* and *Moenchia* were sister taxa, Greenberg & Donoghue (2011) found *Holosteum* and *Dichondra* to be sisters, with that clade a sister to the clade that include *Cerasium* and *Moenchia*.

**Honkenya** Ehrh. in Neues Mag. Aerzte 5: 206. 1783 sec. Bittrich (1993c). – Type: *Honkenya peploides* (L.) Ehrh. Monotypic; circumpolar in sandy coastal areas. Harbaugh & al. (2010) found *Honkenya* and *Wilhelmsia* are sister to each other and both are the closest relatives to the Hawaiian *Schiedea*.


Two species from tropical east Africa. Likely included in the Polycarpaceae, but not yet sampled for DNA.


Three species of central Asia. Sadeghian & al. (2015) found two species formed a clade sister to one including Odontostemma and Pseudostellaria.

Greenberg & Donoghue (2011) noted that L. holostoides clustered with Stellaria monosperma Buch.-Ham. ex D. Don.


Seven species of the Mediterranean, southwestern Asia, and western North America. Fior & al. (2006) and Harbaugh & al. (2010) both showed Loeflingia and Polycarpion clustering together; a result not shown in the Kool & al. (2007) study of Polycarpion.

Greenberg & Donoghue (2011) found it clustered in a poorly resolved clade including eleven other genera of Polycarpaceae.


= Hedona Lour., Fl. Cochinch. 1: 286. 1790.


= Uebelinia Hochst. in Flora 24: 664. 1841.

This circumscription, including around twenty species, is strongly supported as monophyletic (e.g. Popp & al. 2008; Greenberg & Donoghue 2011), with the African Uebelinia nested within. However, its relationships to Silene are not fully resolved (see under Silene).


Three species in Chile. Traditionally placed in Polycarpaceae, but not yet sampled for DNA.


About 54 species, chiefly in Mediterranean Europe and eastward into south-central Asia. While several molecular studies had shown Minuartia to be polyphylectic, Dillenberger & Kadereit’s (2014) study is the most comprehensive to date, including the first sequences for Minuartia sect. Minuartia. They found that the 96 species of Minuartia sampled belonged to ten different clades representing four different tribes. This circumscription restricts Minuartia to two of the twelve sections of Minuartia subg. Minuartia recognized by McNeill (1962).


Four species of the mountains of Turkey and Iran. Treated as Minuartia [sect. Lanceolatae (Fenzl) Graebn.] ser. Dianthifoliae Mattf. by McNeill (1962), Dillenberger & Kadereit (2014) found the sampled taxa forming an isolated clade that could be interpreted as sister to a clade that included Colanthus, Facchinia, Sabulina and Sagina.


A group of 25 north-temperate species. Fior & Karis (2007) found Moehringia could be made monophyletic by transferring four Iberian species to Arenaria.


Three species found in western and central Europe. While Harbaugh & al. (2010) noted that Moenchia and Holosteum were sister taxa, Greenberg & Donoghue (2011) found that Moenchia was a sister to Cerastium.


= Geocarpion Mack. in Torreya 14: 67. 1914.


Nine species of eastern North America. Dillenberger & Kadereit (2014) found Geocarpion was nested within a clade consisting of Minuartia sect. Uninerviae (Fenzl) Mattf.; that clade was sister to a clade containing Triplatea and three species of Stellaria on the basis of matK sequences.
Monotypic; temperate Eurasia. Treatment of the species as Stellaria aquatica L. may be warranted pending a serious review of Stellaria. It was found nesting near species of Stellaria sect. Stellaria by both Harbaugh & al. (2010) and by Greenberg & Donoghue (2011) in a study that more densely sampled Stellaria.


About 65 species of the Himalayas and adjacent southern China. Considered as a subgenus of Arenaria by many (e.g. McNeill 1962), Harbaugh & al. (2010) proposed, and Sadeghian & al. (2015) confirmed, that Odontostemma should be treated as a genus, clustering with Cerastium and Stellaria rather than Arenaria. Work on new combinations necessary for recognizing most species in Odontostemma is underway (R. Rabeler & W. Wagner, unpubl. data).


Monotypic; Italy and Iberian Peninsula. A member of tribe Polycarpaceae, but relationships vary in different studies. Fior & al. (2006) showed Ortegia in a cluster with Loeflingia and Polycarpus; Kool & al. (2007) reported Ortegia clustering with Cardionema and Illecebrum. Curiously, using the matK sequence from the Fior & al. (2006) study, both Harbaugh & al. (2010) and Greenberg & Donoghue (2011) found that Ortega clustered with a Hawaiian collection of Drymarnia cordata (L.) Willd. ex Schult. var. pacifica Mizush.


= Anychia Michx., Fl. Bor.-Amer. 1: 112–113. 1803.

In a study mainly addressing Gymnocarpus, Oxelman & al. (2002) found Paronychia to be polyphylectic, with the subgenera Paronychia and Siphononychia forming a strongly supported sister group to Gymnocarpus, whereas species in P. subg. Anoplonychia (Fenzl) Rchb. were found to be more closely related to Herniaria and Philippiella. This was confirmed by Greenberg & Donoghue (2011). The genus consists of 110 (Hartman & al. 2005) or more than 150 species (Bittrich 1993b). It is one of the large genera in the family that has not yet been extensively studied with DNA sequence data, especially in P. subg. Anoplonychia (Fenzl) Rchb. (only two of 48 species sampled).


Monotypic; Afghanistan. Presumed to be close to Scleranthus, but has not yet been sampled for DNA.


Endemic to the Iberian Peninsula, in particular the Pyrenees. Species-level taxonomy is controversial, with anything between one and 12 species (Cires & Prieto 2015) recognized. Phylogenetically, it occupies a position distinctly outside of the core Silenet Lychnis clade according to several putatively unlinked genes (e.g. Oxelman & Lidén 1995; Oxelman & al. 1997; Popp & Oxelman 2004), but the exact position varies, suggesting a possible ancient hybrid origin (Frajman & al. 2009a). Cires & Prieto (2015) confirmed the genus was monophyletic but noted that additional study was needed to resolve infrageneric relationships.


= Fiedleria Rchb., Icon. Fl. Germ. Helv. 6: 42. 1844.

Comprising 33 species, ranging from the Canary Islands east to Kashmir. Shown to cluster as sister to a clade including Dianthus and Velezia by Harbaugh & al. (2010), Greenberg & Donoghue (2011) and Pirani & al. (2014). The genus has not been widely sampled. Although kept separate by Bittrich (1993c), most recent treatments of the genus include Kohlrussia as a section in Petrochagia following the monograph of Ball & Heywood (1964). This may deserve further investigation since Greenberg & Donoghue (2011) cited three samples in their study; a voucher of "P. velutina Guss." (a later name for P. dubia (Raf.) G. López & Romo) was shown as a sister to a clade including P. saxifraga (L.) Link and a second voucher of P. dubia; the identification of the vouchers should be verified.


Monotypic; Patagonia. Oxelman & al. (2002) and Greenberg & Donoghue (2011) found P. patagonica

Monotypic; Turkey. Possibly related to *Gypsophila*, but not yet sampled for DNA.


Monotypic; central Asia to Himalayas. Possibly related to either *Psammosilene* or *Saponaria* (Bittrich 1993c), but not yet sampled for DNA.


Monotypic; eastern and southern Africa. Kool & al. (2012) placed *P. campesris* as sister to the monotypic *Sphaerocoma*; both genera form a clade that is sister to a clade containing *Polycarpaceae* and *Polycarpum*.


A paleotropical group of 50+ species. Kool & al. (2007, 2012) found it to be polyphylectic; additional sampling is required to treat the genus, resolve infrageneric relationships and decide how small genera (e.g. *Haya*, *Xerotia*) should be treated.


Monotypic; Mediterranean and western North America. Kool & al. (2007) found *Polycarpum* was polyphyletic with species distributed in three clades. Two of these included species of *Polycarpaceae* and were removed from *Polycarpum*. The third included members of the *P. tetrphyllum* group; tight relations in the remaining clade suggested reduction to one polymorphic species.


Monotypic; Angola. Placed in the *Polycarpaceae*, but not yet sampled for DNA.


Four species of central Asia. Most often treated as *Gypsophila* subg. *Macrorhiza*, but both Greenberg & Donoghue (2011) and Pirani & al. (2014) showed *P. muralis* as sister to a clade of *Dianthus* *Petrorhagia*, clearly separate from the remainder of *Gypsophila*.


Monotypic; in montane forests of Yunnan, China. Oxelman & Liden (1995) found *Psammosilene* to be sister to *Cerastium* in both Harbaugh & al. (2010) and Greenberg & Donoghue (2011) found it to be a sister to tribe *Caryophylloideae*, while Greenberg & Donoghue (2011) found the two groups segregated into different clades far from *Minuartia* s.str., proposing the recognition of both genera.


Monotypic; China. Presumed close to *Cerastium*, but not yet sampled for DNA.


Comprises 12 species found in the Caucasus region, arctic Asia and northwestern North America. Formerly included (with *Cherleria*) in *Minuartia* sect. *Pectabiles* (Fenzl) Hayek, Dillenberger & Kadereit (2014) found the two groups segregated into different clades far from *Minuartia* s.str., proposing the recognition of both genera.


A group of about 20 species, mostly in central Asia east to Japan, with one species in Europe and three in western North America. The few species thus far sampled cluster near *Lepidodiclis* and *Odontostemma*. Greenberg & Donoghue (2011) included four species and found the American *P. jamesiana* (Torr.) W. A. Weber & R. L. Hartm. did not cluster with the three Asian species; their report showing *Stellaria jamesiana* Torr. (= *P. jamesiana* (Torr.) W. A. Weber & R. L. Hartm.) clustering among *Cerastium* is based on a misidentified specimen of *C. arvense* L.

Monotypic; northern Africa east to Iran. A member of the Polycarpaceae, clustering with Dic eranthus (Greenberg & Donoghue 2011).


Segregation of Pycophyllis from Pycophyllum has been confirmed (M. Timaná, unpubl. data). Plettkeu may belong here.


Monotypic; Chile. Not yet sampled in a molecular study.


Monotypic; Chile. Not yet sampled in a molecular study.


Comprising c. 65 species (possibly 70, including some eastern European and western Asian taxa not yet transferred to Sabulina: S. Mosyakin, unpubl. data), all but two found in the northern hemisphere (Europe, Asia and North America). Including members of six sections of McNeill’s (1962) Minuartia subg. Minuartia as well as Stellaria fontinalis (Short & Peter) B. L. Rob., these species form a clade that is sister to a clade including Colobanthus, Facchinia and Sagina. Rabeler & al. (2014) suggested this clade may be further subdivided, possibly recognizing four other genera.


A genus of about 30 species, most diverse in temperate and arctic areas with a few taxa found on some tropical mountains. Sampling shows Sagina to be monophyletic, although infrageneric relationships have not been studied.


Monotypic; San Ambrosio Island (Desventurados archipelago), Chile. Kool (2012) reported it nested within a Spergularia clade.


About 40 species, most diverse in the Mediterranean and southwestern Asia. The most comprehensive monograph dates from 1910 (Simmler 1910), with Shults (1989) providing an updated account for Russian taxa. Up to now, sampling has been minimal and offers no information on how related genera (Bolbosacanaria, Cyathophylla, Pleioneura, etc.) may best be treated.


A monophyletic group of 34 species endemic to the Hawaiian Islands. See Wagner & al. (2005) for a monographic/phylogenetic revision and Harbaugh & al. (2010) for comments on the origin of Schiedea.


About 12 species native to Eurasia and Australasia. Smissen & al. (2003) found Scleranthus to be monophyletic and to be treated as two subgenera: S. subg. Scleranthus (three species, Eurasia) and S. subg. Mniarum (J. R. Forst. & G. Forst.) Pax (nine species, southeastern Australasia). Dillonberger & Kadereit (2014) found Scleranthus was sister to one of ten clades of Minuartia s.l., treated by them as Cherleria.


Two species; southwestern United States and Mexico. Hartman (2005b) noted seed and flower characters suggesting a close relationship to Achyronychia; Greenberg & Donoghue (2011) showed this for S. rixfordii (Brandegee) Munz & I. M. Johnst., but S. parryi (Hems.) I. M. Johnst. clustered with Sphaerocoma acheri Boiss. (= S. hookeri T. Anderson subsp. acheri (Boiss.) Kool & Thulin).

Oites Adans., Fam. Pl. 2: 255. 1763.
Silenanthe Griseb. & Schenk in Archiv für Naturschichte 18: 507, 611. 1763. – type:
≡ Schischkiniella steenis in Blumea 15: 278. 1926.
≡ Oberna Adans., Fam. Pl. 2: 255. 1763.

The monotypic Genus Cucubalus L. (C. neriifolius (L.) Borkh.) is distributed in Europe and Asia, and is monophyletic (Kool et al. 2012). It is sister to Sileaeae (except Agrostemma) in Silene (e.g. Greuter 1995), whereas Tzvelev (2001) recognized 23 genera in Europe alone. Molecular evidence clearly supports separation of Agrostemma, Atocion, Endianthe, Heliosperma, Petrocoptis and Viscaria (e.g. Oxelman & Lidén 1995; Oxelman & al. 1997, 2001; Popp & Oxelman 2004; Fraudjman & al. 2009a; b; Greenberg & Donoghue 2011). However, monophyly of Silene, in the sense adopted here, is only rarely supported by individual gene trees. Several studies have identified two major clades (S. subg. Behenantha (Oth) Endl. and S. subg. Silene; e.g. Oxelman & Lidén 1995; Oxelman & al. 1997, 2001; Eggens & al. 2007; Erixon & Oxelman 2008; Rautenberg & al. 2012; Aydin & al. 2014), but their relationship to Lychnis is ambiguous. Silene sect. Atocion Oth. is a small group of annuals from the eastern Mediterranean, appears to be blurring the picture, possibly due to highly elevated substitution rates across the genome (Z. Aydin & al., unpubl. data).


