

Peter V. Bruyns

Euphorbia in Southern Africa

Volume 1

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Peter V. Bruyns
University of Cape Town
Rondebosch, South Africa

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New synonyms published in this work: *Euphorbia grandialata* R.A. Dyer is reduced to synonymy under *E. grandicornis* A. Blanc, *E. halipedicola* L.C. Leach under *E. bougheyi* L.C. Leach, *E. decliviticola* L.C. Leach under *E. graniticola* L.C. Leach, *E. stenocaulis* Bruyns under *E. plenispina* S. Carter.

Lectotypes are designated here for *Euphorbia benguelensis* Pax, *E. caerulescens* Haw., *E. cucumerina* Willd., *E. enopla* Boiss., *E. fleckii* Pax, *E. genistoides* var. *leiocarpa* Boiss., *E. genistoides* var. *major* Boiss., *E. grandicornis* K.I. Goebel, *E. grandicornis* J.E. Weiss, *E. involucrata* var. *megastegia* Boiss., *E. latimammillaris* Croizat, *E. melanosticta* E. Mey. ex Boiss., *E. nodosa* N.E. Br., *E. platymammillaris* Croizat, *E. polygonata* G. Lodd., *E. proteifolia* Boiss., *E. trichadenia* var. *gibbsiae* N.E. Br. and *Tithymalus zeyheri* Klotzsch & Garcke.

A type is also designated for the genus *Tirucalia* Raf.

Euphorbia L., with around 1840 species, is one of the largest genera of flowering plants and is by far the largest genus in the Euphorbiaceae. Common to all species of *Euphorbia* is the copious milky sap (transported to all organs of the plant by unarticulated laticifers), the possession of an unusual but typical ‘inflorescence’, the cyathium and the absence of a perianth in the male florets. Along with its almost cosmopolitan distribution comes a bewildering variety of vegetative forms. Many of the species are small to medium-sized herbs. In stark contrast to these are some spectacular species in Africa, the Arabian Peninsula and Peninsular India, which may form enormous succulent trees reaching 30 m tall (as in *E. ampliphylla*, *E. cussonioides* and *E. ingens*). Even among the succulent species there is remarkable variation, from these huge trees to dwarf spherical or globose plants that often do not exceed 50 mm tall at maturity (such as *E. gymnocalycioides* and *E. obesa*) or small geophytes with a rosette of leaves flat on the ground (such as *E. acaulis*, *E. rubella* and *E. tuberosa*) and even tiny annuals not exceeding 10 × 100 mm (as in *E. prostrata*). The larger members form a conspicuous and characteristic, sometimes dominant component of the vegetation of many of the tropical, semi-arid areas of Africa, the Arabian Peninsula and Peninsular India. Outside the tropics, succulent species of *Euphorbia* are an important component in semi-arid, temperate areas receiving winter-rainfall in southern Africa (in the Greater Cape Flora) and in north-west Africa in some parts of coastal Morocco and on the Canary Islands.

The last revision of *Euphorbia* for southern Africa was contained in N.E. Brown’s accounts in *Flora of Tropical Africa* Vol. 5 (2) and *Flora Capensis* Vol. 5 (2) (Brown 1911–12; 1915). The succulent species received further detailed attention from R.A. Dyer (1931) for the Eastern Cape and for the region as a whole in *The succulent Euphorbieae (Southern Africa)* by Alain C. White, R. Allen Dyer and Boyd L. Sloane, a sumptuous pair of tomes which appeared in 1941. This monograph was largely based on the field-experience of Dyer, who travelled widely to collect and familiarise himself with the species in habitat. Subsequently, regional accounts were



Fig. 1.1. Milky sap oozing from cut branch of *Euphorbia grandidens*, PVB 6870a, Springs, NE of Uitenhage, South Africa, 16 Jul. 2018 (© PVB).

published by P.G. Meyer (1967) for Namibia and by Carter & Leach (2001), where Botswana was included within the area of the Flora Zambesiaca. The 80 years since 1941 have seen much more extensive exploration of southern Africa. During this period some new species have come to light (most of these in formerly inaccessible areas such as Kaokoveld,

Namibia), but the taxonomy of *Euphorbia* in southern Africa has become progressively disorganised, with many names applied in different herbaria in South Africa to quite different species. Further exploration has clarified the distributions of and variation in most of the species. This led to the realisation that some of the ‘species’ discussed by White et al. (1941) were not distinct (though in many such cases they expressed reservations about their distinctness), while a few others mentioned there were undescribed and a few that they had reduced to synonymy were distinct species. Therefore, *The succulent Euphorbieae (Southern Africa)* is now considerably out-of-date and is difficult to use for the identification of recent collections, so that there is an urgent need for a replacement.

This book presents a new account of the southern African species of *Euphorbia*. For our purposes, southern Africa is taken to be most of Africa south of 17°S, including the whole of Botswana, Lesotho, Namibia, South Africa and Swaziland (but leaving out Moçambique and Zimbabwe). The island of Madagascar, with its rich and almost exclusively endemic euphorbiaceous flora, is also not included.

In this area *Euphorbia* is represented by 172 species, which are distributed across all four subgenera. Although none of these subgenera is endemic to the region, there are several sections and subsections that are only found in southern Africa. Of the 172 species found in southern Africa, 128 are endemic. The 44 non-endemic species mainly extend beyond southern Africa into Angola and the southern parts of East Africa but a few, such as *E. ingens*, are found from subtropical South Africa to southern Ethiopia and Somalia. Although fewer than 10% of the species in *Euphorbia* are treated here, 74% of these are endemic and so this book will have little overlap with any account of the species from further north.

This book brings together the results of the exploration and research that has taken place over the past 80 years. The first section introduces the reader to the diversity in *Euphorbia*, especially in the vegetative parts, but also in how the flowers are arranged. The terminology peculiar to the floral organization of *Euphorbia* is explained and illustrated with examples. The second section is the systematic account, where the species are arranged into their sections, subsections and series as these have recently been defined. Keys are provided to all the species within each of these subdivisions, while keys to the subspecies and varieties are provided under the respective species in the systematic account. Of the 172 species in southern Africa, 157 are presented in detail here. Each is illustrated with several colour photographs, with a map showing its known distribution and with line drawings in which some of the minute details of the plant and floral parts are highlighted.

