

Preface

With the constant flow of plant species that reached Europe in the times of the great expeditions in the 18th and 19th century, the demand for any form of cataloguing the steadily growing diversity became inevitable. Succulent plants always fascinated plant-loving people above average, and the first handbooks devoted to succulents were published in the 19th century. Initially, however, interest was focussed on the *Cactaceae*. It was only 1954/55 when Herman Jacobsen (1898 - 1978), the former curator of the Botanic Garden of Kiel, made available a first handbook devoted to succulents (excl. *Cactaceae*), the "Handbuch der sukkulenten Pflanzen". An abridged version of this handbook was published by Jacobsen as "Sukkulentenlexikon" in 1970. It included descriptions, synonymies and numerous illustrations. The "Sukkulentenlexikon" represented the long-awaited reference work supporting both Botanical Gardens as well as amateur or professional growers in the navigation through succulent plant diversity. An English edition followed in 1975 as "Succulent Lexicon", and a revised German edition was published in 1981. This second edition had been finished by Jacobsen's successor in Kiel, Klaus Hesselbarth, who, with regard to the *Asclepiadaceae*, was supported by the senior editor of the present publication.

Over twenty years have passed since then, and the knowledge on succulent plants has increased permanently. We saw monographs of formerly little-known groups and many revisions and re-revisions, which often change the taxonomy within single groups considerably. A large amount of new taxa has been published on one hand, and on the other hand, many taxa have been sunk into synonymy. Therefore, a new lexicon-like contribution covering the whole succulent plant world, incl. the *Cactaceae*, was taken into consideration by various members of the International Organization for Succulent Plant Study (IOS) more than 10 years ago. Gustav Fischer-Verlag Jena, the publisher of both Backeberg's "Kakteenlexikon" and Jacobsen's "Sukkulentenlexikon", encouraged the project, which was informally termed the "New IOS Succulent Plant Lexicon", and later "Synopsis Plantarum Succulentarum". This new work was primarily planned to consist of three volumes (*Cactaceae*, *Aizoaceae*, other Succulents), and after a consensus regarding style and format had been found, the compilation of the *Asclepiadaceae* taxa started in 1994. With the disappearance of Gustav Fischer-Verlag, the project was adopted by Springer-Verlag for the English edition, and by Verlag Eugen Ulmer, for the German edition, and the series finally changed its title to "Illustrated Handbook of Succulent Plants". Also with regard to the enormous array of taxa of other succulents finally found worth to be presented, the early concept was adapted. Accordingly, the series in its English version now appears in six volumes altogether: Two volumes cover the *Aizoaceae* (Hartmann 2001); one volume each treats the Monocotyledons (Eggli 2001), the *Asclepiadaceae* (respectively *Apocynaceae* – *Asclepiadoideae* and – *Periplocoideae*, Albers & Meve 2002, this volume), the *Crassulaceae* (Eggli, in preparation for 2003), and the remaining groups in a mixed volume of Dicotyledons (Eggli 2002). The *Cactaceae* will not become available in time to be included in the present handbook series.

Apart from doubling the number of *Asclepiadaceae* genera covered, and their presentation in one volume solely dedicated to this plant group, this new handbook has many additional features such as the vastly expanded descriptions incl. typification data for all accepted taxa, full synonymy and literature references that lead to published illustrations. Keys to main groups and genera are provided. Although desirable, we do not include keys to the species. This would have made an excessive demand, esp. in species-rich genera such as *Ceropegia*, which could not be performed within the frame of this handbook.

It took us tremendous efforts over the years of compilation to keep the taxonomy as actual as possible. Taxonomy means change – this is esp. true with regard to the last years where asclepiad systematic research saw a powerful renaissance. In 2000, we even lost "our family", the *Asclepiadaceae*, because of the formal transposition of the subfamilies *Asclepiadaceae* – *Asclepiadoideae* and *Asclepiadaceae* – *Periplocoideae* to the *Apocynaceae*. For pragmatic reasons (e.g. avoiding the clumsy new taxon names) we nevertheless stick to the *Asclepiadaceae* in the title of the present work.