A genus of about seven Himalayan species. Sadeghian & al. (2015) found Solitaria clustering as a sister to either Odontostemma or Pseudostellaria.


Five north-temperate species. While López González (2010) suggested Spergularia should be included in Spergula based on morphology, Kool (2012) demonstrated that both genera are monophyletic.


= Delia Dumort. in Fl. Belg. 1: 110: 1827.
About 60 species (Hartman & Rabeler 2005), especially diverse in the Mediterranean and temperate South America. The genus is monophyletic (Kool 2012), but infrageneric relationships are not defined.


Monotypic; in deserts from Somalia east to Pakistan. Kool & al. (2012) noted that Sphaerocoma is sister to the monotypic Pollichia and together they form a sister clade to one including Polycarpaea and Polycarpum.


A genus of about 150 to more likely 200 species of Eurasia and North America, most diverse in the mountains of central Asia. *Stellaria* is in need of a monographic revision; the most recent infragenetic classification is that of Pax & Hoffmann (1934). Greenberg & Donoghue (2011) conducted the most extensive sampling of *Stellaria* to date, including 44 species. *Stellaria* is clearly polyphyletic and in need of further study: *S. obtusa* Engelm. appeared as a sister to a clade including *Honckenya*, *Schiedea* and *Wilhelmsia*; three Mexican/Caribbean species were sister to *Minuartia* sect. *Uninerviae* (Fenzl) Mattf. (= *Mononeuria* of Dillonberger & Kadereit 2014); *S. americana* (Porter ex B. L. Rob.) Standl. clustered with *Pseudostellaria jamesiana* (Torr.) W. A. Weber & R. L. Hartm.; and *S. holostea*, the type of *Stellaria*, appeared as sister to the clade that includes *Cerasitium*, *Dichodon*, *Holosteum*, *Moenchia* and the majority of *Stellaria* species sampled.


**Triplateia** Bartl. in Ord. Nat. Pl.: 305. 1830 sec. *Dillenberger* & Kadereit (2014). – Type: *Triplateia diffusa* Bartl. = *Hymenella* Ser. in Candolle, Prodr. 1: 389. 1824, nom. illeg. Monotypic; endemic to central Mexico. Treated by McNeill (1962) as *Minuartia* subg. *Hymenella* (Ser.) McNeill. Harbaugh & al. (2010) and Greenberg & Donoghue (2011) both reported it as sister to *Geocarpum minimum* Mack., a species endemic to the Ozark region of the United States. Dillonberger & Kadereit (2014) found that it was a sister taxon to three species of *Stellaria* from Mexico and the Caribbean. This clade was, depending on the gene chosen, either sister to *Mononeuria* (*Minuartia* sect. *Uninerviae + Geocarpum*) (matK) or sister to a clade including *Honckenya*, *Schiedea* and *Wilhelmsia* (ITS).

**Vaccaria** Wolf, Gen. Pl.: 3. 1776 sec. *Bittrich* (1993c). – Type: *Vaccaria pyramidata* Medik. One or four species, native to Eurasia. While usually thought to be closely related to *Saponaria*, both Harbaugh & al. (2010) and Greenberg & Donoghue (2011) found a potential relation with *Gypsophila* based on different vouchers: sister to *Gypsophila* in the former study, clustering near the base of a *Gypsophila* clade in the latter.


**Xerologia** Oliv. in Hooker’s Icon. Pl.: t. 2359. 1895 sec. *Bittrich* (1993c). – Type: *Xerologia arubica* Oliv. Monotypic; Arabia. Found to be nested in one of the clades of *Polycarpaceae* by Kool & al. (2012); placement awaits further resolution of polyphyly in *Polycarpaceae*.

**Chenopodiaceae** Vent. sec. Muller & Borsch (2005). The family *Chenopodiaceae* is cosmopolitan predominantly occurring in temperate and subtropical regions, and especially in semi-arid or arid environments (Kühn 1993; Kadereit & al. 2003). Our delimitation of the *Chenopodiaceae* follows the concept of Ulbrich (1934), and Kühn (1993) with the exception of the *Polycnemoidae* (see *Amaranthaceae*). Considering that the core of *Chenopodiaceae* (composed of *Betoideae*, *Camphorosmoideae*, *Chenopodioidae*, *Salsiliniae*, *Salsoloidae* and *Suadeoideae*) is likely to be monophyletic, we
maintain the Chenopodiaceae as a family distinct from the Amaranthaceae in line with a series of current taxonomic treatments and morphological, physiological and phylogenetic studies (Tvzelev & al. 1996; Welsh & al. 2003; Zhu & al. 2003; Kadereit & al. 2005; Kapralov & al. 2006; Voznesenskaya & al. 2007; Akhani & al. 2007; Zacharias & Baldwin 2010; Kadereit & al. 2010; Sukhurok 2010; Flores-Olvera & al. 2011; Sukhurok & Kushunina 2014). We believe that name stability is important as it facilitates the assignment of genera to the respective major Amaranthaceae and Chenopodiaceae clades in line with the vast literature on Chenopodiaceae. The monophyletic core Chenopodiaceae had already been found with maximum support based on matK-trnK sequence data (Müller & Borsch 2005a), although relationships of the six major subfamilies were not clear. Much progress has been made in the last decade on the internal relationships of Chenopodiaceae. Schütze & al. (2003) found two major clades of Suaedoideae Ulbr., to which Bienertia is sister. The Salicornioideae were clearly identified as monophyletic and are a lineage of about 90 species growing worldwide in coastal and inland saline habitats (Kadereit & al. 2006) with often succulent-articulated stems. Phylogenetic analysis yielded good support for the Camphorosmoideae that include several major lineages of mostly steppe, semi-desert and desert plants (Kadereit & Freitag 2011), although genera of the Chenopodiaceae (Kühn 1993a; Kadereit & al. 2003). Carpo logically it is closely related to Corispermum (Kühn 2014).


The genus belongs to Salsoleae s.str. and comprises c. nine species (Akhani & al. 2007).


Atriplex is the most species-rich genus within Chenopodiaceae with c. 300 species. This cosmopolitan genus comprises annual or perennial herbs, subshrubs and shrubs that are often prominent floristic elements of steppes, semi-deserts and coastal habitats (Kadereit & al. 2010). Most species of Atriplex are C₄ plants that all belong to one large C₄ lineage. Many species of the genus are halophytes and possess salt glands. Ontogenetic studies showed that the two more or less concrescent "bracteoles" that envelope the fruit and that are characteristic of Atriplex are better interpreted as two tepals (Flores-Olvera & al. 2011). The circumscription of Atriplex has changed over time, and several infrageneric classifications have been proposed (Flores & Davis 2001; Kadereit & al. 2010). Recent phylogenetic studies based on molecular data (Kadereit & al. 2010; Zacharias & Baldwin 2010) show that Atriplex in its traditional circumscription is not monophyletic and includes several satellite genera that have been separated in the past. A new infrageneric classification is needed. Previously Atriplex was placed in the tribe Atripliceae. However, because the previous Chenopodiaceae are paraphyletic to Atripliceae the tribes were merged together by Fuentes-Bazán & al. (2012b). The accepted name of the tribe in the new, monophyletic definition is Atripliceae.


Axyris, together with Ceratocarpus and Krasheninnikovia, constitutes the Axyriadeae (Kadereit & al. 2010). The genus consists of six species mainly concentrated in the mountains of central Asia and eastern Siberia (Sukhorukov 2011); some species (especially A. amaranthoides L.) occur as alien weeds in Eurasia and North America beyond their native range. Investigated species of the genus show heterocarpy (Sukhorukov 2005, 2011).


The phylogenetic position of this rare monotypic genus from China is unknown. According to Kühn (1993a) it belongs to the Chenopodioidaeae.


≡ Londesia Fisch. & C. A. Mey. in Index Seminum [St. Petersburg (Petropolitanus)] 2: 40. 1836.

≡ Panderia Fisch. & C. A. Mey. in Index Seminum [St. Petersburg (Petropolitanus)] 2: 21. 1836.


Bassia belongs to Camphorosmoideae–Camphorosmeae and in the circumscription adopted here consists of c. 20 C₄ annuals or perennials. The genus is distributed from the western Mediterranean to eastern Asia (Kadereit & Freitag 2011), with the main centre of diversity in central Asia. It represents an interesting example of C₄ leaf-type diversity (Freitag & Kadereit 2014) and multiple reduction of water-storage tissue (Akhani & Khoshravesh 2013; Kadereit & al. 2014).


Beta comprises seven species of annuals or biennial and perennial herbs with a storage root. Beta is subdivided into two sections and is the only genus of tribe Betaeae. Beta sect. Procumbentes Ulbr. (= B. [unranked] Patellaires Tranzschel) was excluded from Beta on the basis of molecular phylogenetic and morphological results (see under Patellifolia; Hofmann & al. 2006; Kadereit & al. 2006b). Beta vulgaris and its various cultivated varieties (sugar beet, beetroot, fodder beet and chard) are the economically most important crops within Caryophyllales (McGrath & al. 2011). For B. vulgaris the chloroplast genome (Li & al. 2014) and the nuclear genome (Doehm & al. 2013) have been sequenced recently.


In the last century, the Linnaean Blitum, with its two species, B. capitatum and B. virgatum L., was usually merged with Chenopodium s.l. (e.g. Aellen 1929; Ilijin & Aellen 1936; Aellen & Just 1943; Aellen 1960–1961; Grubov 1966; Brenan & Akeroyd 1993; Mosyakin 1996; Uotila 1997, 2001a, b; Clemants & Mosyakin 2003), or rarely recognized in the original Linnaean circumscription (Scott 1978a). However, the resurrection of this genus based on phylogenetic reconstruction supports a monophyletic lineage and a wide concept of Blitum including c. ten species (Fuentes-Bazán & al. 2012b), most of them in the northern hemisphere and one (B. atriplicium F. Muell.) in Australia. Blitum belongs to the tribe Anserineae.


The genus Caroxylon was resurrected by Tzvelev (1993) and then confirmed and re-circumscribed based on molecular and morphological evidence (Akhani & al. 2007). In that circumscription, it is the most diverse genus in Salsoloideae with c. 100 species distributed in central and southwestern Asia, the Mediterranean region and northern and southern Africa (Feodorova 2011). Feodorova & Samigullin (2014) revealed four clades within Caroxylon s.l. and provisionally advocated further splitting of the genus, with recognition of Caroxylon s.str., a re-circumscribed Nitrosalsola, and possibly two other segregate genera, based on molecular and morphological evidence.


This monotypic genus comprises one annual widespread Eurasian species and belongs to the Axyranaeae G. Kadereti & Sukhor. (Kadereit & al. 2010).


This genus is distributed in southern Africa and comprises two perennial species (Snijman & Manning 2013; Kadereit & al. 2014). Other taxa previously placed in Chenolea are now mainly included in Bassia s.l. or Chenoleoidae (see discussion under Bassia).


Chenopodiastrum is a widespread new genus with six or seven species and segregated from Chenopodium s.l. Its recognition is based mainly on molecular phylogenetic studies (Fuentes-Bazán & al. 2012a, b). The genus is subdivided into two groups, for which sectional rank was proposed (Mosyakin 2013).


= Einadia Raf., Fl. Tellur. 4: 121. 1838.


Chenopodium has been considered one of the most diverse genera within Chenopodiaceae with c. 150 species (Kühn 1993), or even up to 250 species (under a narrow species concept). The circumscription has considerably changed over time, and several infrageneric classifications have been proposed. In a wide sense, Kühn (1993) and Mosyakin & Cleman (1996) recognized three subgenera: C. subg. Ambrosia A. J. Scott, C. subg. Blitum (L.) Hiitonen and C. subg. Chenopodium, and this classification was followed by several authors in recent treatments for the genera. However, it was proposed, based initially on morphological data, to include C. subg. Ambrosia into the re-circumscribed genus Dysphania R. Br. (Mosyakin & Cleman 2003, 2008; Mosyakin & Mosyakin 2003; Zhu & al. 2003). Recent phylogenetic studies based on molecular data (Fuentes-Bazán & al. 2012a, b) have shown that Chenopodium in its traditional circumscription is not monophyletic and consists of six independent lineages. Fuentes-Bazán & al. (2012b) also gave the morphological descriptions of the segregates, including Chenopodium s.str., which still remains the most species-rich and most widespread genus of the group. Chenopodium belongs to Atripliceae (earlier Chenopodiaceae), which is monophyletic in the circumscription by Fuentes-Bazán & al. (2012b). The typification of the genus Chenopodium is debated. If the same solution is adopted for Chenopodium as that proposed for Salsola by Akhani & al. (2014), i.e. the recognition of the lectotype proposed under the “American Code” (Arthur & al. 1907) (C. rubrum L. in our case), then the genus recognized here as Oxybasis should be called Chenopodium s.str., and the genus containing C. album L. (the lectotype of Chenopodium as recognized here) should probably be called Rhagodia, which will have disastrous consequences for taxonomy and nomenclature of the group (see discussion in Mosyakin & Cleman 1996; Fuentes-Bazán & al. 2012b).


A monotypic genus from Anatolia, closely related to Girgensohnia and Hammada of Salsoleae s.str. (Akhani & al. 2007).


A monotypic genus from North America that is probably phylogenetically nested within Dysphania (Dysphaniaceae; G. Kadereit, unpubl. data).


This monotypic genus belongs to the Australian Camphorosmeae and is closely related to Dissocarpus and Erinociton (Cabrera & al. 2009). The genus is endemic to Australia (Wilson 1984).


Four species are currently recognized in Dissocarpus (Australian Camphorosmeae). The genus is endemic
to Australia (Wilson 1984). It is closely related to Didymanthus and Eriochiton (Cabrera & al. 2009).