This book would not have been possible without the generous help received over many years from many individuals. My early interest in succulents was particularly fostered by excursions into the field with Walter Wisura, formerly the curator for succulents at Kirstenbosch and by M. Bruce Bayer, formerly the curator of the Karoo Botanic Garden,

Worcester. Succulent species of *Euphorbia* were collected and recorded during my earlier collecting work on stapeliads, which led to the development of a large data-base of collections in otherwise poorly explored areas. Many kind and helpful farmers have allowed access to their properties to look for *Euphorbia* and other plants. I particularly wish to thank the following for their hospitality and help: Johann and Odile Becker, Rolf Becker and Alma Möller, Susanne Bell, Susan and Richard Dean, Elke Erb, Wilfried Friedrich, the late Johan Geldenhuys, Michael and Joanne Kroon, Frans and Duberette Labuscagne, Molly, Chris and Marina Lochner, Paul and Linda Loffler, Douglas McMurtry and Shane Burns, Steven, Alicia and Pieter Theron, James and Regina van Vuuren and Gordon and the late Ada Whittal. David Cumming, Sean Geldenhuys and P.J.D. Winter shared valuable information on several little-known species.

Paul E. Berry of the University of Michigan involved me in the Planetary Biodiversity Inventory-working-group on *Euphorbia* and gave financial assistance for visits to some European herbaria. He also provided very helpful criticism of some papers which contributed towards this work and commented on most parts of this work itself. Erich van Wyk and Jean J. Meyer provided regular assistance during visits to the herbarium at PRE, the largest collection of *Euphorbia* in southern Africa. Christiane Anderson and Rafaël Govaerts have frequently assisted with nomenclatural questions, while Gill Challen at Kew (K) and Arne Anderberg at Stockholm (S) arranged for many scans of specimens in their respective institutions. I am also grateful to the Keeper of the Herbarium, Royal Botanic Gardens, Kew for permission to publish the illustrations by George Bond and Thomas Duncanson of several types of Haworth’s species, as well as several of the lovely water-colour sketches by Nell Lugard. All of these were scanned for me with great care at Kew by Patricia Long. Dmitry Geltman assisted with the world-wide distribution of subg. *Esula*. John Burrows, Steven P. Fourie, Graham & Kate Grieve, Pavel Hanáček, Niels Jacobsen, J.A.R. de Paiva (Coimbra), Ralf Peckover, Ernst Schmidt and Geoff Tribe each allowed me to use several of their photographs.

Finally, I wish to thank Cornelia Klak for her support and encouragement and also for many useful suggestions, which have helped to improve this book substantially.

1.1 Historical Sketch

Since *Euphorbia* is well-represented in Europe and Asia, it has been known as long as interest in plants has existed. Members of *Euphorbia* have long been held to have medicinal value and the name itself is derived from ‘*Euphorbos*’, ostensibly a ‘physician’ to Juba, ruler of the ancient kingdom of Mauretania in West Africa. Nevertheless, the species of the northern hemisphere are rarely succulent. The succulent species have an unusual appearance and were reputed to yield sap

that had great curative value. The first such succulents were recorded from Morocco, the Canary Islands and southern India as early as 1570 (Croizat 1934), as European exploration of these areas began to gather steam. Around 1680 the distinctive and characteristic plants of *Euphorbia* of southern Africa began to appear in European accounts of exploration at the Cape. Several were cultivated at Cape Town (especially in the garden of Colonel Robert Gordon) and soon cuttings and seed of these were taken to and cultivated in Europe. It was immediately obvious that these succulent species exhibited greater diversity than those known from elsewhere. How this diversity was to be dealt with taxonomically was not quite understood. This one sees from the account of *Euphorbia* in Linnaeus' *Species Plantarum* of 1753, which contains 56 species and is surprisingly confused about the southern African succulent species (see for example what he included under *E. caput-medusae*). Some of this confusion arose in the doctoral dissertation from 1752 of his student Johannes J.F. Wiman and was taken over into the *Species Plantarum* (Croizat 1934).

The documentation of *Euphorbia* in southern Africa can really be said to have begun in earnest with the explorations of C.P. Thunberg and Francis Masson between 1772 and 1795. Thunberg spent nearly 3 years at the Cape and during this time he and Masson explored some areas together. Masson spent a total of about 12 years at the Cape during two visits and left for England for the last time early in 1795. Thunberg made specimens of several species of *Euphorbia*, including several succulents. Such novelties as *Euphorbia meloformis* were among the many remarkable species that they encountered and which Masson sent back as live specimens to England. Nevertheless, neither seems to have had a particular interest in *Euphorbia* and the same is true of the famous collectors Ecklon & Zeyher and the brothers Drège, who discovered many other species before 1840. These were gathered during their general collecting activities, which were so comprehensive that the first floristic accounts for South Africa could be compiled from them. Several new species were described by Haworth from among the many succulents sent back to Kew by James Bowie, who explored at the Cape from 1816 until 1823.

During his preparation of the accounts of *Euphorbia* for the *Flora of Tropical Africa* and the *Flora Capensis*, N.E. Brown (1911–12; 1915) was especially aided by the collecting activities in South Africa of Rudolf Marloth. Marloth was the first botanist who took a particular interest in *Euphorbia*, discovering many new species and describing many of these himself. Marloth also tried to clarify the identity of some of the lesser-known species, such as *E. virosa*. He and others in South Africa assisted Brown with material of some of the succulent species, which were generally poorly represented in herbaria. Marloth knew and documented most of the widely distributed species and completed the basic exploration for *Euphorbia* in South Africa. Nevertheless, significant discoveries have been made subsequent to his work. In particular, many quite local species

have been discovered since then, especially in the north-east of South Africa (where many were discovered by F.Z. van der Merwe) and in the north-west of Namibia, where Major Hahn and Max Otzen found several for the first time. Most of these were described by R.A. Dyer and a few more were named later by L.C. Leach.