Sometimes, publications like revisions or monographs that could serve as base for our compilations do not exist. This is esp. true for the two largest genera of the *Asclepiadaceae* – *Ceropegieae*, *Ceropegia* (\pm 180 species) and *Brachystelma* (122 species), as well as for *Hoya* (\pm 200 species), the largest genus of the tribe *Marsdenieae*. While for *Ceropegia* the revision of H. Huber (1957) is outdated, a complete generic treatment has never been produced for *Brachystelma*. Own research and literature studies were unavoidable here. Although not all problems could be solved, the *Brachystelma* treatment published in this volume is the first complete "critical" presentation of this interesting genus at all. The last and only full generic treatments of *Hoya* originate from the 19th century (Decaisne 1844, Hooker 1885). Since then, due to the enormously increased number of taxa described, further revisions of *Hoya* were restricted to a regional scale, their sum being far away from representing a complete generic revision. The presentation of *Hoya* in this handbook is therefore restricted to the better known, mostly cultivated and predominantly succulent taxa.

The core and most popular asclepiadaceous succulents are represented by the stem-succulent stapeliads. Here, recent revisions often compete against each other, and made it difficult to decide which should be followed. Usually, only one revision is followed, though sometimes a pragmatic concept considering the different revisions available plus own assessments have been applied. For the genus *Caralluma* s.l., a conservative circumscription is presented despite the editors' knowledge of the necessary recircumscription of *Caralluma* and its division into a few smaller genera. However, the new taxonomy was not available within the deadline of the present work. In parts, this is also true for the recircumscription of *Cynanchum*.

Apart from the classical succulents of the tribe *Ceropegieae*, several less well-known groups or taxa are presented in this book. Inclusion has been mainly influenced by horticultural value.

Several persons helped during the production process, whether as compiler of texts (Anke Brennecke, Christiane Hoffmann, Janine Kiel, Rainer Kranz, Dr. Sigrid Liede, Birgit Müller, Petra Stegemann, Beate Willke and Ruurd van Donkelaar) or as authors of additional illustrations (Josef Bogner, Dr. Wiebe Bosma, Dr. Urs Eggli, Dr. David Goyder, Dr. Sigrid Liede, Ernst Specks, Dr. Joachim Thiede and Ruurd van Donkelaar). The support of various journals and their editors in publishing necessary new combinations or names is gratefully acknowledged. Many of the above named and further unnamed persons contributed with literature/photocopies, provided us with additional specimens or living plants for study (namely the Sukkulenten-Sammlung Zürich under its former director Dieter Supthut), or with a wide array of any kind of information on taxa, types, distribution etc. We gratefully acknowledge their long-standing interest in the project.

We would like to thank Dr. Johanna Schlüter, Gustav Fischer-Verlag Jena, for fruitful cooperation during the first years of the project. Finally, the endless patience and painstaking accuracy of the series editor responsible for this volume, Dr. Urs Eggli, in transposing our texts into the standard format, tracing the many nomenclatural problems, and composing the final layout of text and colour plates is gratefully acknowledged.

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What is a succulent ?

It is probably impossible to define what constitutes a *succulent plant* – at least in view of the several competing definitions. For the purpose of this handbook, a pragmatic approach has been selected, and apart from the multitude of unambiguous succulents, many borderline cases are included as well, especially if the species in question are encountered in cultivation together with other succulents, and if they are native to more or less semi-arid regions and consequently show some degree of xerophytic adaptation. This, then, includes most of the caudex and pachycaul plants now popular in cultivation.

Other borderline cases included are a number of bulbous and rhizomatous monocotyledons, where examples from several genera are covered, as well as several weakly developed leaf succulents from the *Gesneriaceae* (e.g. *Columnnea*).