- **Botrydium** Spach, Hist. nat. vég. 5: 298. 1836.


- **Meiomeria** Standl., N. Amer. Fl. 21(1): 7. 1916.


- **Chenopodium sect. Margaritaria** Brenan in Kew Bull. 11: 166. 1956.


The widespread genus *Dysphania* comprises c. 50 species native mostly to South America (D. sect. *Adenois*), Eurasia and Africa (D. sect. *Botryoides*) and Australia (D. sect. *Dysphania*, D. sect. *Orthospora* and D. sect. *Tetraspalea*). Traditionally, only native Australian taxa were included in *Dysphania* (Scott 1978; Wilson 1983, 1984); later an expanded circumscription of the genus was proposed (Mosyakin & Clemants 2002, 2008) based on morphological evidence. Further molecular phylogenetic studies (Kadereit & al. 2003, 2010; Fuentes-Bazán & al. 2012a, b) demonstrated that *Dysphania* is phylogenetically distant from *Chenopodium* and forms the tribe *Dysphanieae* together with the closely related *Suckleya* and *Teloxys*. The latter was included in *Dysphania* based on morphology (Mosyakin & Clemants 2002, 2008; Clemants & Mosyakin 2003; Zhu & al. 2003), but should be recognized as a separate genus based on molecular results (Kadereit & al. 2010; Fuentes-Bazán & al. 2012a, b).


*Enchyelaena* seems to be polyphyletic (Cabrera & al. 2009). However, more molecular data for this genus of Australian *Camphorosmeae* are needed before taxonomic rearrangements can be done.


The genus is endemic to Australia and belongs to the *Camphorosmeae*. It is closely related to *Neobassia* (Cabrera & al. 2009).


A monotypic genus distributed in South Africa. It belongs to the *Archiatriplex* clade within *Chenopodieae*, formerly *Atripliceae* (Kadereit & al. 2010).


The two species of *Extriplex* are endemic to the California Floristic Province. *Extriplex* belongs to the *Archiatriplex* clade within *Chenopodieae*, formerly *Atripliceae* (Kadereit & al. 2010; see Zacharias & Baldwin 2010 for detailed information on the genus).

*Girgensohnia* comprises five annual species in central Asia and Iran (Sukhorukov 2007). The genus belongs to the *Salsoleae* s.str. and is closely related to *Cytathobas and Hammadna* (Akhani & al. 2007).


*Zuckia* Standl. in J. Wash. Acad. Sci. 5: 58. 1915. A small North American genus that belongs to the *Architriplex* clade within *Chenopodiaceae*, formerly *Atripliceae* (Kadereit & al. 2010; see Zacharias & Baldwin 2010 for detailed information on the genus).


A central Asian genus comprising three annual C₃ species previously included in *Bassia* and/or *Kochia*. *Grubovia* is sister to the speciose clade of Australian *Camphorosmeae* (Kadereit & Freitag 2011).


The monotypic genus belongs to the *Habitizieae–Betoideae* (Hohmann & al. 2006; Kadereit & al. 2006). *Habitizia tammoides* is one of the very few climbing *Chenopodiaceae*. Annual shoots grow from a fleshy root in this species, which is endemic to Caucasus and NW Iran.


Phenotypically this monotypic genus from Afghanistan fits into *Halimocnemis* s.l. However, several attempts to generate sequences for this species have failed (H. Akhani, pers. comm.).


*Halimione* consists of three species (one annual, two perennial), which are distributed in Europe, the Mediterranean and western Asia. The genus is often included in *Atriplex*. Molecular and morphological data, however, support the generic status of *Halimione* (Kadereit & al. 2010), which is sister to the species-rich *Atriplex* in the tribe *Chenopodiaceae*, formerly *Atripliceae*.


= *Halanthium* K. Koch in Linnaea 17: 313. 1844.


*Halimocnemis* is an aggregate of Irano-Turanian annual species that is phylogenetically not well resolved. Based on phylogenetic studies (Akhani & al. 2007), a broad concept was adopted in which *Gamanthus, Halanthium* and *Halotis* are included. Further phylogenetic studies are required for possible inclusion of genera such as *Halarchon, Physandra* and *Piptoptera*.


*Halocharis* comprises seven annual species and belongs to the *Caroxyleae* (Akhani & al. 2007).


*Halocnemum* belongs to *Salicornioideae* and comprises two hygrohalophytic species of shrubs. The genus is distributed in the southern Mediterranean and southern, western and west-central Asia and is closely related to *Halopeplis* and *Halostachys* (Kadereit & al. 2006).


*Halogenet* belongs to *Salsoleae* s.str. and is likely monophyletic (Akhani & al. 2007). This Eurasian genus, one species of which is also found in the southwestern and partly central United States as a widespread invasive alien, comprises c. five annual and perennial species and is often found in saline habitats.


*Halopeplis* comprises three species of annual and perennial hygrohalophytes distributed in the southern Mediterranean, South Africa and southern, western and central Asia. The genus belongs to *Salicorniae* and is closely related to *Halocnemum* and *Halostachys* (Kadereit & al. 2006).


This monotypic genus of *Salicorniae* is distributed in central, southern and western Asia and southern and eastern Europe. It is closely related to *Halocnemum* and *Halopeplis* (Kadereit & al. 2006). Nomenclatural note: Pfeiffer (1874) had chosen *Halostachys songarica* Schrenk as the type of *Halostachys*, but this species was by that time already placed in the new genus *Halopeplis* (see Piirainen 2015 for details). A proposal has been published to
conserve the name *Halostachys* with *H. caspica* as its conserved type (Piirainen 2015).


*Halothamnus* belongs to *Salsoleae* s.str. and is likely monophyletic (Akhani & al. 2007). The genus comprises 21 species, most of which are small shrubs or subshrubs, only two species are annuals. It is found from Somalia in the west to Kazakhstan in the east in desert and semi-desert habitats (Kothe-Heinrich 1993).


Generic circumscription of *Hammada* requires more studies. The molecular phylogeny of three studied species showed paraply of the studied samples (Akhani & al. 2007).


This halophytic genus belongs to the *Salicornioideae* and comprises two species in Central and South America. It is closely related to *Allenrolfea* (Kadereit & al. 2006).


A monotypic South American genus of *Chenopodioideae* (incl. *Atripliceae*) (Kadereit & al. 2010; Zacharias & Baldwin 2010). It is one of the rare *Chenopodioideae* with berry-like fruits.


A likely monophyletic genus within *Salsoleae* s.str. comprising six annual species distributed in desert habitats in central and western Asia (Akhani & al. 2007).


This presumably monotypic genus likely belongs to *Salsoleoidae*, but has not yet been included in molecular studies.


The genus comprises c. 20 C₄ annual species with spiny leaf tip, except for the shrubby species *Kali gryphitii* (Bunge) Akhani & Roalson, an endemic of southeastern Iran, southern Afghanistan and adjacent Pakistan. The genus is native to Asia, Europe and the Mediterranean basin and is also widely introduced in Australia, South Africa and North America (Brullo & al. 2015a, b). However, it is likely that some species are native to Australia and North America (see Hrusa & Gaskin 2008; Chinnock 2010). The typification and nomenclature of *Kali* are discussed in Akhani & al. (2014). See also under *Salsola*.


This genus belongs to the *Salicornioideae* and comprises five perennial halophytic species that are distributed in central and southwestern Asia as well as southern and southeastern Europe. The monophyly of *Kalidium* is only weakly supported by molecular data (Kadereit & al. 2006).


This genus belongs to *Caroxyleae* and includes c. ten xerohalophytic species mainly distributed in deserts of central and southwestern Asia (Akhani & al. 2007).


= *Eurotia* Adans., Fam. Pl. 2: 260. 1763, nom. illeg. *Krascheninnikovia*, according to a molecular study (ITS phylogeny only) by Heklau & Röser (2008), comprises only one widespread and highly polymorphic species with two subspecies (Eurasian and North American ones). However, considerable morphological diversity and wide geographical distribution (from southern Europe through central Asia to southwestern and west-central North America) of representatives of the genus suggest recognition of several species and/or subspecies (Grubov 1966; Zhu & al. 2003). The genus belongs to the *Axyrideae* (Kadereit & al. 2010).


The genus likely belongs to *Salsoleoidae*, but has not yet been included in molecular studies.

A monotypic genus distributed in western North America and likely closely related to *Chenopodium* (Kadereit & al. 2010).

A genus of c. ten closely related xerophytic species that are distributed in central Asia (Pratov 1985). *Brachymelum* is related to *Halocnemum* and *Kaviria* based on phyletological studies (Akhani & al. 2007).

A small genus endemic to Australia and belonging to *Camphorosmoideae* (Wilson 1984, Cabrera & al. 2009).

A small genus of three xerophytic C₄ species distributed in western North America and likely closely related to *Chenopodium* (Kadereit & al. 2010).

A monotypic genus distributed in southern Africa. It belongs to the *Archiatrilex* clade within *Chenopodiaceae*, formerly *Atripliceae* (Kadereit & al. 2010).

A small genus endemic to Australia and belonging to *Camphorosmoideae* (Cabrera & al. 2009).

A monotypic genus distributed in western North America and likely closely related to *Chenopodium* (Kadereit & al. 2010).

**Camphorosmoideae** (Wilson 1984, Cabrera & al. 2009).

A small genus endemic to Australia and belonging to *Camphorosmoideae* (Wilson 1984, Cabrera & al. 2009).

A genus of c. ten closely related xerophytic species that are distributed in central Asia (Pratov 1985). *Camphorosmoideae* is related to *Halocnemum* and *Kaviria* based on phyletological studies (Akhani & al. 2007).

A small genus endemic to Australia and belonging to *Camphorosmoideae* (Wilson 1984, Cabrera & al. 2009).

A small genus of three xerophytic C₄ species distributed in southwestern and central Asia (Akhani & al. 2007).

A monotypic genus endemic to southeastern Europe, southwestern Siberia, and central Asia. It is closely related to *Petrosimonia* (Akhani & al. 2007).

A small genus endemic to Australia and belonging to *Camphorosmoideae* (Cabrera & al. 2009).

A small genus endemic to Australia and belonging to *Camphorosmoideae* (Cabrera & al. 2009).

A small genus endemic to Australia and belonging to *Camphorosmoideae* (Cabrera & al. 2009).

A small genus endemic to Australia and belonging to *Camphorosmoideae* (Cabrera & al. 2009).

A monotypic genus distributed in western North America and likely closely related to *Chenopodium* (Kadereit & al. 2010).


A monotypic genus distributed in western North America and likely closely related to *Chenopodium* (Kadereit & al. 2010).


Oxybasis was described by Karelin & Kirilov (1841) and included at that time only one species, O. minitiflora Kar. & Kir. (= Oxybasis chenopodioides (L.) S. Fuentes & al.) The phylogenetic studies by Fuentes-Bazán & al. (2012b) and Sukhorukov & al. (2013) supported the monophyly of this widespread genus as a member of Chenopodiaceae and enlarged its circumscription with species segregated from Chenopodium s.l. At least ten species are currently known (some recently transferred from Chenopodium: see Mosyakin 2013; Sukhorukov 2014), and some occur in saline habitats. Since Oxybasis contains O. rubra (L.) S. Fuentes & al., and its basionym, C. rubrum L., is considered by some authors to be lectotype of Chenopodium, the adoption of that lectotype would result in Oxybasis becoming a synonym of Chenopodium (see there).


A genus of c. 12 species distributed in saline soils of central and southwestern Asia, westwards to the eastern Mediterranean. Petrosimonia is a typical genus with bifurcate hairs. It forms a monophyletic group with Ofaiston within Caroxyleae (Akhani & al. 2007).

Physandra Botsch. in Chorn. fl. Akad. Sukachev 114. 1956 sec. Botschantzev (1956). – Type: Physandra halimocnemis (Botsch.) Botsch. Physandra has not yet been included in any phylogenetical study. It is presumably a member of Halimocnemis s.l. (Akhani & al. 2007).


See notes under Halimocnemis on the possible synonymy of Piptoptera.


Pyankovia is a recent segregate of Climacoptera and Salsola s.l.: it was initially described as a monotypic genus (Akhani & al. 2007). Further studies showed that the genus contains more than one species (Wen & al. 2010). There are probably at least three species distributed from southeasternmost Europe through the Caspian area, the Caucasus, and Iran to central Asia (A. Mosyakin, unpubl. data).


A monotypic genus from central Asia belonging to the tribe Salsoleae of Salsoloideae (Akhani & al. 2007).


A small genus comprising three species, endemic to Australia (Wilson 1984).


The genus is distributed worldwide (except for Australia and South America) in salt marshes and saline inland habitats and consists of annual species. It is nested within the perennial Sarcocornia. For recent molecular and morphological studies see Kaderiet & al. (2007, 2012), Akhani (2008), Teege & al. (2011), Slenzka & al. (2013) and Steffen & al. (2015).

A small genus belonging to the *Camphorosmoideae* and endemic to Australia (Wilson 1984; Cabrera & al. 2009).


This monotypic genus belongs to *Camphorosmoideae*, with an annual species distributed from Hungary to southern Siberia and showing a C4 intermediate photosynthetic pathway (Kadereit & al. 2014). The illegitimate name *Salsola sedoides* Pall. (the basionym of *Sedobassia sedoides*) was proposed for conservation against *Salsola sedoides* L. (Freitag & Sennikov 2014). If this proposal is accepted, the name *Sedobassia sedoides* (Pall.) Freitag & G. Kadereit will remain in use.


A monotypic African genus.


The small Eurasian genus *Spinacia* is supported as monophyletic and sister to *Blitum*, both genera belonging to the tribe *Anserineae* Dumort. (Fuentes-Bazán & al. 2012a).


A monotypic genus in *Camphorosmoideae* comprising an annual species distributed from the northern Mediterranean to southern Siberia.