Fig. 1.2. Rudolf Marloth in 1887 (© Stellenbosch University Archives).



Fig. 1.3. Rudolf Marloth in the field near Cape Town in 1912 (© Stellenbosch University Archives).

After Marloth, possibly the person with the greatest interest in *Euphorbia* was Robert Allen Dyer. Dyer worked from 1925 until 1930 at the Albany Museum in Grahamstown. Initially he was the Botanical Survey Officer and later, after the retirement of S. Schönland, he became curator of the Museum's Herbarium. This is an ideal place for someone interested in succulents and particularly in *Euphorbia*, which is especially diverse in that area. His investigations there led to an account of *Euphorbia* in the Eastern Cape (Dyer 1931), where he placed on record many of his discoveries. From 1931 to 1934 he worked at the Herbarium at Kew, England and this experience turned his attention away from ecology towards taxonomy. After returning to South Africa he continued collecting while employed at the Botanical Research Institute in Pretoria. He documented the distribution of *Euphorbia* widely over South Africa and made more specimens of the succulent spe-

cies than any previous collector, with the intention of producing a monograph of the southern African species (Dyer 1979). However, Alain Campbell White (1880–1951) and Boyd Lincoln Sloane (1886–1955), after completing their first monograph *The Stapelieae* of 1937, decided that succulent *Euphorbia* was their next project. For this, they approached Dyer, who later joined them in it, but insisted that the monograph be restricted to the southern African species and that he was made a co-author. For this work he supplied many photographs of plants in habitat and in cultivation in South Africa and he also provided the keys and most of the detailed discussion of the species. Together, the three authors produced the now famous two volumes on the southern African representatives of the Succulent Euphorbieae (White et al. 1941). Further volumes were planned, together with P.R.O. Bally, but they never materialized (Sloane 1952; Dyer 1979).



Fig. 1.4. R.A. Dyer in the field. Left: on Tristan da Cunha, 1937 (© Albany Museum). Right, camping on the Blouberg, Jan. 1955 (© Tristan Dyer).

A further major contributor to the study of the succulent species of *Euphorbia* in southern Africa was the amateur botanist Leslie Charles (Larry) Leach (1909–96). Born in Essex in England, Leach worked as an electrical technician in the army in Britain until he emigrated to Southern Rhodesia (later Zimbabwe) in 1938. There he set up a business supplying electrical equipment, especially batteries for vehicles. His business was successful enough for him to sell it off and ‘retire’ in 1956 before he was 50. This gave him more time to pursue his programme of collecting and documenting the succulent members of *Euphorbia* as well as stapeliads and *Aloe* in Zimbabwe and other parts of Africa south of the equator. He had begun these studies in 1950 and continued them in Zimbabwe, working as Honorary Botanist at the National Herbarium in what was then Salisbury until he emigrated to South Africa in December 1981. This

research and exploration in areas that were previously little-collected (such as Angola and Moçambique) resulted in many papers on the taxonomy of *Euphorbia*. Most of these involved descriptions of new taxa, but there were also several that clarified the identity of previously misunderstood species, such as *E. berotica*, *E. candelabrum* and *E. virosa*. Once in South Africa, he briefly established himself at the Botanical Research Institute in Pretoria and then was employed at the ‘Karoo Botanic Garden’ at Worcester from 1982 to 1989. After this he worked as Honorary Research Fellow in the Department of Botany at the University of the North in what was then Pietersburg (now Polokwane) until his death on 18 July 1996 at the age of 86. From 1982 onwards he described several new species from southern Africa, but not all of these have stood the test of further collecting.



Fig. 1.5. L.C. Leach, Nov. 1962 (© Larry Leach Herbarium, University of the North).

The relatively thorough exploration of the Namibian flora, from 1897 until 1935, by Moritz Kurt Dinter brought to light hardly any species of *Euphorbia* that had not already been discovered in South Africa or were not found around the same time in Namibia and described by Marloth. The extensive collecting by Merxmüller, Giess and Volk between 1956 and 1968, prior to the publication of *Prodromus einer Flora von Südwestafrika*, also revealed almost no new species of *Euphorbia*. In the remote north-west (the Kaokoveld), which neither Dinter nor Marloth visited, there were species whose identities were uncertain. In several cases, these were first noticed by Max Otzen (4 Jan. 1871–10 Aug. 1948). One is even mentioned in White et al. (1941, with figures 1095 and 1096). Some (such as *E. eduardoi*) were recorded later again by the botanist P.G. Meyer during his preparation for the account of *Euphorbia* in the *Prodromus* but Meyer did not describe any of these and they were later mostly described by Leach.

White et al. (1941) gave a very thorough account of people who had discovered species of *Euphorbia* and the general progress of this discovery. This is not repeated here and, for additional biographical information, the reader is referred to Gunn & Codd (1981) and Glen & Germishuizen (2010).



Fig. 1.6. L.C. Leach, c. 1962, finding directions out of Magde, Moçambique, with his trusted VW-Kombi close by (© Larry Leach Herbarium, University of the North).



1.2 Classification of *Euphorbia*

With some 5000 species, the Euphorbiaceae is one of the larger families of flowering plants. It is divided into five sub-families, with five tribes making up the subfamily Euphorbioideae (Webster 1994). Of these tribes, the Euphorbieae includes somewhat under half the total number

of species and consists of *Euphorbia* and several very small genera that are mainly found in the tropical parts of both the Old and the New Worlds. A feature common to all members of the tribe Euphorbieae is the greatly reduced flowers that are tightly gathered together inside flower-like structures known as cyathia (for more details of these structures, see below).

Webster (1975) divided the tribe Euphorbieae into three subtribes, of which the nearly cosmopolitan Euphorbiinae is by far the largest. In this subtribe the involucre is made up of five fused bracts (rather than four), the male flowers lack a perianth and the female flowers are also mostly devoid of a perianth.