On the other hand, purely halophytic succulents (such as *Salicornia*) are omitted from these pages since they are as a whole neither adapted to climatically dry conditions nor encountered in collections devoted to succulent plants.

Finally, some families with undoubted claim to (xerophytic) succulence have been excluded from this set of volumes. This notably is the case for the *Cactaceae*, which will be treated elsewhere. In addition, the families *Bromeliaceae* and *Orchidaceae* are also excluded. Both count with a considerable number of mostly leaf succulents, but for both, vast specialist literature and numerous specialist societies are in existence, and this effort does not need to be duplicated here. For all these excluded families, however, a family description is included in the present volumes for the sake of completeness.

How to use this handbook

Since all information is presented in strictly alphabetical sequence of families, genera and species (except that monocotyledons and dicotyledons are treated separately, and that the families *Aizoaceae*, *Asclepiadaceae* and *Crassulaceae* occupy their own volumes), it is easy to find the entry for a given species as long as its family placement is known.

An alternative way is to use the taxonomic cross-reference index supplied at the end of the

volume. This index contains all the names treated in the volume and for accepted names indicates the page where a treatment can be found, or in the case of synonyms gives the name of the accepted taxon and a page reference as above. For names merely mentioned in the text, the index gives the page reference and the name under which information can be found.

If a completely unknown plant is to be identified, the handbook supplies keys to the genera with succulent representatives for each family. Please note that these keys are designed to work for the succulent taxa treated, and do not necessarily include the total variation encountered in a genus. If the family is not known, the reader is referred to general botanical books that include keys to plant families. Rowley (1980) and Egli (1994) provided keys for flowering and non-flowering succulents, and Geesink & al. (1981) produced a well-known book of keys to all flowering plants worldwide.

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The following families are included as a whole, i.e. with all their component species: *Agavaceae*, *Aloaceae* and *Doryanthaceae* in the present volume covering the Monocotyledons, and the *Didiereaceae*, *Fouquieriaceae* and *Nolanaceae* in the Dicotyledons volume. The *Aizoaceae* and *Crassulaceae* are covered in their entirety in separate volumes within this series, and the succulent taxa of the *Asclepiadaceae* likewise occupy a separate volume of the Handbook.

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This is followed by notes on the distribution, classification and economic importance of the family, and the occurrence of succulence if this is not a general feature of the family as a whole. Also, a key to genera with succulents is included, and special terminology used for genera and species descriptions is discussed.

The family concept adopted more or less follows Mabberley (1987), except for the monocotyledons, where Dahlgren & al. (1985) is used as a base, with a number of small modifications.

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The entries for genera and species follow the same layout. Names of authors are given in full, with initials added where necessary according to Brummitt & Powell (1992). The literature reference of the original description or combination is followed by information on typification (where available, see below). In the case of genera, important literature is then cited. This is followed by information on geographical distribution (including notes on ecology where available) and an explanation of the etymology for generic names.

The main part of the entry is made up by the diagnostic description of the taxon, followed by a discussion of its variability, circumscription and/or application where necessary. It should be noted that these descriptions reflect major variability only, but do not include all the reported minor variations.

For larger genera, an outline of the accepted formal or informal classification is also given, with individual taxa or groups numbered in sequence. These sequence numbers are then given at the start of each taxon description to indicate its placement within the genus.

If recent conflicting classifications are available for a given group, this is shortly discussed and the classification adopted is indicated.

Minor spelling variants of epithets are not indicated; instead, the 'corrected' spelling is used throughout for accepted names and synonyms.