**Borsczowia** Bunge in Linnaea 17: 120. 1843.

**Calvelia** Moq. in Candolle, Prodr. 13(2): 47. 1849.

**Helicilla** Moq. in Candolle, Prodr. 13(2): 47. 1849.


Molecular phylogenetic studies clearly show that
Alexandra and Borsczowia should be included in a monophyletic Suaeda (Kapralov & al. 2006), despite the arguments by Lomonosova & Freitag (2011), who preferred a paraphyletic Suaeda by keeping Alexandra as a separate genus. The study by Schütze & al. (2003) is currently the most comprehensive molecular and morphological study of the genus. The pollen morphology of Suaeda was studied by Dehghani & Akhani (2009).


The monotypic North American genus Suckleya belongs to the Dysphaniaeae, in which it is sister to Cycloloma and Dysphania (Kadereit & al. 2010).


A genus of Salicornioideae with c. 25 hydrohalophytic species, largely endemic to Australia.


Since the treatment of Beck (1907–1909), Teloxys was included and mostly accepted in Chenopodium subsect. Teloxys. For the flora of North America, Mosyakin & Clemants (2002) transferred this species to Dysphania. However, the phylogenetic studies of Kadereit & al. (2010) and Fuentes-Bazán & al. (2012a) recovered an isolated position of the monotypic Teloxys, supporting its first circumscription (Moquin 1834) and also revealing its close relationship to Cycloloma, Dysphania and Suckleya.


A small genus belonging to the Camphorosmoideae and endemic to Australia (Wilson 1984; Cabrera & al. 2009).


A small segregate genus of Salsola s.l. complex, with three species endemic to Aralo-Caspian sandy deserts.


A segregate genus of Salsola s.l. consisting of small or large shrubs occurring in sandy or gravelly habitats of the central Asian and Iranian deserts (Tzevelev 1993; Akhani & al. 2007).


A family with six genera and 20 species (Bruyns & al. 2014). Traditionally, Didiereaceae included xerophytic shrubs and trees endemic to Madagascar with short lateral shoots bearing spines or alternate leaves (Kubitski 1993a; Cuénoud 2003). However, molecular phylogenetic studies (Applequist & Wallace 2001, 2003; Nyffeler & Eggli 2010a; Bruyns & al. 2014) showed a well-supported clade including the traditional Didiereaceae plus the African genera Calyptrothece, Ceraria and Portulacaria, previously placed in Portulacaceae. This expanded circumscription of the family is accepted here, which includes also much-branched plants with opposite leaves and without spines. Applequist & Wallace (2003) divided the family into three subfamilies: Calyptrotheceoideae, Didiereoideae (= traditional Didiereaceae) and Portulacarioideae. The recent molecular phylogeny of Bruyns & al. (2014) supports the monophyly of these subfamilies and the inclusion of Ceraria within Portulacaria.


Portulacaria Jacq. in Coll. 1: 160. 1787 sec. Carolin (1993). – Type: Portulacaria afra Jacq. – Fig. 4F.
Dioncophyllaceae Airy Shaw sec. APG (2009).
A small family of woody lianas comprising three monotypic genera endemic to the Guineo-Congolian forest (Porembski & Barthlott 2003). The family is characterized by leaves with grapnels on branches or paired at the leaf apex, elongated funicules and large discoid and winged seeds (Heubl & al. 2006). The family is considered as partially carnivorous because it includes both carnivorous (Triphyophyllum) and non-carnivorous taxa (Dioncophyllum and Habropetalum). The studies by Heubl & al. (2006) and Renner & Specht (2011) concluded that within Dioncophyllaceae occurred a partial secondary loss of carnivory. See also notes under Ancistrocladaceae.


Triphyophyllum Airy Shaw in Kew Bull. 1951: 341. 1952 sec. Porembski & Barthlott (2003). – Type: Triphyophyllum peltatum (Hutch. & Dalziel) Airy Shaw – Fig. 4G.

Droseraceae Salisb. sec. APG (2009).
The family includes perennial or annual carnivorous herbs and sometimes submerged aquatics (Kubitzki 2003b) characterized by having perception of tactile and chemical stimuli, leaf blade and tentacle movement and genetically by a loss of the rpl2 intron (Heubl & al. 2006). The family comprises three genera, two of them monotypic: Aldrovanda distributed in Eurasia, southeastern Africa and northeastern Australia, and Dionaea endemic to the southeastern United States. Drosera is cosmopolitan and comprises probably more than 100 species (Kubitzki 2003b; Rivadavia & al. 2003). The family is well known to attract, capture, retain and digest small prey animals (mainly small arthropods) with active snap-traps (Aldrovanda [waterwheel plant] and Dionaea [Venus flytrap]) or with active sticky flypaper traps (Drosera [= sundews]) and to absorb the resulting nutrients (Poppinga 2013). The relationships of Droseraceae to the other carnivorous families of the Caryophyllales remain unclear; the results of several molecular phylogenetic studies resulted in three main hypotheses: Droseraceae as sister of Nepenthaceae (e.g. Nandi & al. 1998: rbcL; Cuénoud & al. 2002; Brockington & al. 2009: combined nuclear and plastid data; Schäferhoff & al. 2009: petD); Dioncophyllaceae as sister of a clade including Droso­phyllaceae + [Ancistrocladaceae + Dioncophyllaceae] (e.g. Schäferhoff & al. 2009: petD) and Droseraceae as sister of the rest of the carnivorous families (e.g. Meimberg & al. 2000: partial matK; Schäferhoff & al. 2009: complete matK; Renner & Specht 2011: combined nuclear, ribosomal and plastid data).


Drosera L., Sp. Pl. 1: 281. 1753 sec. Kubitzki (2003b). – Type: Drosera rotundifolia L. – Fig. 5A & B.

= Sondera Lehnn., Nov. Stirp. Pug. 8: 44. 1844.


Drosera has a worldwide distribution, but the majority of species are found in the southern hemisphere, especially in southwestern Australia and New Zealand (Kubitzki 2003b; Rivadavia & al. 2003). Several classifications have been proposed for the genus; the last one was that by Seine & Barthlott (1994), who recognized three subgenera and 11 sections based on morphological, anatomical, palynological and cytotaxonomical characters; the molecular phylogenetic study that included the most representative subgenera and sectional sampling so far (i.e. Rivadavia & al. 2003) supported the monophyly of only some of these groups.

A monotypic family that includes carnivorous subshrubs distributed in Spain, Portugal and Morocco (Kubitzki 2003c). These are characterized by reverse circinate leaves, basal placationment, polyporate pollen and a chromosome base number x = 6 (Heubl & al. 2006). Historically, the single genus Drosophyllum was placed within Droseraceae, but its position as an independent lineage has been well supported by several molecular phylogenetic studies (e.g. Meimberg & al. 2000; Cuénoud & al. 2002; Hilu & al. 2003; Brockington & al. 2009; Schäferhoff & al. 2009). These studies also revealed the closer relationship of Drosophyllaceae with the clade Ancistrocladaceae + Dioncophyllaceae rather than Droseraceae.


A monogenic family with 70–80 species of halophytic and xerophytic shrubs, subshrubs and herbs (Whalen 1987; Kubitzki 2003d) distributed throughout the warmer dry regions of the world (Kubitzki 2003d). Kubitzki (2003d) recognized two genera: Frankenia and the monotypic Hypericopsis; however in the same year Olson & al. (2003) supported the inclusion of Hypericopsis within Frankenia based on wood-anatomical characters. The position of Hypericopsis within the Eurasian and Australian clade of Frankenia has also been well supported by the molecular phylogenetic study of Gaskin & al. (2004).

= **Beatsonia** Roxb. in Beatson, Tracts St. Helena: 300. 1816.
= **Niederleinia** Hieron. in Bol. Acad. Nac. Ci. 3: 218. 1879.
= **Anthobryum** Phil. in Anales Mus. Nat. Santiago de Chile 1891: 51. 1891.

**Gisekiaceae** Nakai sec. APG (2009).

*Gisekia* was excluded from *Aizoaceae* and raised to family level by Nakai (1942). Recent molecular studies support the family status and show an isolated position of *Gisekiaceae* within core-*Caryophyllales* (Brockington & al. 2009; Schäfferhoff & al. 2009; Crawley & Hilu 2012; Bissinger & al. 2014).


- Type: *Gisekia pharmacofoide* L.

  Gilbert (1993) revised the genus and accepted seven species; however, Bissinger & al. (2014) found all species to be polyphyletic and suggested to treat them as one polymorphic species or species complex, *Gisekia pharmacofoide* agg. *Gisekia pharmacofoide* is a C₄ species with atriplicoid Kranz anatomy and NAD-ME biochemical type. The lineage originated in South Africa and presumably migrated along arid areas of eastern Africa during the late Miocene/Pliocene (Bissinger & al. 2014).

**Halophytaceae** A. Soriano sec. APG (2009).

A monotypic family of succulent monoeious herbs, endemic to semi-deserts of western and southwestern Argentina (Hunziker 1998; Bittrich 1993c; Pozner & Cocucci 2006). For many years the position of the only species, *Halophytum ameghinoi* (Speg.) Speg. was uncertain. When the species was described, it was placed in *Aizoaceae* and later transferred to *Chenopodiaceae* (e.g. Cronquist 1981). Several molecular phylogenetic studies have shown that it represents a well-supported independent lineage within the *Portulacinae* (Brockington & al. 2009, 2011; Nyffeler & Eggl 2010a; Ocampo & al. 2010; Arakaki & al. 2011), but its relationships with the other families in this group remain uncertain. The most recent phylogenetic study, based on data from several nuclear and chloroplast markers, supports a close relationship between *Halophytum* and *Basellaceae* and a close relationship of both with *Di-diereaceae* (Anton & al. 2014).

*Halophytum* Speg. in Anales Mus. Nac. Buenos Aires 7: 152. 1902 sec. Bittrich (1993d). – Type: *Halophytum ameghinoi* (Speg.) Speg. – Fig. 5C.

**Kewaceae** Christenh. sec. Christenhusz & al. (2014).

Monogeneric family segregated from *Molluginaceae* (Christenhusz & al. 2014) based on results from Christin & al. (2011).


Eight species, distributed in Africa and Saint Helena; checklist of species in Christenhusz & al. (2014). These species were formerly included in *Hypertelis* (*Molluginaceae*), but have been shown to occupy an isolated position in *Caryophyllales* (Christin & al. 2011).

**Limeaceae** Shipunov ex Reveal sec. APG (2009).

A monogeneric family with c. 20 species, distributed mainly in southern Africa with a few species in Sudan, Ethiopia and southern Asia (Endress & Bittrich 1993). Traditionally, the single genus *Limeum* was placed in *Molluginaceae*. However, the position of the genus as an independent lineage and its distant placement from *Molluginaceae* has been well supported by several molecular studies (Brockington & al. 2009; Schäfferhoff & al. 2009; Christin & al. 2011). The family includes herbs and subshrubs characterized by pseudomonomeros two-chambered ovaries (Endress & Bittrich 1993).


**Lophiocarpaceae** Doweld & Reveal sec. APG (2009).

Small family of about six species distributed in Africa, mainly in the southwest, and southwestern Asia (Endress & Bittrich 1993; Rohwer 1993). The family includes the genus *Lophiocarpus*, previously placed in *Phytolaccaceae* subfamily *Microteoideae* and the genus *Corbichonia*, previously placed in *Molluginaceae*. The clade *Lophiocarpus* + *Corbichonia* was first recovered and well supported in the molecular phylogeny based on *matK* sequences by Cuenoud & al. (2002). The family was described by Doweld and Reveal (2008) and the clade was later confirmed by Schäfferhoff & al. (2009) and Brockington & al. (2011). The two genera included in *Lophiocarpaceae* are morphologically very different. While members of *Lophiocarpus* are herbs and sometimes suffrutescent, characterized by flowers in spikes (with five tepals and four stamens) and achenes (Rohwer 1993), members of *Corbichonia* are herbs or subshrubs, characterized by flowers in cymes (with five sepals and several petaloid staminodes and stamens) and capsules (Endress & Bittrich 1993; Boulos 1999; Sukhorukov & Kushunina 2015).


**Macarthuriaceae** Christenh. sec. Christenhusz & al. (2014).

A monogeneric family restricted to Australia. The poorly known genus *Macarthuria* has been shown to be sister to
all core Caryophyllales (Brockington & al. 2011; Christin & al. 2011) and a separate family Macarthuriaceae was proposed (Christenhusz & al. 2014).


About ten species of rush-like shrubs from Australia, especially southwestern Australia.

Microteaceae Schäferh. & Borsch sec. APG (2009). A monogeneric family restricted to the Neotropics and distributed from Central America and the Antilles to South America (Rohwer 1993; Schäferhoff & al. 2009). Based mainly on the presence of single-ovuled ovaries, Nowicke (1969) placed Microtea, together with Lophiocarpus, in Phytolaccaceae subfamily Microteoideae. However, Schäferhoff & al. (2009) showed that these two genera are not closely related and the position of Microtea as an independent lineage was well supported, resulting in the description of the new family. These results were later confirmed by Brockington & al. (2011).


A poorly studied genus of annual herbs from Central and South America and the Antilles. The number of species is estimated to c. 12 (Schäferhoff & al. 2011); a modern monograph is lacking. Microtea was found in an isolated phylogenetic position (Schäferhoff & al. 2011; two species have been sampled).

Molluginaceae Bartl. sec. APG (2009). A family with nine genera and c. 90 species mainly distributed in southern Africa, but also found in the tropics around the world. The circumscription has been problematic and some of the taxa formerly assigned to Molluginaceae are now considered as members of other families (especially Aizoaceae and Phytolaccaceae) or as independent families within the Caryophyllales (e.g. Kewaceae, Limaceae, Lophiocarpaceae) (Endress & Bittrich 1993; Schäferhoff & al. 2009; Christin & al. 2011; Christenhusz & al. 2014). The family as currently circumscribed is characterized by an undifferentiated perianth with alternitepalous stamens, except for Glinus, which occasionally has small petals (Brockington & al. 2013).