In the past (as, for example, in Webster 1994), the subtribe Euphorbiinae consisted of the seven genera: *Chamaesyce* (with \pm 300 species), *Cubanthus* (3 spp.), *Endadenium* (1 sp.), *Euphorbia* (\pm 1450 spp.), *Monadenium* (\pm 80 spp.), *Pedilanthus* (14 spp.) and *Synadenium* (4 spp.). The genera *Poinsettia* (24 spp.) and *Elaeophorbia* (4 spp.) have also occasionally been recognised. In Africa *Chamaesyce*, *Elaeophorbia*, *Endadenium*, *Euphorbia*, *Monadenium* and *Synadenium* occur naturally and all of these except *Chamaesyce* and *Euphorbia* are endemic. *Chamaesyce* was distinguished by vegetative features (apical abortion of the main shoot followed by sympodial growth from buds lower down, the presence of interpetiolar stipules and opposite pairs of often asymmetrical leaves), the infrequently recognised *Elaeophorbia* was distinguished by its indehiscent fruit (a feature also found in several species of *Euphorbia*). *Endadenium*, *Euphorbia*, *Monadenium* and *Synadenium* were separated purely on details of the cyathium (Carter 1988; Carter and Leach 2001).

The very large, almost cosmopolitan genus *Euphorbia* has been subdivided in many different ways. For example, Wheeler (1943) recognised eight subgenera: *Agaloma*, *Chamaesyce*, *Eremophyton*, *Esula*, *Lyciopsis*, *Poinsettia*, *Rhizanthium* and *Tithymalus*. For the naturally occurring tropical and southern African species of *Euphorbia*, Gilbert (1987) recognised four subgenera: *Chamaesyce*, *Esula*, *Euphorbia* and *Lacanthis*. This was modified to six subgenera in Gilbert (1995). On the other hand, eight subgenera were recognised by Carter (1988) for the naturally occurring Tropical East African species and by Holmes (1993) for the naturally occurring Somalian species: namely *Chamaesyce*, *Eremophyton*, *Esula*, *Euphorbia*, *Lacanthis*, *Lyciopsis*, *Tirucalli* and *Trichadenia*. These arrangements differed considerably, since Carter's concepts of the subgenera *Eremophyton*, *Lyciopsis*, *Trichadenia* and *Tirucalli* fell under a broadly defined subgenus *Esula* of Gilbert (1987). In their account for *Flora Zambesiaca*, Carter & Leach (2001) abandoned these subgenera and instead recognised 14 sections, though they mentioned that sect. *Euphorbia* 'would be better regarded as a Subgenus'.

Clearly then, the subgeneric classification of *Euphorbia* is complex and confusing (Leach 1976c). This confusion is much aggravated by

- (a) the very large number of species involved.
- (b) the broad distribution of the genus as a whole and of each of the subgenera.
- (c) the complexity of previous classifications and

- (d) the extent of convergence in many vegetative features and the consequent uncertainty as to which features define natural groups.

The problem of convergence in *Euphorbia* is especially acute. Convergence is now known to have taken place in vegetative features such as annual habit, geophytic habit, succulence of the shoots, development of thorns (even its development from the same organ, e.g. the tips of the shoots, has occurred several times independently), succulents with photosynthetic shoots and conspicuous, deciduous leaves, succulents with terete photosynthetic shoots with reduced leaves, the so-called 'pencil-plant' which developed in Australia (in *E. sarcostemmoides*), several times independently in South Africa (as in *E. burmanni*, *E. dregeana*, *E. gregaria* and *E. mauritanica* for example, each belonging to a different subgenus but all considered to be closely related in White et al. 1941), in South America (as in *E. apparicana*) and in North America (as in *E. antisiphilitica*), tuberculate stems with leaves borne on tubercles or phyllopodia and the phenomenon of shiny, peeling bark on the thicker and older shoots.

As in many groups of plants (as well as other organisms), analysis of the wealth of new data derived from DNA-sequences has provided entirely new insights into relationships within the Euphorbiaceae. As a consequence of these new results, the Euphorbiaceae was split into three families: Euphorbiaceae, Phyllanthaceae (including *Phyllanthus*) and Picrodendraceae (including *Hyaenanche*) (APG IV). Of greater interest here is that these new techniques significantly sorted out the previously intractable problems of relationships between the major groups within *Euphorbia* (Leach 1976c) and enabled a new classification of *Euphorbia* to be developed. These techniques were first applied to *Euphorbia* by Steinmann & Porter (2002) who assembled and analysed data from DNA-sequences from the nuclear ITS and plastid *ndhF* gene-regions of 192 species from *Chamaesyce*, *Endadenium*, *Euphorbia* (including a few from *Elaeophorbia* and *Poinsettia*), *Monadenium*, *Pedilanthus* and *Synadenium*. Other preliminary studies reconstructing the phylogeny of *Euphorbia* with DNA-data (Bruyns et al. 2006, 2011; Park and Jansen 2007; Zimmermann et al. 2010) yielded similar results, often with much improved resolution and support, but all entirely different from the results obtained when morphological characters were analysed (Park 1996; Park and Elisens 2000). Subsequently data from all three different genomes (mitochondrial, nuclear and plastid) was used to try to strengthen the support for relationships among major groups in the genus revealed by previous work (Horn et al. 2012).

Steinmann & Porter (2002) and Horn et al. (2012) found that three subtribes of the Euphorbieae of Webster (1975) were very well-supported. Surprisingly, the subtribe Euphorbiinae broke into four clades (initially termed A, B, C and D), which did not correspond to any taxa that had been

recognised before. Three of them (A, C and D) contain a remarkable mix of subgenera and sections of *Euphorbia*, while the fourth (clade B) was mainly made up of *Euphorbia* subg. *Esula* (in the sense put forward by Wheeler in 1943). Even this clade exhibited some novel features, since a small group of African and Arabian succulents usually placed in 'sect. *Tirucalli*' (e.g. Carter 1988; Holmes 1993; Gilbert 1995; Carter and Leach 2001) was nested within it, while *E. tirucalli* itself was not part of it (corroborating suggestions along these lines made by Leach 1975a, 1976c). At the generic level, the universally accepted segregate genera *Cubanthus*, *Endadenium*, *Monadenium*, *Pedilanthus* and *Synadenium* as well as the less widely recognised genera *Chamaesyce*, *Elaeophorbia* and *Poinsettia* were all nested among species traditionally placed in *Euphorbia*. At the subgeneric and sectional levels, most of the previously recognised taxa were not monophyletic. Also, the relationships among the species have turned out to be quite different to those suggested before (e.g. for sect. *Euphorbia*, compare the relationships found in Dorsey et al. 2013 with those suggested by Carter 1994).