Infraspecific taxa

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Asclepiadaceae

Shrubs, woody or herbaceous left-twining climbers, perennials with deciduous herbaceous above-ground parts or stem succulents, with watery or milky sap; **L** decussate, rarely whorled, simple and entire (rarely lobed or divided), sometimes much-reduced, absent or spinescent (in stem succulents); **Inf** cymose (terminal thyrses), rarely racemose; **Fl** actinomorphic, bisexual; **Sep** 5, basally connate; **Pet** 5, usually connate; **Cl** occasionally forming outgrowths on the upper face (→ petaloid corona, Fig. 1A); **St** 5, alternating with the **Pet**; **Fil** free, basally fused with the **Cl**, **Anth** coherent (→ *Periplocoideae*) or all **St** postgenitally fused with the **Sty** head into a column (= gynostegium, **Gy**) (→ *Secamonoideae*, *Asclepiadoideae*); **Gy** mostly with a simple (staminal) or double (staminal plus interstaminal) corona (**Cn**, Fig. 2A); **Anth** 4-locular (→ *Periplocoideae*, *Secamonoideae*) or 2-locular (→ *Asclepiadoideae*), pollen in tetrads and freely presented on pollen-carriers (translators, Fig. 1B) (→ *Periplocoideae*) or pollen grains of each pollen sac coherent into a pollinium (**Poll**) and adjacent **Poll** united into a pollinarium by means of a translator (→ *Secamonoideae*, *Asclepiadoideae*) (Fig. 2B); gynoeceum of 2 apically connate **Ca**, which are united by means of the 5-angular **Sty** head; **Fr** paired or single follicles, with few to many **Se**, not fleshy, slender to inflated; **Se** usually flattened, with or without wing, with a terminal silky tuft of **Ha** (coma).

Distribution: Worldwide, esp. subtropics and tropics.

Literature: Liede & Albers (1994); Sennblad & Bremer (1996); Swarupnandan & al. (1996); Liede (1997); Endress & Bruyns (2000).

The family consists of some 240 genera with 3400 species. Of these, 61 genera can be referred to as succulents in the widest sense.

In the present account, the *Asclepiadaceae* are treated as a family, which according to Schumann (1895), Bruyns & Forster (1991) and Liede & Albers (1994) is subdivided into the 3 subfamilies *Periplocoideae*, *Secamonoideae* and *Asclepiadoideae*. This conservative taxonomic view has been taken, since this is the system still widely accepted among scientists and amateurs alike. However, as has already been implied by earlier morphological studies, progress in molecular research suggests to include all 3 subfamilies into the *Apocynaceae* and to abandon the *Asclepiadaceae*, see Olmstead & al. (1993) or Sennblad & Bremer (1996). This concept has been formally transformed into taxonomy by Endress & Bruyns (2000).

The widely accepted suprageneric system of the *Asclepiadaceae* by Bruyns & Forster (1991), which

largely relies on morphological data, is based on the classification of Brown (1810) and Schumann (1895), to which the newly described tribe *Fockeeae* by Kunze & al. (1994) has to be added. The inclusion of the tribes *Marsdenieae* into the *Stapeliaceae* by Swarupnandan & al. (1996) and *Gonolobeae* into the *Asclepiadeae* by Liede (1997) still needs to be corroborated and are not adopted here. The technical terms used in the keys and descriptions that follow are explained in the longitudinal flower sections and detail illustrations presented in Fig. 1 and Fig. 2.