Montiacae Raf. sec. APG (2009). A family with 13 genera and around 200 species distributed around the world (Nyffeler & Egli 2010a). The species of this family are traditionally considered as members of Portulacaceae; however, molecular phylogenetic studies have shown that the traditional Portulacaceae are not monophyletic (Hershkovitz & Zimmer 1997; Applequist & Wallace 2001; Nyffeler 2007; Nyffeler & Egli 2010a; Ocampo & Columbus 2010). Nyffeler & Egli (2010a) proposed the segregation of the traditional Portulacaceae into four families (Anacampserotaceae, Montiaceae, Portulaceae and Tilmaceae) based on morphological and molecular data. The circumscription of Montiaceae follows the proposal of Hershkovitz (1993, 2006) and Hershkovitz & Zimmer (2000). Montiaceae also includes Hectorrellaceae (Applequist & al. 2006; Wagstaff & Hennion 2007; Nyffeler & Egli 2010a).


Calyptridium is a North American genus with eight species (Guilliams 2009). Although Hershkovitz (1990) treated Calyptridium as a section of Cistanthe, phylogenetic analyses have shown that this consideration makes Cistanthe a non-monophyletic group


See under Calyptridium (Montiaceae).


Monotypic; endemic to New Zealand (South Island). The taxonomic position of Hectorella remained controversial for a long time and was even treated in a separate family along with Lyallia (Hectorellaceae; Philipson & Skipworth 1961). However, phylogenetic analyses have confirmed that this monotypic genus is nested in Montiaceae (Applequist & al. 2006; Wagstaff & Hennion 2007; Nyffeler & Eggli 2010a).


= Oroebroma Howell in Erythea 1: 31. 1893.


Lyallia Hook. f., Fl. Antarct. 2: 548. t. 122. 1847 sec. Philipson (1993). – Type: Lyallia kerguelensis Hook. f. Monotypic; endemic to the subantarctic Kerguelen Islands. Lyallia kerguelensis was found to be sister to Hectorella and both are nested in Montiaceae (Wagstaff & Hennion 2007; see also under Hectorella).


Based on phylogenetic analyses (Hershkovitz 1996), Hershkovitz (1998) transferred 35 Australian Calandrinia species to the new genus Parakeelya. However, the relationships of the species of this genus within Montiaceae are not well supported (Hershkovitz 1996; Hershkovitz & Zimmer 2000), so further studies are needed to evaluate its affinities. Australian botanists still continue to use the name Calandrinia for species assignable to Parakeelya. The relationships of the Australian genus Rumicastrum are not clear. It was considered as a genus closely related to Atriplex (Chenopodiaceae). Carolin (1987) and Hershkovitz (1993) used the name to represent the Australian calandrinias (Montiaceae); however, Hershkovitz & Zimmer (2000) opted to use the name Parakeelya for those taxa. Further studies are required to clarify the correct use of Rumicastrum.


Species of Phemeranthus were considered as members of Talinum. However, morphological and molecular analyses have shown that c. 30 New World species that have terete to semi-terete leaves represent a lineage different from Talinum (Talinaceae; Carolin 1987; Hershkovitz & Zimmer 2000; Applequist & Wallace 2000; Nyffeler & Eggli 2010a; Ocampo & Columbus 2010).

An enigmatic monotypic genus, placed here with doubts, and not included in any recent analysis.

**Nepenthaceae** Dumort. sec. APG (2009).

A monogenic family comprising 120–138 species (McPherson 2009, 2011) native to tropical Asia, distributed from Madagascar through Indo-Malesia to New Guinea and New Caledonia (Kubitzki 2003e; Meimberg & Heubl 2006). The family includes woody climbers or scrambling shrubs and some epiphytes (Kubitzki 2003e) widely known as the carnivorous “pitcher plants”. They are characterized by unisexual flowers, axilar placentation, filaments united into a column, three- or four-locular ovaries and the loss of vascularization in glands (Heubl & al. 2006). The affinities of **Nepenthaceae** have long been discussed (Meimberg & al. 2001). Traditionally, the family was placed in the order **Nepenthales**, either as a monofamilial order (e.g. Takhtajan 1980) or together with **Droseraceae** and **Sarraceniacae** (e.g. Cronquist 1988). The placement of the family within **Caryophyllales** was shown by the early molecular phylogenetic study of Nandi & al. (1998). Several molecular phylogenetic studies have shown (although with moderate support) the close relationship of **Nepenthaceae** and **Droseraceae** (Nandi & al. 1998; Cuénoud & al. 2000; Brockington & al. 2009; Schäferhoff & al. 2009; further information under **Droseraceae**). Another study, based on parsimony analysis of combined rbcL and matK shows with high support **Nepentes** as sister to the rest of the carnivorous families, whereas the study of Renner & Specht (2011), based on the ML and Bayesian analysis of the combined data of nuclear, ribosomal and plastid DNA, shows also with high support the relationship of **Nepenthaceae** with the **Drosophyllaceae + [Dioncophyllaceae + Ancistrocladaceae] clade**.


- Type: **Nepentes distillatoria** L.

**Nyctaginaceae** Juss. sec. APG (2009).

This family comprises c. 30 genera and 300–400 species (Bittrich & Kühn 1993; Spellenberg 2003) of trees, shrubs and herbs. These are found in all warmer areas of the world (Douglas & Spellenberg 2010), but mostly in the Americas, with two centres of distribution: arid western North America (southwestern U.S.A. and northern Mexico) and the Neotropics (tropical and subtropical South America and the Antilles). Some genera, such as **Boerhavia**, **Mirabilis** and **Pisonia**, have some species occurring in the Old World, but some of them are introduced (Mirabilis), whereas Comnicarps, with few American species, is most diverse in Africa; **Phaeopitium** is endemic to southwestern Africa and Botswana (Bittrich & Kühn 1993; Douglas & Spellenberg 2010). Recently, Douglas & Spellenberg (2010), based on the molecular phylogeny of the family by Douglas & Manos (2007), made some adjustments to Bittrich and Kühn’s classification of 1993, so that seven tribes were recognized: **Boldoeae**, **Bougainvilleeae**, **Caribeeae**, **Colignoniaceae**, **Leucasteraceae**, **Nygctaginaceae** and **Pisonieae**; the relationship of **Caribeeae** with the others is unknown since it is known only from the type. Several genera, especially those of North America that include the suffrutescent and herbaceous taxa, have been the focus of interest of various studies. However, most of the taxa distributed in the Neotropics, including the trees and shrubs in the diverse genera **Guapira**, **Neea** and **Pisonia**, are poorly known.


- Type: **Abronia californica** J. F. Gmel.


- Type: **Acleisanthes crassifolia** A. Gray = **Selinocarpus** A. Gray in Amer. J. Sci. Arts ser. 2, 15: 262. 1853.

- **Anmocodon** Standl. in J. Wash. Acad. Sci. 6: 631. 1916.


- Type: **Andradea floribunda** Allemão


- Type: **Anulocaulis eriosolenus** (A. Gray) Standl.


- Type: **Belemia fusioides** Pires


- Type: **Boerhavia erecta** L.

**Boerhavia**, with c. 40 species, is distributed in warm-tropical and tropical regions worldwide (Spellenberg 2003) and has been recognized as a natural group by Douglas & Manos (2007). Several authors (Fay 1980; Spellenberg 2001, 2003) have highlighted that at the species level this is a taxonomically difficult group due to morphological variation. Especially among annuals of the Sonoran desert and the pantropical **B. diffusa** Vahl and **B. coccinea** Mill. complex (Spellenberg 2001, 2003), apparently factors such as wide dispersal, hybridization and autogamy have contributed to that variation (Fay 1980; Spellenberg 2001, 2003). The genus is in need of a critical revision.


- Type: not designated.

The genus is monotypic, with **B. purpurascens** Cav. ex Lag. distributed from Mexico and the Antilles to northern South America. Along with **Cryptocarpus** and **Salpianthus**, **Boldoa** is placed within the tribe **Boldoeae** (Douglas & Spellenberg 2010), and in
several treatments (Standley 1911, 1918, 1931; Fay 1980; Pérez & al. 2000; Spellenberg 2001; Hernández-Ledesma & Flores 2003; González 2007) the genus has been included in the wide concept of the genus *Salpianthus*. Here we follow Bittrich & Kühn (1993) and Harling (2010), who consider them as separate genera because of differences of the perianth: *Boldoa* has a campanulate perianth (2–3.5 mm long) with glandular and uncinate hairs, *Salpianthus* has a tubular perianth (6–7 mm long) with straight hairs, while *Cryptocarpus* has a pyriform perianth (1.5–2 mm long). A revision and phylogenetic analysis including all the species of the tribe is necessary to evaluate the circumscription of the genera.

*Bougainvillea* Comm. ex Juss., Gen. Pl.: 91. 1879, nom. cons. sec. Bittrich & Kühn (1993). – Type: *Bougainvillea spectabilis* Willd. – Fig. 5E.

Standley and Steyermark (1946) state that *Bougainvillea* contains c. 14 species native to South America, three of which were cultivated in tropical and subtropical regions of the world. According to Fay (1980), the genus includes ten species, but that author argued that artificial selection processes, hybridization and the spread of clonal variants have produced a complex pattern of variation only loosely related to any natural group. Gillis (1976) treated the bougainvilleas of cultivation, considering three species and one hybrid. The biology, artificial selection as well as the lack of a monographic treatment make it difficult to determine the current number of species.

*Caribea* Alain in Candollea 17: 113. 1960 sec. Bittrich & Kühn (1993). – Type: *Caribea litoralis* Alain An endemic genus from Cuba that has a unique morphology among the *Nyctaginaceae* (Douglas & Spellenberg 2010). *Caribea* includes compact bush-forming taprooted perennial shrubs characterized by opposite leaves forming a stipulariform sheath at the base (Bittrich & Kühn 1993; Douglas & Spellenberg 2010). Because the genus is known only from the type collection, the most recent classification system for the family (Douglas & Spellenberg 2010) included it in its own tribe, *Caribeeae*. It is awaiting its rediscovery in the field.


The genus is monotypic with *C. pyriformis* restricted to Ecuador, Peru, and the Galápagos Islands. For further information see notes under *Boldoa*.


A monotypic genus, *C. vulcanicola* is a perennial herb reported from El Salvador.


*Guapira* Aubl. in Hist. Pl. Guiane: 308. 1775 sec. Bittrich & Kühn (1993). – Type: *Guapira guianensis* Aubl. – Fig. 5F.

= *Torrubia* Vell., Fl. Flumin.: 139. “1825” [1829].

A neotropical genus with c. 70 species, distributed from southern Florida to South America and the Antilles. It is closely related to *Neea*, also being dioecious and having fleshy fruits. Both genera form a complex and their distinctness has been questioned by several authors (e.g. Standley 1931; Burger 1983; Pool 2001; Douglas & Manos 2007) because they are distinguished only by the presentation of the stamens, which are included in *Neea* and exserted in *Guapira*.

In the phylogenetic analysis by Douglas & Manos (2007), the two genera form a clade in which both are paraphyletic; however, those authors questioned if this result was the effect of their sampling (*Guapira*, two species; *Neea*, three species) or whether the paraphyly is due to the lack of resolution between both genera. *Guapira* needs a taxonomic revision and also needs to be evaluated in a phylogenetic analysis that includes an extensive sampling along with *Neea*.


= *Quanoclidion* Choisy in Candolle, Prodr. 13(2): 429. 1849.


A genus with 50–60 American and one Asiatic species. It includes herbs, suffrutescent herbs and subshrubs characterized by the presence of involucres of accrescent bracts, often connate, which surround one or more flowers. Traditionally the genus was classified into six sections, some of them corresponding to previously separated genera. Molecular phylogenetic studies, which have mainly been focused on the...
North American species, support the monophyly of the genus (Levin 2000; Douglas & Manos 2007; P. Hernández-Ledesma & al., unpubl. data) but not the monophyly of the sections (P. Hernández-Ledesma & al., unpubl. data). In order to achieve a natural subgeneric classification, the South American species should be included in the sampling.


*Neea* shows extensive morphological variation in habit, leaves, pubescence, inflorescences, flowers and fruits (Burger 1983). Some authors (e.g. González 2007) have considered it the taxonomically least understood group in the Neotropics. *Neea* seems to be the most species-rich genus within Nyctaginaceae; Douglas & Spellenberg (2010) mentioned that the genus has c. 80 species. However, the lack of a revision, along with the morphological variation and dioecy, has generated many species names (c. 150), whereas the actual number of species remains uncertain. For further information see notes under *Giuapira*.


**Pisoniella** L., Sp. Pl. 1753 1: 1026. 1753 sec. Bittrich & Kühn (1993). – Type: *Pisonia aculeata* L. – Fig. 5G.


This genus includes shrubs, trees and woody climbers characterized by stout spines on the stems and co-riaceous fruits with stipitate glands. Its distribution is pantropical with a centre of diversity in the Neotropics. Molecular phylogenetic studies (e.g. Douglas & Manos 2007; León de la Luz & Levin 2012) supported the monophyly of *Pisonia*, although the genus was poorly sampled in both studies. *Pisonia* has not been monographed, and the number of species is uncertain; some treatments considered 40 species (e.g. Spellenberg 2001; DeFilipps & Maina 2003; González 2007) whereas others (e.g. Spellenberg 2003) considered a range between 10–50 species; in the literature there are numerous accepted and unresolved names.


The genus includes shrubs with alternate leaves, a four- or five-lobed tubular petaloid perianth with straight glandular hairs, three to four long-exserted stamens and a linear style (Bittrich & Kühn 1993). Three species are recognized following this concept: *S. aequalis* Standl., *S. arenarius* and *S. macrodonthus* Standl., all of them with restricted distributions in Mexico. *Salpianthus* was assumed to be monophyletic by Douglas & Manos (2007); however, only *S. arenarius* was included in their study. For further information see notes under *Boldoa*.