This new information made it clear that major taxonomic re-organization was necessary within *Euphorbia* to achieve a classification that reflected these results. The process of establishing a monophyletic *Euphorbia* was initiated by Steinmann (2003), who placed all species of *Pedilanthus* in *Euphorbia*, where they now reside in sect. *Crepidaria* of subg. *Euphorbia*. It was taken a step further in Bruyns et al. (2006), who recognised Clades A–D of *Euphorbia* as four subgenera and moved all species of *Endadenium*, *Monadenium* and *Synadenium* into subg. *Euphorbia* (clade C). Steinmann et al. (2007) completed this process and moved the species of *Cubanthus* into *Euphorbia*, where they now form sect. *Cubanthus* in subg. *Euphorbia*.

Under the auspices of the *Planetary Biodiversity Initiative* project on *Euphorbia* based at the University of Michigan, USA, investigations were conducted on each of the four subgenera in much greater detail, to infer relationships among the species and to classify each subgenus into sections. These investigations by Yang et al. (2012) for subg. *Chamaesyce* (where 291 of the 566–574 species were sampled), Dorsey et al. (2013) for subg. *Euphorbia* (216 of 661 species sampled), Peirson et al. (2013) for subg. *Athymalus* (88 of 148 species sampled) and Riina et al. (2013) for subg. *Esula* (273 of 457 species sampled) placed virtually all known species in their respective subgenera, in the process obtaining sequences for 868 species out of 1840 or around 47% of the total. The monophyly of each of the four subgenera was confirmed and no species has yet been found that does not fit into these four subgenera.

The notion that *Euphorbia* is 'too large' has inspired various attempts to break it up. Early efforts were those of Haworth (1812) and Klotzsch & Garcke (1860a, 1860b). In the latter case *Euphorbia* was split into seven genera, while Haworth had slightly more. All the spiny species remained in *Euphorbia* and this included such distant relatives as *E.*

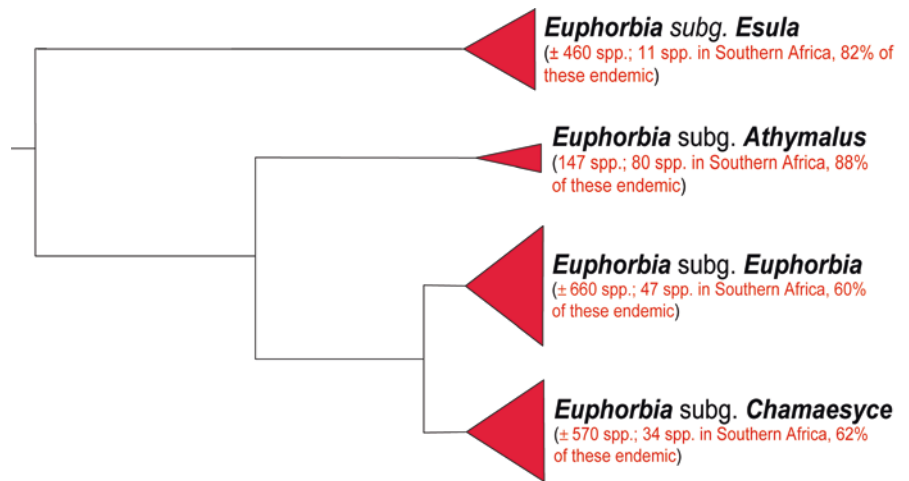
polygona and *E. canariensis*, for example. A. Berger (1906) and N.E. Brown (1911–12; 1915) placed all of them back in *Euphorbia* except for a few, such as *Monadenium*, which were considered to be florally sufficiently distinctive to remain separate from *Euphorbia*. The splitting of *Euphorbia* began again with Koutnik (1984b, 1987, for example), who re-established *Chamaesyce* (sect. *Anisophyllum* in the present arrangement). This directly contradicted Webster (1967: 420–421), who assessed the pros and cons of recognising *Chamaesyce* as a genus and showed that there were no significant features to distinguish it from *Euphorbia*. For this reason attempts to split off *Chamaesyce* from *Euphorbia* did not find general favour, though Carter & Leach (2001) still maintained (without substantiation) that the evidence for recognising their 'sect. *Chamaesyce*' (sect. *Anisophyllum* in the present arrangement) as a genus 'has been accepted by almost all workers'. In the same manner, it was suggested by Gilbert (1987, 1995) and Carter (1994) that some of the groups that they recognised in *Euphorbia* could be split from *Euphorbia* into separate genera. For example, Gilbert (1995) stated that each of the six subgenera he recognised could be treated as a genus and that the species bearing spine-shields (now recognised as sect. *Euphorbia*), were 'a distinctive group lacking obvious relatives elsewhere in the genus'. Analysis of DNA-data (as well as better graphical methods for displaying the relationships revealed and a statistical assessment of the confidence in these relationships) has made it clear that the groups singled out for being split off (such as sect. *Euphorbia* or sect. *Anisophyllum*) and others that were split off previously (like *Cubanthus*, *Monadenium*, *Pedilanthus* and *Synadenium*) are deeply nested within *Euphorbia*. For example, the species of *Monadenium* and *Synadenium* were found to be closer to *E. antiquorum* (the type of *Euphorbia*) than such 'typical' species of *Euphorbia* as *E. mauritanica* or *E. clavarioides*. Here, one possibility is to break up *Euphorbia* and recognise many smaller genera. If the spine-shield-bearing species (i.e. sect. *Euphorbia*) were recognized as a genus, this would involve anything up to 1500 name-changes (since *E. antiquorum*, the type of *Euphorbia*, is a spine-shield-bearing species and so all but the \pm 350 species of sect. *Euphorbia* would remain in *Euphorbia*). Such a treatment would replace the relatively easily recognised, widely known and almost cosmopolitan *Euphorbia* with many new and often small genera. Even more importantly, these new genera would be difficult to separate from one another, especially now that the extent of convergence within *Euphorbia* is better understood. Following Steinmann & Porter (2002), recent work has moved even further from the scenario of carving up *Euphorbia* and placed all members of the Euphorbiinae within the single genus *Euphorbia*. *Euphorbia* is then recognised as a fairly ancient radiation that has evolved into many species-rich lineages over most of the globe. This endorses the view of Dyer (1957: 493) that *Euphorbia* provides a per-