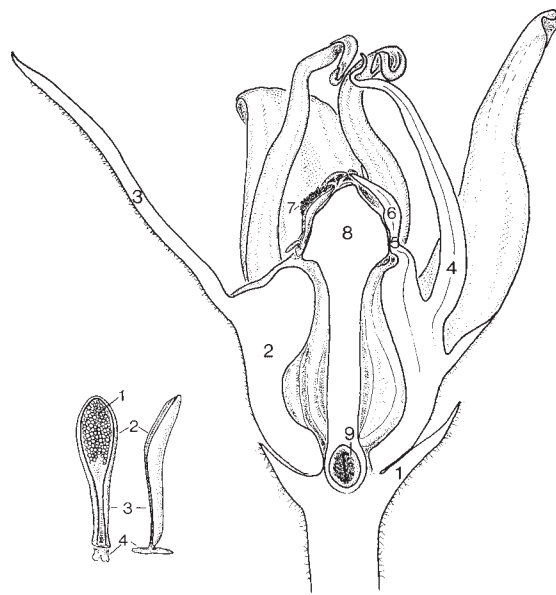


Fig. 1: *Raphionacme madiense*. – **Right:** Longitudinal section through a flower (1 sepal (**Sep**); 2 corolla tube; 3 corolla lobe; 4 (petaloid) corona; 5 filament (**Fil**); 6 anther (**Anth**); 7 translator; 8 style head; 9 ovary). **Left:** Translator, left in top-view, right in side-view (1 heaps of pollen tetrads; 2 scutellum; 3 stipes [= stalk]; 4 adhesive disc [= viscidium])

The *Asclepiadaceae* constitute a derived family showing complex floral structures, which are dedicated to the service of a highly specialized pollination biology (→ Figs. 1 and 2). The presence of fascinating floral structures and colours in connection with facilities fostering deceit, trapping and attachment as well as the possession of pollen-masses (pollinia) warrant the *Asclepiadaceae* to be seen as the ‘orchids’ among the dicotyledons. This, combined with numerous forms of succulence, has made members of this family attractive objects for the plant lover – in particular ceropegias and stapeliads with their pitfall and carrion flowers. Notwithstanding, they are often fairly difficult to cultivate in comparison to cacti, which may occasionally diminish the pleasure taken in them. The question of suc-

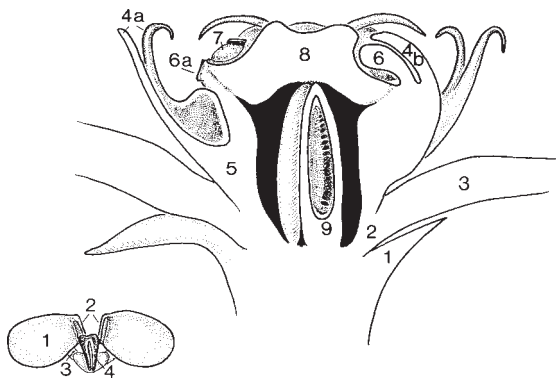


Fig. 2: *Caralluma adscendens*: – **Right:** Longitudinal section through a flower (1 sepal (**Sep**); 2 corolla tube; 3 corolla lobe; 4a interstaminal corona (**CI**); 4b staminal corona (**CS**); 5 filament tube; 6 anther (**Anth**); 6a guide rail; 7 pollinium (**Poll**); 8 style head; 9 ovary). **Left:** Pollinarium (1 pollinium (**Poll**); 2 germination crest; 3 caudicle; 4 corpuscle)

culence is one of definition on the one hand (e.g. whether root succulence constitutes genuine succulence or not). On the other hand, in particular cases it may prove difficult to delimitate succulents against other xerophytic life forms. The term succulence is used here in a very broad sense, not least to allow the inclusion of all taxa being worthy of cultivation or actually encountered in cultivation. Nevertheless, as a rule all taxa treated have at least one fleshy-thickened organ, be it root, stem or leaves. Thus, some 1000 succulent species, subspecies etc. of 61 genera from all tribes of the *Asclepiadaceae* (excl. *Secamoneae*) are included. Except for a few species of the genera *Asclepias*, *Marsdenia* and *Matelea*, succulence in this family is confined to the Old World. In the subfamily *Periplocoideae*, succulence occurs almost exclusively in Africa and usually in the shape of huge storage tubers (e.g. *Raphionacme*). Succulence is likewise made up by usually subterranean storage organs in the tribes *Fockeeae*, *Asclepiadeae* and *Gonolobeae* of the subfamily *Asclepiadoideae*. In contrast, the tribe *Marsdenieae* is characterized by the large number of leaf succulent members of the generally epiphytic genera *Dischidia* and *Hoya* from Australasia. Finally, most succulents, esp. stem succulents, belong to the tribe *Ceropegieae* with 34 genera of almost exclusively African origin.