**Physeneaceae** Takht. sec. APG (2009).

A monogeneric family with two species endemic to Madagascar (Dickson 2003). Traditionally, the only genus *Physena* was placed in Capparales/Capparaceae (e.g. Pax & Hoffmann 1936) or Flacourtiaeae (e.g. Perrier de la Bâthie 1946). Later, it was considered as a family of its own and placed in the order Sapindales (e.g. Takhtajan 1980, 1987) and was then even transferred to the separate order Physenales (e.g. Takhtajan 1997). However, already the early molecular phylogenetic studies of Morton & al. (1997) showed the affinities of *Physeneaceae* with Caryophyllales and its close relationship to Asteroeicaceae. These results were confirmed by subsequent molecular phylogenetic studies (e.g. Cuénoud & al. 2002; Brockington 2009, 2011; Solits & al. 2011). The relationship between Asteroeicaceae and Physeneaceae is also supported by wood-anatomical characters. For further information see notes under *Asteroeicaceae*.


**Phytolaccaceae** R. Br. sec. APG (2009).

This family comprises herbs, trees or lianas dis-
tributed mainly in the Americas, including the Antilles, but with some members distributed in Australia and New Caledonia. They are characterized by styloids, elongate crystals, racemes or spikes and four or five tepals (Rohwer 1993a; Stevens 2001 onwards). The circumscription of the family has long been controversial. Following the treatment by Rohwer (1993a), *Phytolaccaceae* have been disintegrated step by step according to the results of molecular phylogenetic studies (e.g. Cuenoud & al. 2002; Hilu & al. 2003; Schäfferhoff & al. 2009; Brockington & al. 2011), which have shown that the subfamilies *Agdestioidae*, *Barbeuioideae* and *Microteioideae* (sec. Rohwer 1993a) are well-supported independent lineages. Therefore, these taxa are now treated at family level (see further notes under those families). These studies have also shown that *Phytolaccaceae* s.l. comprising the subfamilies *Phytolaccoidae* and *Rivinoidae* (sec. Rohwer 1993a) are not monophyletic. The most recent study by Brockington & al. (2011) included most of the genera recognized in these subfamilies and showed that the *Phytolaccoidae* (= *Phytolaccaceae* s.str.) represents a well-supported independent lineage, while the support for *Rivinoidae* is present but weak. Recent studies (J. Petersen, T. Borsch & P. Hernández-Ledesma, unpubl. data) show that the latter is as an independent family within *Caryophyllales* by Stevens (2001 onwards). However, the correct family name for a clade that includes the genera *Petiveria* and *Rivina* would have to be *Petiveriaceae* C. Agardh (1824) and not *Rivinaceae* C. Agardh (1824). Both family names were published in the same work (Agardh 1824) but Meissner (1836) included *Rivina* under *Petiveriaceae* separate from *Phytolaccaceae*. This gives priority to *Petiveriaceae*. The taxon has a complicated taxonomic history. In some early treatments members were classified either within *Phytolaccaceae* and distinct from *Petiveriaceae* C. Agardh (Lindley 1853), or vice versa (e.g. Hutchinson 1959; Brown & Varadarajan 1985), or at an infrageneric or infrageneric level within *Phytolaccaceae* (e.g. *Petiveriaceae*, *Rivinoidae*, *Phytolaccoidae*) (including *Petiveria* and related genera) (e.g. Heinrich 1889, 1934; Rohwer 1993a).


**Plumbaginaceae** Juss. sec. APG (2009). A cosmopolitan family of perennial herbs or shrubs, rarely climbers, mainly distributed in the temperate zones of the northern hemisphere, especially in the Mediterranean and Irano-Turanian regions but also in southern Africa, southern South America and Western Australia. The family comprises 25–35 genera and 650–1000 species, which predominantly occur in arid and saline environments and often in coastal habitats. The family is characterized by flowers that have stamens opposite the petals and a single basal anatropous ovule with a curled funicle. Molecular studies based on different markers have shown that *Plumbaginaceae* are well supported as monophyletic family within *Caryophyllales* and sister to *Polygonaceae* (e.g. Cuenoud & al. 2002; Hilu & al. 2003). Lledó & al. (1998, 2001) confirmed the classification of *Plumbagi-
naceae into two subfamilies, Limonioideae and Plumbaginoideae, well differentiated by morphological, chemical and molecular characters. Plumbaginoideae are mostly distributed in the pantropical region and comprise four genera; Plumbago with c. 20 species is the largest. Limonioideae have diversified in regions with a Mediterranean climate and are morphologically more diverse. This subfamily is divided into two tribes: Aegialitideae (one genus with two species) and Limonieae. Most species of Limonieae (> 85%) are grouped into three genera: Acantholimon, Armeria and Limonium, while the remaining species belong to monotypic or small genera (Kubitzki 1993b) mostly segregated from Acantholimon and Limonium. The status of most of these genera is unclear; generic concepts and relationships are in need of revision.

Acantholimon Boiss. in Diagn. Pl. Orient., ser. 1, 7: 69. 1846, nom. cons. sec. Kubitzki (1993b). – Type: Acantholimon glaucaceum (Jaub. & Spach) Boiss. – Fig. 6C.

A large genus of cushion-forming subshrubs; 150–200 species (including many narrow endemics) are distributed in the deserts of Chile and Peru. One sampled species was found in a clade together with Armeria–Psylliostachys, Myriolimon and Saharanthus (Kubitzki & al. 2005).


Two species, distributed in the deserts of Chile and Peru. One sampled species was found in a clade together with Armeria–Psylliostachys, Myriolimon and Saharanthus (Kubitzki & al. 2005).


Monotypic; from Afghanistan. No sequence data are available for this species yet.


Monotypic; B. cabulica is distributed in Afghanistan and Pakistan. Not yet included in molecular studies.


Two(?) species from Afghanistan and central Asia. One species was sampled (C. coelicolor (Rech. f.) Rech. f.) and found in a clade together with Acantholimon acerosum (Willd.) Boiss. and Dictyolimon macrorrhabdos (Boiss.) Rech. f. (Kubitzki & al. 2005).

Sequence data for C. turcomanicum Popov were generated by Akhani & al. (2013).


Ceratolimon, a segregate from Limoniastrum, includes four species of dwarf shrubs with disjunct distributions on the Atlantic and Indian Ocean edges of the Sahara Desert (Crespo & Lledó 2000). Three species sampled by Lledó & al. (2000) formed a well-supported clade, that is sister to Limoniastrum.


A genus of about eight species; distributed in Asia, especially in China and the Himalayas; one species in eastern Africa.


Four species distributed in Afghanistan, Pakistan, and India. One representative was sampled (*D. macrorrhados*) and found in a clade together with *Anctholimon acerosum* (Willd.) Boiss. and *Cephalorrhizum coelolor* (Rech. f.) Rech. f. (Lledó & al. 2005).


Three species of shrubs or subshrubs; from India, Arabia, Socotra and southern Africa.


Monotypic; from Afghanistan. No sequence data are available yet.


Monotypic; distributed in Afghanistan. No sequence data are available yet.

*Gonolimon* Boiss. in *Candolle, Prodr.* 12: 667. 1848

≡ *Gonolimon arborescens* (Boiss.) Sauvage & Vindt, Fl. Maroc 1: 47, 74. 1952


≡ *Myriolepis ferulaceum* (Lincz.) Lincz.

Two species distributed along the central and western coasts of the Mediterranean region.


Monotypic; distributed in central Asia. No sequence data are available yet.


Two species, *Limoniopsis davissii* Bohkari and *L. overinii*, distributed in eastern Turkey and Caucasus, respectively. Not yet tested in any molecular studies.


The largest genus of the family with an estimated c. 350 species with a preference for coastal habitats; distributed worldwide but mainly in the Mediterranean region. *Afrolimon* was shown to be nested in *Limonium* and related to *L. vulgare*, the type of *Limonium* (Lledó & al. 2005). *Limonium* is divided into two major clades corresponding to subgenera, but otherwise the current infrageneric classification proved to be artificial (Lledó & al. 2005). Akhani & al. (2013) studied the Irano-Turanian taxa of *Limonium*. They stated that segregation of *Eremolimon* is not supported by morphology or molecular data (Akhani & al. 2013). Evolutionary studies of this group are complicated by hybridization, many microspecies and apomictic taxa.


Monotypic genus; halophytic *M. salicorniaceum* distributed in Western Australia. Related to *Gonolimon* (Lledó & al. 2005).


Two species distributed along the central and western coasts of the Mediterranean region.


Monotypic; distributed in central Asia.


A genus of 10–20 species ("leadworts") with pantropical distribution.


Monotypic; distributed in Turkmenistan. No sequence data are available yet.


Two or three species; distributed in Asia (former Soviet central Asia, Iran, Afghanistan). *Psylliostachys* species formed a well-supported clade (Moharrek & al. 2014) and were shown to be sister to representatives of *Armeria* (Lledó & al. 2001, 2005; Moharrek & al. 2014).

The genus *Antigonon*, with three to six species, consists of woody or herbaceous perennial lianas that grow in Mexico and Central America, with the exception of *A. leptopus* Hook. & Arn., which is widely cultivated as an ornamental (Brandbyge 1993). Sanchez & Kron (2009), Sanchez & al. (2009), Burke & al. (2010) and Burke & Sanchez (2011), based on consistent and highly supported molecular data, proposed that *Antigonon* and *Brunnichia*, two genera with suffrutescent habit and tendril-bearing lianas, are clearly distinguished from the rest of the subfamily *Eriogonoideae*. According to Brandbyge (1993), the described species are poorly defined and a taxonomic revision is needed.


**Coccoloba** includes c. 120 Neotropical species, which are grouped in four areas with distinguished endemism: the Antilles, Central America, northern South America and the Amazon region of Brazil (Stohr 1982; Brandbyge 1993). The presence of an ocrea (also ochrea), flowers with five tepals and eight stamens and the globose or trigonous achenes are the fundamental characteristics that support the relationships among *Coccoloba*, *Neomillspathia* and *Podopterus* (Sanchez & Kron 2009; Burke & al. 2010; Burke & Sanchez 2011). The particular ecological conditions and ecological isolation of the Antilles allow inferring a radiation, mainly in Cuba and Hispaniola, with c. 40 endemic species; however, there is no biogeographic hypothesis for the genus. Currently, *Coccoloba* is classified in several sections, which have not been phylogenetically evaluated.


A new genus segregated from Muehlenbeckia, based on the molecular study by Schuster & al. (2011). The genus comprises three species restricted to Australia, and is characterized by erect shrubs with thornlike branches. This habit it not found in any other Muehlenbeckia (as studied by Schuster & al. 2011). In addition, Duma does not possess extraloral nectaries at the petiole base, which are present in most species of Fallopia, Muehlenbeckia and Reynoutria.


This genus has been considered as a synonym of Fagopyrum, based on pollen morphology (Hong 1988). However, recent molecular analyses did not place it in Fagopyrum (Ohsako & al. 2001; Galasso & al. 2009; Sanchez & al. 2011). Since there are morphological characters that suggest placement in Fagopyrum, but no molecular evidence for that relationship, Eskemukerjea was left as incertae sedis by Sanchez & al. (2011).


= Bilderdykiacum Dumort., Fl. Belg. 1: 18. 1827.


The genus Gymnopodium was originally described with three species, growing as shrubs or small trees on limestone soils in Belize, Guatemala, and the Yucatán Peninsula in Mexico (Blake 1921; Brandbyge 1993). Sanchez & al. (2009) and Burke & al. (2010) showed that Gymnopodium is strongly supported as monophyletic in the subfamily Eriogonoideae (sec. Burke & Sanchez 2011); based on leaf shape and pubescence characters, the genus should be recognized with only one polymorphic species (Burke & Sanchez 2011).


– Type: Knorrningia sibirica (Laxm.) Tzvelev

The genus was segregated from Polygonum s.l. (or from Aconogonon) and placed in the Coccolobaeae by Hong (1989). Later on it was included within Persicaria (Persicarieae) by Brandbyge (1993) and after that considered as incertae sedis within Polygonaceae by Galasso & al. (2009). Its isolated position from Persicaria was statistically well supported by molecular data in Sanchez & al. (2011). The taxon is sister to the remaining members of the Polygonaceae, with which it shares characters such as tepal nerveature, structure of the exocarp and pollen morphology (Galasso & al. 2009).


Leptogonum is an interesting genus of small trees or shrubs, endemic to Hispaniola (Liogier 1983; Brandbyge 1989). In Burke & al. (2010), this genus was placed in the subfamily Eriogonoideae and recognized as its own subtribe Leptogoneae (Burke & Sanchez 2011), based on the lack of accrescent tepals
in the fruit, the reduction to three stamens, and the leaves clustered at the stem spicules.


This recently published genus comprises two species distributed in Brazil, Bolivia and Venezuela, and it was segregated from *Ruprechtia* based on molecular and morphological characters (Sanchez & Kron 2011). *Magoniella* is characterized by a strict liane- cous habit, and it shares with *Salta* and *Triplaris* the presence of a scar at the base of the perianth in the fruit.


= *Homalocladium* (F. Muell.) L. H. Bailey in Gentes Herb. 2: 56. 1929.


With only two recognized species, the genus is re- stricted to the dry forests of Mexico and Central America (Brandbyge 1993; Burke & al. 2010). Previous to their assignment to a new genus by Blake (1921), species of *Neomillspaughia* had been placed in either *Campderia* Bentham. (Donnell Smith 1899) or *Podopterus* (Gross 1913). Roberty & Vautier (1964) included *Neomillspaughia* in the genus *Podopterus*; however, based on molecular data, *Neomillspaughia* receives strong support as sister to *Coccoloba* (Sanchez & al. 2009; Burke & al. 2010).