fect and beautiful phylogenetic example of how great diversity in plant forms can be derived ‘from a common stock’. It also substantiates the opinion of Croizat (1972), who believed that *Monadenium* made more sense phylogenetically as part of *Euphorbia*.

1.2.1 Relationships among and within the Subgenera

The relationships between the four subgenera in *Euphorbia* that were revealed first by Steinmann & Porter (2002) were

Fig. 1.7. Relationships between the four subgenera in *Euphorbia* as derived from analysis of DNA-data. The total number of species, the numbers of species in southern Africa and the number of southern African endemics is given for each. The length of the vertical side of each of the triangles is proportional to the number of species in that subgenus (© PVB).



refined with successively increasing support by later work (Bruyns et al. 2006, 2011; Park and Jansen 2007; Zimmermann et al. 2010). Horn et al. (2012) used nine loci from all three genomes (chloroplast, mitochondrial and nuclear) to place this on a firmer basis, once more finding the relationships between the four subgenera as in Fig. 1.7. Here the earliest diverging branch is subg. *Esula*, with subg. *Athymalus* arising after that and the other two the most recent. Each of the four subgenera spread into southern Africa between two and six times, so that *Euphorbia* in southern Africa is not a monophyletic entity but is made up of survivors from many distinct invasions.

1.2.2 Species Concepts in *Euphorbia*

As with many plants, a simple, intuitive ‘folk concept’ of species (Cronquist 1988) has mostly been applied, where species are groups of ‘essentially similar’ individuals. In this sense, as with most genera, *Euphorbia* contains many easily recognised species that are impossible to confuse with any other (e.g. *E. hallii*, *E. phylloclada* and *E. stellispina*). It also contains complexes, where the limits of the species are harder to discern. Examples are the species around *E. procumbens* in subsect. *Medusea* and the complexes around *E. rhombifolia* and *E. spartaria* in sect. *Articulofruticosae*. In the past, where only small amounts of material were available and variability was impossible to assess, this led to the recognition of ‘species’ that do not occur in nature as distinct elements. This phenomenon is especially noticeable in sect. *Articulofruticosae*. Here, in several widely distributed species of the winter-rainfall region one finds a distinct dwarfing and thickening of branches as one proceeds northwards into the more arid Northern Cape. This is not clear without the considerably expanded herbarium-record that now exists and such information on variability was not available to N.E. Brown

and earlier workers. Especially obvious examples of this are in *E. burmanni* (with the thick-branched forms often known as *E. karroensis*), in *E. rhombifolia* (where the dwarfed coastal forms were known as *E. angrae* and the much larger ones were often called *E. chersina*) and also in the distinctive *E. stapelioides* (where the more slender southern forms were named *E. lumbricalis*). Outside this section, the same phenomenon is found in *E. celata* of sect. *Anthacanthae*, where the names *E. miscella* and *E. namuskluftensis* were applied to the stouter-branched forms occurring to the north of more slender ones. In the complex surrounding *E. rhombifolia*, N.E. Brown (1911–12; 1915) recognised at least nine different names which cannot be located as distinct species in nature and exist only as the types of his names. White et al. (1941) did not know these species well and so did not reduce many of these names. In the complex around *E. heptagona*, where White et al. (1941) recognised the three species *E. atrispina*, *E. enopla* and *E. heptagona*, they (i.e. Dyer) knew the plants well in habitat and expressed scepticism as to their distinctness. Here their scepticism has been corroborated by further collections and observations in habitat, which have shown the presence of only a single entity

across a relatively wide range. Field-work has also shown that the many names applied to *E. caput-medusae* do not express the actual relationship between the plants involved, where there is continuity between the largest, most robust plants of the Olifants River valley (formerly *E. tuberculata*) through to the smaller, more slender-stemmed plants on the Cape Peninsula (*E. caput-medusae*), the even more slender-stemmed, often rhizomatous ones in the sandy areas around Cape Town and further east (*E. marlothiana* and *E. muirii*) to the very dwarfed plants found in coastal Namaqualand (*E. ramiglans* etc.). Over this range there is considerable vegetative variation in this species (mainly in the length and thickness of the branches) but the floral parts are indistinguishable in all of them.

Among the succulent Aizoaceae, revisions based on extensive field-work revealed as many as five times (and sometimes up to 20 times) as many names as species (Ihlenfeldt and Gerbaulet 1990; Hammer 1993; Klak and

Linder 1998). L.C. Leach found that certain species of stapeliad (such as *Ceropegia mixta* = *Orbea variegata* and *C. lutea* = *O. lutea*) also have many synonyms. In *Euphorbia*, Leach established important synonymy for such species as *Euphorbia virosa*. While he was also instrumental in showing how to separate the members of sect. *Tirucalli* in the Namib Desert of Angola, Namibia and South Africa, he used the existence of differences in the material before him to define species. Where he worked on material from previously unexplored regions (such as Angola and northern Mozambique), this was not problematic. In the much better-explored southern Africa, this relatively simplistic view was not always backed up by adequate field-experience and knowledge of the variability of the species. Differences that could be found among the relatively few collections before him did not necessarily exist in the wild and led him to describe too many taxa. Examples of this are *E. miscella* and *E. namuskluftensis* = *E. celata*; *E. mira* = *E. silenifolia*; *E. glandularis* = *E. exilis* and several others.