Apart from their use as ornamentals and of the seed-hairs as poor-quality floss, the family has no economically important taxa. A few species are utilized as natural remedies owing to their content of alkaloids, cardenolides, pregnane esterglycosides (Hegnauer 1989).

Key to the subfamilies and tribes with succulents

- 1 **Anth** 4-locular, pollen tetrads loosely on a shovel-shaped translator, translator basally with an adhesive disc (viscidium): 2 (*Periplocoideae*)
 - **Anth** 2-locular, pollen coherent in masses (pollinia, **Poll**), translator with a corpuscle: 4 (*Asclepiadoideae*)
- 2 **CI** rotate with very short **CI** tube, **St** arising from the base of the **CI**:
 - Periplocoideae** – **Periploceae**
 - **CI** with conspicuous cylindrical to campanulate **CI** tube, **St** arising from within the **CI** tube: 3
 - 3 **St** and **Cn** originating from the upper margin of the **CI** tube: **Periplocoideae** – **Gymnanthereae**
 - **St** originating from the base to the middle of the **CI** tube, **Cn** arising from the base to the margin of the **CI** tube:
 - Periplocoideae** – **Cryptolepideae** (**Stomatostemma**)
- 4 **Poll** with a asymmetrical marginal zone that is not serving as germination zone for the pollen:
 - Asclepiadoideae** – **Gonolobeae** (**Matelea**)
 - **Poll** without conspicuous marginal zone or with symmetrical marginal zone serving for the germination of pollen (germination crest): 5
 - 5 **Poll** pendent: **Asclepiadoideae** – **Asclepiadeae**
 - **Poll** erect: 6
 - 6 **Anth** without sterile (connective) appendage:
 - Asclepiadoideae** – **Ceropegieae**
 - **Anth** with sterile (connective) appendage: 7
 - 7 **Poll** attached to the corpuscle by means of a translator arm: **Asclepiadoideae** – **Marsdenieae**
 - **Poll** directly attached upon the corpuscle:
 - Asclepiadoideae** – **Fockeeae**

Key to the succulent genera of the *Periplocoideae*

Tribe *Periploceae*

- 1 Robust lianas with huge caudex, **CI** lobes widely spreading, 12 - 15 mm long: **Petopentia**
 - Shrubs, partly epiphytic, with several ovoid tubers, **CI** lobes ascending, overlapping, 5 mm long: **Sarcorrhiza**

Tribe *Gymnanthereae*

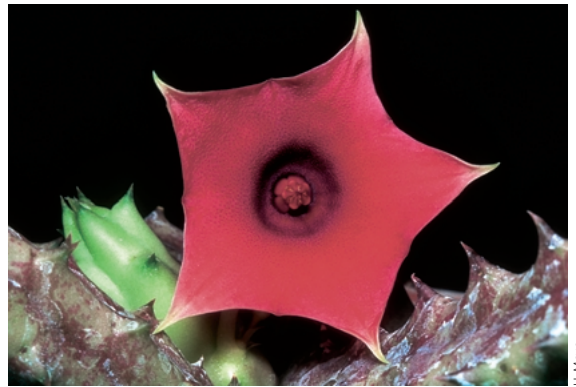
- 1 Shrubs with many small tubers, **L** (seemingly) 3-partite, linear, **Cn** basally fused to the **Fil**:
 - Ischnolepis**
 - Herbaceous perennials or lianas, (usually) with 1 tuber only, **Cn** only fused with the **CI**: 2
- 2 **Fl** robust, pollen loosely on the translator:
 - Raphionacme**
 - **Fl** delicate, short-lived, pollen in 2 pollen-masses (**Poll**) on each translator/**Anth**: **Schlechterella**



a *Huernia keniensis* var. *keniensis*



b *Huernia leachii*



c *Huernia lenewtonii*



d *Huernia macrocarpa*



e *Huernia nouhuysii*



f *Huernia saudi-arabica*



g *Huernia tanganyikensis*