*Oxygonum* comprises c. 35 species and is confined to the African continent and Madagascar (Graham 1957; Ortíz & Paiva 1999). Several studies have placed the genus in *Polygoneae* (Haraldson 1978; Brandbyge 1993; Hong & al. 1998; Galasso & al. 2009); however, Haraldson (1978) suggested a close affinity to *Fagopyrum* and genera in *Rumicaceae*. Ronse Decraene & Akroyd (1988) suggested an affinity with *Polygonum*. *Oxygonum* has not been sampled in any molecular study; therefore it was left as incertae sedis by Sanchez & al. (2011).


**Podopterus** Bonpl., Pl. Aequinoc. 2: 89. 1812 sec. Brandbyge (1993). – Type: *Podopterus mexicanus* Bonpl. *Podopterus* includes three species restricted to Mexico and Guatemala (Brandbyge 1993). The genus has strong morphological affinities to *Neomillspaughia* and *Coccoloba*, based on habit and the presence of five tepals (Burke & al. 2010). Although the placement of *Podopterus* is not well supported, Burke & Sanchez (2011) included the genus in the tribe *Coc­ coloebae* alongside *Coccoloba* and *Neomillspaughia*. *Neomillspaughia* and *Podopterus* share the presence of accrescent and membranous inner tepals (Blake 1921; Roberty & Vautier 1984).


= *Polygonella* Michx., Fl. Bor.-Amer. 2: 240. 1803.


A monotypic genus found in China. The genus was considered part of *Fagopyrum* (Haraldson 1978; Ronse Decraene & Akroyd 1988) but molecular studies do not support this placement (Sun & al. 2008; Sanchez & al. 2009; Tavakkoli & al. 2010). Sun & al. (2008) suggested that this genus should be placed in *Persicariaceae*, but in Sanchez & al. (2009) the position is unresolved. In Tavakkoli & al. (2010) there is conflicting placement of *Pteroxygonum* depending on the gene region. Therefore, Sanchez & al. (2011) decided to leave this genus as incertae sedis.


A monotypic genus distributed in Afghanistan, Pakistan, India and China (Quiser 2001). The taxonomy of
Rubrivena is complex; its members have been included in Polygonum (P. polystachyum; Li & al. 2003) and Persicaria (P. wallichii; Freeman 2005), and both names are accepted by Tropicos (undated). However, based on molecular studies, the placement of Rubrivena is strongly supported as sister to Aconogonon and Koenigia (Sanchez & al. 2011).


≡ Enneatypus Herzog in Meded. Rijks-Herb. 46: 3. 1922.


A new monotypic genus described in Sanchez & Cron (2011), based on morphological and molecular data. This genus is commonly found in Argentina, Bolivia, Brazil and Paraguay, and is characterized by a pronounced development of brachylasts and the short axis of the inflorescences borne on a short shoot (Pendry 2004; Sanchez & Cron 2011). Molecular studies have strongly supported the placement of this genus as sister of a clade that includes Magoniella, Ruprechtia and Triplaris (Burke & al. 2010; Sanchez & Cron 2011).


Triplaris Loeffl., Iter. Hispan.: 256. 1758 sec. Brandbyge (1993). – Type: Triplaris americana L. – Fig. 6G.


Although the circumscription of the genus has been relatively stable, the infrageneric classification remains controversial. Previous proposals (von Poellnitz 1934; Legrand 1958; Geesink 1969) are only in part consistent with the results of a recent phylogenetic analysis (Ocampo & Columbus 2012). The genus is monophyletic and has two main lineages: one whose members have opposite leaves (OL clade) and are distributed in Africa, Asia and Australia (except P. quadrifida L., which is a pantropical weed), and a second lineage whose species have alternate to subopposite leaves (AL clade), are more widespread and originated in the New World. These major clades and their subclades have anatomical and morphological features (Ocampo & Columbus 2012; Ocampo & al. 2013) that will be used to amend the classification of Portulaca.
family includes shrubs characterized by having thorny branches, ebracteolate and unsexual flowers, stamine flowers arranged in spikes, whereas the pistillate ones are solitary (Wels & al. 2003). Traditionally, the only genus, Sarcobatus, was placed in Chenopodiaceae (for a detailed taxonomic history until the 1990s see Behnke 1997). The early molecular phylogenetic study by Downie & al. (1997) supported the position of Sarcobatus as an independent lineage. In this study, Sarcobatus showed a close relationship with members of Nyctaginaceae and Phytolaccaceae rather than Chenopodiaceae. Based on these results in addition to characters of the sieve-element plastids and some morphological characters, Behnke (1997) described the new family; nevertheless, some authors continued to treat the genus as part of Chenopodiaceae (e.g. Hils & al. 2003). The position of Sarcobatus as an independent lineage was confirmed by other molecular phylogenetic studies (e.g. Cuénoud & al. 2002; Hilu & al. 2003; Brockington 2009, 2011; Soltis & al. 2011; Schäferhoff & al. 2009), which showed a close but only moderately supported relationship of the family with Agdestidaceae.


Simmondsiaceae Tiegh. ex Reveal & Hoogland sec. APG (2009). A monotypic family native to the Sonoran Desert of northwestern Mexico and to neighbouring regions in Arizona and southern California (Vázquez Yanes & al. 1999); it is also introduced in some countries of South America, Europe, Asia and Africa. The family includes evergreen dioecious shrubs with opposite and thick leaves, clearly articulated near the stem; the stamine flowers are small and borne in terminal inflorescences, while the pistillate flowers are single and axillary; the calyx is much enlarged in fruit (Stevens 2001 onwards; Köhler 2003). Traditionally, the family was placed in Hamamelidales (sensu Takhtajan 1980), Euphorbiales (sensu Cronquist 1988) or in its own order Simmondsiales (sensu Takhtajan 1997), in some cases within Buxaceae or close to it. However, the early molecular phylogenetic study by Fay & al. (1997) showed the affinities of Simmondsiaceae with Caryophyllales: this agrees also with several morphological characters of the stylodia, calyces and secondary growth (Köhler 2003). The affinities of the family with Caryophyllales were confirmed by subsequent molecular phylogenetic studies (e.g. Cuénoud & al. 2002; Brockington 2009, 2011; Soltis & al. 2011), which showed that Simmondsiaceae are closer to Rhabdodendraceae and/or to the remainder of the caryophyllid clade. For further information see notes under Rhabdodendraceae.

Simmondsia Nutt. in London J. Bot. 3: 400. 1844 sec. Köhler (2003). – Type: Simmondsia californica Nutt. The only species, Simmondsia chinesis C. K. Schneider, is known as a dominant shrub in its native distribution area. The species is well appreciated for the liquid wax, extracted from the seeds, which is used mainly in the cosmetic industry (jojoba; Vázquez Yanes & al. 1999).

Stegnospermataceae Nakai sec. APG (2009). A monogenic family with three species occurring from northwestern Mexico to Nicaragua and the Antilles (Rohwer 1992). The family includes small trees and shrubs characterized by bisexual flowers with a two-whorled perianth, one whorl consisting of five free green sepals, and the other whorl of five white narrow-based petals adherent to the alternate-petalous stamens at the base. The fruits are capsules and the seeds are arillate (Rohwer 1993). When the only genus, Stegnosperma, was described in 1844, it was placed in Phytolaccaceae and accepted by other authors (e.g. Heimerl 1934). Nakai (1942) elevated the genus to the family level. Recognition as a family was also supported by morphological, palynological and wood-anatomical characters (e.g. Nowicke 1969; Bell 1980; Carlquist 1999). For a detailed taxonomic history until the 1980s see Bell (1980). The early molecular phylogenetic studies of Downie & al. (1997) and Fay & al. (1997) showed the position of Stegnosperma as an independent lineage. However, both classifications, the recognition of Stegnospermataceae (e.g. Rohwer 1993; Takhtajan 1997) and Stegnosperma within Phytolaccaceae (e.g. Stevens 2001), continued to be used. Subsequent phylogenetic studies (e.g. Salolainen & al. 2000; Cuénoud & al. 2002; Schäferhoff & al. 2009; Qiu & al. 2010; Brockington 2009, 2011; Soltis & al. 2011) confirmed the findings of Downie & al. (1997) and Fay & al. (1997), resulting in the wide recognition of Stegnospermataceae as a separate family.


Talinaceae Doweld sec. Nyffeler & Eggli (2010a). A family with three genera and around 28 species mainly distributed in Africa, but with a few taxa in the Americas and the tropics around the world (Nyffeler & Eggli 2010a). The species of this family are traditionally considered as members of Portulacaceae; however, molecular phylogenetic studies have shown that the traditional Portulacaceae are not monophyletic (Hershkovitz & Zimmer 1997; Applequist & Wallace 2001; Nyffeler 2007; Nyffeler & Eggli 2010a; Ocampa & Columbus 2010). Nyffeler & Eggli (2010a) proposed the segregation of the traditional Portulacaceae into four families (Anacampserotaceae, Montiaceae, Portulacaceae and Talinaceae) based on morphological and molecular data.
Amphipetalum Bacigalupo in Candollea 43: 409. 1988


Molecular and phylogenetic analyses have shown that the New World species with terete to semi-terete leaves formerly treated as members of Talinum form a monophyletic genus within Montiaceae (Phermeranthus; Carolin 1987; Hershkovitz & Zimmer 2000; Applequist & Wallace 2000; Nyffeler & Eggli 2010a; Ocampo & Columbus 2010).

Tamaricaceae

Five genera and c. 80 species occurring in Africa, Asia and Europe with major distribution in the Irano-Turanian and Mediterranean regions (Gaskin 2003). Phylogenetic studies support the monophyly of the genera. Three well-supported clades have been recovered: Hololachna and Reaumuria; Myricaria and Myrtyma; and Tamarix. Tamarix is sister to the clade comprising Myricaria and Myrtyma, and this group is sister to Hololachna and Reaumuria (Gaskin & al. 2004). The main feature in most genera of Tamaricaceae is the presence of salt glands, which enable successful growth in salty and riparian habitats.

Hololachna Ehrenb. in Linnaea 2: 273. 1827 sec. Gaskin (2003). – Type: Hololachna sonangrica (Pall.) Ehrenb. This is a monotypic genus restricted to central Asia and Mongolia. Hololachna is sister to Reaumuria (Gaskin & al. 2004).


The monotypic genus Myrtyma is variously interpreted in taxonomic references, both as an independent genus or as a synonym of Myricaria (Yang & Gaskin 2007) or Tamarix (Baum 1978).


Tamarix L., Sp. Pl. 1: 270. 1753 sec. Gaskin (2003). – Type: Tamarix gallica L. – Fig. 7B. Tamarix with c. 60 species is most diversified in saline and wet habitats of the Old World and is naturalized in Australia and the Americas, sometimes as aggressive invasive plants. It is one of the few lineages in Caryophyllales that contain large trees and shrubs with a significant role in carbon sequestration and vegetation under harsh and salty conditions. The taxonomy and phylogenetic reconstruction of Tamarix are challenging due to the absence of reliable constant characters and the occurrence of hybridization even among morphologically very different species (Gaskin & Kazmer 2009; Mayonde & al. 2015; Samadi & al. 2013; H. Akhani & T. Borsch, unpubl. data).

Tamaricaceae Link sec. APG (2009).

Incertae sedis

Summary: current knowledge, trends, gaps
Phylogenetic sampling as a basis for classification

The synopsis of the genera currently accepted in Caryophyllales along with a discussion on the recent work dealing with these genera provides a comprehensive source of information on the current knowledge of this group of plants. In the context of global undertakings, such as the World Flora Online (WFO; CBD-SBSTTA 2012), this study forms the basis for a gap analysis on the availability of treatments for a major group of flowering plants. The results indicate that there is a substantial taxonomic turnover when comparing the current classification with generic concepts available in the complete treatment of the order in Kubitzki’s “Families and genera of vascular plants” (FGVP; Kubitzki & al. 1993; Kubitzki & Bayer 2003; Table 2). The number of families has increased substantially (27 vs 39 families), reflecting changes necessary because families were not monophyletic (e.g. Portulacaceae). In addition, several isolated lineages have been recovered that were consequently elevated to family rank (e.g. Kewaceae, Macarthuriaceae). The most diverse families in terms of numbers of genera are...
the Cactaceae, Aizoaceae, Chenopodiaceae and Caryophyllaceae (all with over 100 genera), while 28 families comprise only one to six genera (Table 2). At the generic level, the numbers have increased by more than ten percent in comparison to the last complete treatments in the FGVP volumes (Table 2). While the number of genera has remained equal (or nearly so) in 18 families, generic boundaries have changed dramatically in some families, especially in Cactaceae and Caryophyllaceae.

It is also clear that sampling at the species level is far from complete, so that many genera or entire tribes lack data needed to assert their monophyly and/or their exact position in the families, while others are already known to be polyphylectic but are insufficiently sampled to be reclassified. In addition, for many taxa no taxonomic revision is available or the existing one is clearly outdated.