Fig. 1.8. Variation in *E. silenifolia*. The plant on the left would be *E. silenifolia*, while that on the right would be '*E. mira*'. However, it was clear from its lack of flowers and small tuber that the plant on the left is a juvenile, while that on the right is mature. PVB 13737, just north of Arniston, South Africa, 29 Jun. 2019 (© PVB).

How populations and individuals can be grouped into species was summarized in detail by Luckow (1995) and it is widely accepted that persistent discontinuities in at least two 'good' characters define species (e.g. Stebbins 1950; Hedberg 1957; Wiley 1981; Sidwell 1999). Among flowering plants, a 'good' character is taken to be one which is readily observed (i.e. usually a morphological character for which a magnification of $\times 10$ is enough) and where variation in these characters is assessed by measuring or counting. These discontinuities are believed to result from reproductive isolation, since interbreeding normally causes such differences to disappear. Species are generally defined here in this way. Nevertheless, in a few cases taxa separated by consistent differences in only one character have been found to co-exist but maintain their distinctness. A good example of

this is *E. rhombifolia* and *E. spartaria*. These differ in the shape of their leaf-rudiments but are florally indistinguishable and occur together frequently, without any sign of hybridizing. Consequently, one must assume that they are reproductively isolated (despite their floral similarity) and so they are recognized as distinct species.

For taxa which are spatially separated but which differ only very slightly in morphological features, some authors have taken the view that they could interbreed if they co-existed and so they ought to be treated as the same species (Mayr 1964, but Cracraft 1992 took a very different view). Here such taxa are often recognised at levels below the rank of species. In this account the rank of subspecies is applied where two geographically complementary taxa occur which differ in only one 'reasonably reliable' character. An example

is the pair of ‘species’ *E. obesa* and *E. symmetrica*. In nature they occur far apart and cannot interbreed. However, they differ only in minor (and somewhat unreliable) features of their floral parts and in cultivation they interbreed readily to produce fertile offspring. Here they are treated as subspecies. The rank of variety is only rarely used (as in *E. lydenburgensis*): where taxa that occur together differ in a single, often quite distinctive character, but where intermediates may be found.

1.3 Morphology of *Euphorbia* (mainly in Southern Africa)

It has been suggested (Dressler 1957; Steinmann and Porter 2002; Horn et al. 2012) that the ancestors of *Euphorbia* were non-succulent, woody shrubs or trees. When mature, such



Fig. 1.9. Ancestral growth-form of *Euphorbia*, here seen in *Euphorbia guerichiana*, tree \pm 4 m tall, on sparsely wooded slope overlooking Namib Desert and Hartmann Mountains, SE of Camp Synchro on Kunene River, Namibia, 27 Dec. 2014 (© PVB).

plants consist of roots, stem (or trunk), branches, leaves, flowers and fruit. Although the size of the plant varies in *Euphorbia*, most species conform to this basic structure. There is a particularly wide range of sizes within subg. *Chamaesyce* and subg. *Euphorbia* (from minute herbs 10–20 mm tall or small geophytes not exceeding 20 mm tall above the ground to trees 20 m tall or more). This variety of sizes is less pronounced in subg. *Athymalus* (which contains trees 3–5 m tall to small geophytes rising 1–5 cm above the ground) and the range is the least within subg. *Esula*, where most species are shrubs.

In *Euphorbia* the ancestral shrub or tree has evolved in many directions. Among the southern African species the following are among the most striking:

- (1) Reduction of the plant in size. This has developed further along at least five lines:
 - (a) shoots are short and packed into dense mounds or mat-like plants, as in *E. clavarioides* and *E. polyccephala* in subg. *Athymalus* or *E. mosaica* in subg. *Euphorbia* from NE Africa.
 - (b) geophytic habit (see below under ‘Rootstock’)
 - (c) horizontally spreading, underground rhizomes up to 0.3 m long (as in *E. stapelioides* of subg. *Chamaesyce*, shorter in *E. patula* and *E. polygona* of subg. *Athymalus*; *E. knuthii* and *E. namuliensis* of subg. *Euphorbia*). Subterranean rhizomes are slender and without angles or tubercles and become thicker, erect, often tuberculate and even angled on emerging from the soil.
 - (d) loss of branches with the plant reduced to a single, often quite small and short stem, as in *E. meloformis* and *E. obesa* of subg. *Athymalus*; *E. gymnocalycioides* and *E. turbiniformis* of subg. *Euphorbia* from NE Africa. Here the juvenile form, consisting of a stem only, has become reproductive without developing the additional shoots of a fully-sized adult.
 - (e) development of a ‘medusoid habit’: thick stem often greatly reduced in length, with slender often short branches radiating from it. This is well-known in many members of subsect. *Medusea* in subg. *Athymalus*. In subg. *Euphorbia*, the succulent trees and robust shrubs with a trunk in sect. *Euphorbia* have the same form (thick, many-angled stem, slender, fewer-angled branches) and here the ‘medusoid habit’ varies from these large forms to dwarfs such as *E. schizacantha* in NE Africa, *E. clavigera* and *E. stellata* in South Africa.



Fig. 1.10. Modified growth-form into dense low mound in *Euphorbia clavarioides*, PVB 13079, Ubala, north of Kokstad, South Africa, 21 Dec. 2015 (© PVB).

- (2) Increasing succulence. In *Euphorbia* this is usually associated with reduction in the size of the leaves, which become increasingly ephemeral and their photosynthetic function is taken over by the shoots, where the epidermis is long-lived and not rapidly replaced by bark. In southern Africa, of the 172 species of *Euphorbia*, 135 or 79% are succulent (Table 1.1). This includes all 47 members of subg. *Euphorbia*, three of the 11 species of subg. *Esula*, 67 of the 80 species of subg. *Athymalus* (where the other ten are only slightly succulent or woody shrubs) and 18 of the 34 species of subg. *Chamaesyce*.