For example, in the Aizoaceae of South Africa, 55% of taxa are in need of revision, 52% of the recognized taxa in the family have not been treated in any revision, with an additional 12% of taxa revised prior to 1970 (von Staden & al. 2013). In the Ruschioidae the five largest genera, Ruschia (206 species), Lampranthus (194 species), Delosperma (142 species), Drosanthemum (107 species) and Antimima (96 species) have never been comprehensively revised at species level (i.e. there is no key to the species). The same is true for numerous smaller genera such as Stomatium (39 species), Hereroa (27 species) and Malephora (16 species). In addition, a recent extensive phylogenetic study of Ruschieae, the most speciose clade in Aizoaceae, showed that numerous genera are not monophyletic, including the large genus Ruschia (Klak & al. 2013). Despite the lack of resolution in parts of the tree due to the lack of variable gene regions, the many cases of polyphyly detected in the phylogeny were an indication of misplaced taxa and narrow generic concepts upheld by traditional taxonomists (Klak & al. 2013). In particular, mono- and bitypic genera in Ruschieae, which were found to be nested within larger genera, need critical re-evaluation (Klak & al. 2013). In contrast, the Mesembryanthemoideae a phylogeny is available with an almost complete sampling of species (Klak & al. 2007) as well as detailed morphological studies and revisions published for most clades over the last 30 years (e.g. Bittrich 1986; Klak & Linder 1998; Klak & al. 2006; Gerbaulet 1995, 1996a–c, 1997, 2001). However, a conflict in genus delimitaton has erupted between taxonomists with regard to the number of genera that should be recognized in Mesembryanthemoideae. Whereas Klak & Bruyns (2013) favoured a generic concept based on monophyly, Gerbaulet (2012) supported the traditional system of “many genera”, which upholds also genera shown to be paraphyletic (e.g. Phyllobolus). No detailed phylogeny is available for the Aizooidae, which include c. 108 species in seven genera. Finally, a further phylogeny including 18 species from Tetragonioideae indicated that several genera, such as Aizoanthemum, Aizoon and Gunniop-

Available treatments in modern floras are patchy on a global level

Monographic work provides the in-depth synthetic information, and the checklist and gap analysis presented here is aimed at defining part of the baseline for such analysis in the Caryophyllales where it is still missing. However, for the aim of creating a global synthesis of knowledge in the Caryophyllales it is indispensable to consider also the information published in floras.

It is difficult to know in how many floras or related works the Caryophyllales have been treated in the past, especially in regions with a long history of botanical activity such as C and W Europe. In fact, if we take the establishment of the Linnaean classification system and naming as a starting point, we can commence right away in the 18th century, for example with Linnaeus’s own Flora suecica (Linné 1745). Flora treatments are numerous; setting aside the numerous works of mostly historical interest, Frodin (2001) in the second edition of “Guide to standard floras of the world” gave information on nearly 1000 general floras distributed in ten major regions of the world. Only in a few cases is there specific information about the families or groups treated in each flora (e.g. Flora of Nigeria: Caryophyllales by Ghazanfar 1991); for the other floras it is necessary to review each flora individually in order to identify works of significance for a global synthesis.

Our approach for uniting the information available for the global synthesis is partly based on taking advantage of information technologies, and fortunately floras are increasingly published on the World Wide Web. An initial review of such publication has revealed that many historical floras that include treatments of Caryophyllales are already available online, for example the pre-1900 floras of the Alps, Australia, Barbados, Brazil, India, Jamaica, Niger, Sri Lanka and Syria, and pre-1990 treatments from Chile, Costa Rica, Fiji, Guatemala, Japan, Madagascar, Panama, South Africa and Taiwan. The bibliographic references of these floras are cited in Frodin (2001), but can also be accessed through
the Biodiversity Heritage Library (BHL 2005+), JSTOR (JSTOR 2000+), Gallica (1997+) and Google Books (2015). More recent floras including the Caryophyllales are those from China, Nicaragua, the Malesian region (Indonesia, Malaysia, Singapore, Brunei Darussalam, the Philippines, and Papua New Guinea) and the Zambesi river basin (Botswana, Malawi, Mozambique, Zambia, Zimbabwe and the Caprivi Strip), in which the last treatments for some families of Caryophyllales were printed in the 2000s. Incomplete floras (and incomplete for Caryophyllales so far) treat Argentina, the Hawaiian Islands, North America north of Mexico, the Marquesas Islands, Mesoamerica, Madagascar, the Neotropics, Pakistan, Palestine and Tasmania.

Most of these are simply digitized print treatments (representing images of the actual print work, which, depending on their quality, may or may not be searchable after optical character recognition – OCR). In contrast to this, very few “true” e-floras exist, i.e. floras produced with the online publication as their principal output and making full use of existing biodiversity informatics techniques. An example of the latter is the Flora of Western Australia (Western Australian Herbarium 1998+).

However, increasingly various intermediates between electronic representations of print media and true e-floras are becoming available, partly as a result of the computerized editing process of the print publication, and partly because printed floras are “marked up” in order to database their content, for example the treatments of Flora Malesiana (see Hamann & al. 2014).

Another important source of information on Caryophyllales are checklists, which are mostly available online, because most of them were developed over the past two decades. Some of them refer to taxa treated in previously printed floras, some of them are continuously updated and others are in progress. Such checklists are available for Africa, Argentina, Australia, Bolivia, Botswana, Brazil, central Africa, Cono Sur (Argentina, southern Brazil, Chile, Paraguay and Uruguay), Costa Rica, Croatia, Cyprus, Ecuador, Europe plus the Mediterranean region, Germany, the Guiana Shield (Guyana, Suriname, French Guiana and part of Venezuela), Iran, Ireland, Israel, Lesotho, Madagascar, Mexico, Micronesia, Mongolia, Myanmar, Namibia, Nepal, New Zealand, the pan-Arctic region, Paraguay, Peru, Portugal, the Philippines, Singapore, South Africa, southern Africa, Suriname, Swaziland, Switzerland, Taiwan and the United States.

All of these floristic projects have generated valuable information that has increased our knowledge about the Caryophyllales. An online bibliography of such sources of information focussing on Caryophyllales is in preparation, and we envision using this as the base of a comprehensive gap analysis for the order, and also as the basis for an analysis of regional differences in taxon concepts. It became clear from the preliminary survey that such gaps exist, and that there is a lack of synchronization of taxon concepts, partly due to the state of knowledge at the time of the production of the treatment, but often also caused by a specific local perspective that needs to be placed into a wider geographic context. This was one of the reasons for the decision to use the EDIT Platform for Cyber-taxonomy for data management, because this is currently the only taxonomic software system natively supporting different classifications, taxonomic concepts and taxon-concept relationships. It indicates also the need for increased efforts to share and integrate the information generated and to promote the filling of gaps in both geographic and taxonomic coverage. This will be facilitated by the application of information technology, making the information openly available in electronic form and thus furthering the process of future revision and dissemination. Additionally, it enables new kinds of links to current data, including those available only in virtual form, which has not readily been possible in the past (Frodin 2001).

Conclusions and future work

While the published version of this treatment only includes citable publications as its basic reference, there will be a dynamic online version of this generic synopsis that will not only be continuously updated but also become more extensive. To facilitate both interaction in the scientific community and to inspire further research on the Caryophyllales, key data to relevant current projects and research underway will be presented. One of the key steps on the way to a synthesis of Caryophyllales will be identifying specialists who are working at the species level; some of them are those who contributed to this generic synopsis, but others have already been identified and agreed to collaborate. Within the network, we then have to organize the work on taxonomic groups with several specialists and to develop a format, as standardized as possible, for the species-level taxonomic treatments. In addition, directories of specialists, of electronic resources and an online bibliography for the Caryophyllales will be developed. Starting with the Caryophyllales 2015 conference in Berlin (September 2015), regular meetings of the Caryophyllales community will drive this process.

Role of authors

The draft of the generic checklist and the initial data entry was the work of PH, who also provided the treatments of Achatomacraeae, Agdestidaceae, Ancistroleaceae, Asteropeiaeae, Barbeuiaceae, Didiereaeae, Dioncophyllaceae, Droseraceae, Drosophyllaceae, Frankeniaeae, Halophytaceae, Limeaeae, Lophiocarpaceae, Microteaceae, Nepenthaceae, Nyctaginaceae, Phynenaceae, Rhabdodendraceae, Sarcobataeae, Simmondsiaceae and Stegnospermataeae and collaborated in some notes of Chenopodiaceae, Phytolaccaceae and

Terms of Use: https://bioone.org/terms-of-use
Downloaded From: https://bioone.org/journals/Willdenowia on 19 Sep 2019

Downloaded From: https://bioone.org/journals/Willdenowia on 19 Sep 2019
Terms of Use: https://bioone.org/terms-of-use
**Polygonaceae.** The following groups were revised by specific authors: *Aizoaceae*: CK, with contributions by GK (*Sesuvioideae*); *Amaranthaceae*: TB, with contributions by GK (*Polycenomeoidae*); *Anacampserotaceae*, *Molluginaceae* and *Portulacaceae*: GO; *Montiaceae* and *Talinaceae*: GO, with contributions by UE; *Cactaceae*: SA, UE, NK, RN, BOS; *Caryophyllaceae*: RR, BO (*Silenae*), with contributions by SVM; *Basellaceae*: RE; *Chenopodiaceae*: HA, HFO, SFB, GK, PU; *Gisekiaceae*: GK; *Plumbaginaceae*, *Kewaceae*, *Macarthuriaceae* and contributions to other families (*e.g.* *Deeringia*, *Hypertilis*, *Microtea*): SVM; *Polygonaceae*: ICN, AS; *Tamaricaceae*: HA. WGB extensively rechecked the nomenclatural references and standardization of database entries. SVM edited entries and updated the database. Introduction and summary were prepared as a draft by PH, TB and WGB. Comments from co-authors were incorporated, and the final text edited by WGB, SVM, NK and TB.

**Acknowledgements**

We would like to acknowledge the technical support by Katja Luther, Andreas Müller and Cherian Mathew at the BGBM during work with the EDIT Platform software and the production of the generic list directly from the database. There was a productive exchange with James Solomon (Missouri Botanical Garden) while checking our nomenclatural data against the Tropicos database. Werner Greuter, Nicholas Turland, and Wolf-Henning Kusber are advised for advice on complicated cases of nomenclature. Demet Töre provided literature on *Plumbaginaceae*.

Wilhelm Barthlott, Peter Bruyns and Nicholas Turland are thanked for granting permission to use their photographs. David Hunt, John McNeill, Sergei Mosyakin, Kai Müller, Louis Ronse de Craene, Nigel Taylor and one anonymous reviewer are thanked for their valuable comments on an earlier version of the manuscript.

**References**


Akhani H. & Khoshravesh R. 2013: The relationship and different C₄ Kranz anatomy of *Bassia eriantha* and *Bassia eriophora*, two often confused Irano-Turanian and Saharo-Sindian species. – Phytotaxa 93: 1–24.

Akhani H. & Khoshravesh R. 2015: Taxonomic novelties from Irano-Turanian region and NE Iran: *Oresalsola*, a new segregate from *Salsola* s.l., two new species in *Anabasis* and *Salvia*, and two new combinations in *Caroxylon* and *Seseli*. – Phytotaxa (in press).

Akhani H., Lara M. V., Ghasemkhani M., Ziegler H. & Edwards G. E. 2009: Does *Bienertia cycloptera* with the single-cell system of *C₄* photosynthesis exhibit a seasonal pattern of delta C¹³ values in nature similar to co-existing *C₄* *Chenopodiaceae* having the dual-cell (Kranz) system? – Phot. Res. 99: 23–36.


Albert V. A., Williams S. E. & Chase M. W. 1992: Car-

Barthlott W. & Taylor N. P. 1995: Notes towards a mono-
graph of Rhipsalideae (Cactaceae). – Bradleya 13: 43–79.


Calvente N., Zappi D. C., Forest F. & Lohmann L. G. 2012a: Molecular phylogeny of tribe Rhipsalideae (Cactaceae) and taxonomic implications for Schlum-
Hernández-Ledesma & al.: A taxonomic backbone for Caryophyllales

366


Charles G. 2009: Gymnocalycium in habitat and culture. – Stamford: Published by the author.


Cruz D. R. & Alcántara A. O. 2000: Anormalidad floral en Phylolaccaceae icosandra L.. (Phylolaccaceae) en


Ghaffari S. M. 2004: Cytotaxonomy of some species of Acanthophyllum (Caryophyllaceae) from Iran. – Biologia (Bratislava) 59: 53–60.
González R. J. 2007: Nyctaginaceae. – Pp. 785–796 in:


Hochstättler F. 2005: The genus *Sclerocactus* tribe *Cacteae*, family *Cactaceae*. – Mannheim: Published by the author.


Hoffmann A. & Walter H. 2005: Cactáceas en la flora sil­vestre de Chile, ed. 2. – Santiago de Chile: Ediciones Fundación Claudio Gay.


McPherson S. 2009: Pitcher plants of the Old World 1. – Poole: Redfern Natural History Productions.

McPherson S. 2011: New Nepenthes 1. – Poole: Redfern Natural History Productions.


Mosyakin S. L. 1996: Chenopodium. – Pp. 27–44 in:


Mosyakin S. L., Rilke S. & Freitag H. 2014: (2323) Proposal to conserve the name Salsola (Chenopodiaceae s.str.; Amaranthaceae sensu APG) with a conserved type. – Taxon 63: 1134–1135.


Ocampo G. & Columbus T. 2010: Molecular phylogenetics of suborder Cactineae (Caryophyllales), including insights into photosynthetic diversification and historical biogeography. – Amer. J. Bot. 97: 1827–1847.


Ogundipe O. T. & Chase M. 2009: Phylogenetic Analyses of Amaranthaceae based on matK DNA sequence...


Pitirainen M. 2015: (2353) Proposal to conserve the name Halostachys (Chenopodiaceae s.str.; Amaranthaceae sensu APG: Salicornioideae) with a conserved type. – Taxon 64: 386–387.


Ritter F. 1980: Kakteen in Südamerika 2. – Spangenberg: Published by the author.

Ritz C. M., Martins L., Mecklenburg R., Goremykin V. & Hellwig F. H. 2007: The molecular phylogeny of Rebutia (Cactaceae) and its allies demonstrates the influence of paleogeography on the evolution of South American mountain cacti. – Amer. J. Bot. 94: 1321–1332.


Ronse De Craene L. P., Volgin S. A. & Smet E. F. 1999: The floral development of Pulearepalatum darwinii,
Snijman D. A. & Manning J. C. 2013: Chenolea convallis, a new species from Western Cape Province, South Africa. – Bothalia 43: 80–84.