Fig. 1.11. Rhizomatous growth-forms. **A**, rhizomatous branches excavated in *Euphorbia stapelioides* (green parts to ± 5 mm thick), PVB 3947, foot of Kortdoringberg, east of Alexander Bay, Namaqualand, South Africa, 13 Jul. 1997. **B**, rhizomatous branches excavated in *Euphorbia patula* subsp. *patula* (green parts to ± 12 mm thick), PVB 12550, NE of Addo, near Port Elizabeth, South Africa, 16 Dec. 2012. **C**, *Euphorbia knuthii* subsp. *knuthii*, rhizomatous growth and small tubers excavated (green parts to ± 10 mm thick), PVB 4466, near Ndumu, South Africa, 11 Jan. 2004 (© PVB).



Fig. 1.12. Plant reduced to single short, squat stem partly embedded in the ground. Left, in subg. *Athymalus*, *Euphorbia meloformis*, ± 10 cm diam., PVB 12255, NE of Peddie, South Africa, 5 Dec. 2012. Right, in subg. *Euphorbia*, *Euphorbia gymnocalycioides*, ± 4 cm diam., south of Negele, Ethiopia, 18 Nov. 2009 (© PVB).



Fig. 1.13. Medusoid growth-form with thick partly subterranean stem and slender branches radiating near its apex. Left, in subg. *Athymalus*, *Euphorbia crassipes*, just south of Britstown, South Africa, 25 Mar. 2013. Right, in subg. *Euphorbia*, *Euphorbia schizacantha*, PVB 12749, between Garissa and Garsen, Kenya, 19 Jun. 2014 (© PVB).

Whereas shoots in cacti have been elaborately modified in almost all aspects, succulents in *Euphorbia* are anatomically similar to their non-succulent relatives and lack many of the specialized features associated with other desert-adapted plants (Mauseth 2004a, b).

In *Euphorbia* as a whole, nearly 500 species out of the total of 1840 exhibit succulence, so that the preponderance of succulents in southern African is not typical for the genus elsewhere in the world. Most of these nearly 500 succulent species belong to subg. *Euphorbia* in the Old World of tropical Africa, Madagascar, the Arabian Peninsula and SE Asia and to subg. *Athymalus* in southern Africa. In contrast, there are only a few succulents in subg. *Esula* (these are only found in Africa, Macaronesia and Madagascar) and in subg. *Chamaesyce*. Although *Euphorbia* is well represented in the New World (i.e. the Americas), only relatively few species in subg. *Euphorbia* and subg. *Chamaesyce* in Brazil, Chile and Mexico are succulent (Yang et al. 2012; Dorsey et al. 2013).

1.3.1 Rootstock

In *Euphorbia* the base of the stem often continues into a strongly-developed tap-root anchoring the plant firmly in

the ground. Most roots arising from the tap-root are fine and fibrous. However, in several species, such as *E. hallii*, *E. inermis*, *E. oxystegia* and *E. quadrata* in subg. *Athymalus* (usually with relatively conspicuous, deciduous leaves), in *E. espinosa* of subg. *Chamaesyce* and also in some tropical members of sect. *Monadenium*, the tap-root and some side-roots may be swollen and fleshy. These are not to be confused with geophytes.

In true geophytes, the stem forms part of an underground tuber whose apex is below the surface of the ground. Here the lower part of the tuber is the rootstock, the upper part is the stem and usually the two are not clearly separated either within the tuber or externally. In the rainy season leaves develop above the ground from the apex of the tuber, often in rosettes on the surface. They are lost during dry periods, when the plant ‘retreats’ underground. Geophytes have evolved many times independently in subg. *Euphorbia* (in several lineages, as in *E. rubella* from NE Africa and *E. acaulis* from SE Asia), in two lineages in subg. *Athymalus*, in *E. gueinzii* of subg. *Chamaesyce* and in *E. striata* and allies of subg. *Esula*. Most geophytes are reduced to a short stem bearing leaves, but others may develop an almost shrub-like structure underground with leaves at the tips of the shoots (as in *E. tuberosa*).

Table 1.1. The subgenera of *Euphorbia*, showing the numbers exhibiting different growth-forms.

| Subgenus | Number of species | Distribution | Number of sections (southern Africa) | Southern Africa (endemic) % endemic | Namibia (endemic) % endemic | South Africa (endemic) % endemic | Annuals % of total | Perennial, non-succulent herbs % of total | Woody shrub to tree % of total | succulents % of total | geophytes % of total |
|-------------------|-------------------|--|--------------------------------------|--|--------------------------------|-------------------------------------|-----------------------|--|-----------------------------------|--------------------------|-------------------------|
| <i>Athymalus</i> | 147 | Africa, Arabian Peninsula to Iran, Macaronesia | 7 (3) | 80 (70) 88% | 19 (2) 11% | 72 (55) 76% | 4 5% | 1 1% | 2 3% | 67 84% | 6 8% |
| <i>Chamaesyce</i> | ± 570 | cosmopolitan | 15 (6) | 34 (21) 62% | 20 (5) 25% | 22 (6) 27% | 10 29% | 3 9% | 2 6% | 18 53% | 1 3% |
| <i>Esula</i> | ± 460 | cosmopolitan (mainly Eurasia) | 21 (2) | 11 (9) 82% | 4 (1) 25% | 9 (4) 44% | 0 | 5 45% | 0 | 3 23% | 3 23% |
| <i>Euphorbia</i> | ± 660 | cosmopolitan (especially Africa, Madagascar) | 21 (3) | 47 (28) 60% | 13 (3) 31% | 35 (20) 58% | 0 | 0 | 0 | 47 100% | 0 |
| Total | ± 1837 | cosmopolitan | 64 (14) | 172 (128) 74% | 55 (12) 22% | 138 (85) 62% | 14 8% | 9 5% | 4 2% | 135 78% | 10 6% |



Fig. 1.14. Swollen roots emanating from the tap-root in *Euphorbia inermis*, PVB 11005, Port Elizabeth, South Africa, 29 Dec. 2008 (© PVB).



Fig. 1.15. Small geophyte \pm 3 cm tall in flower among pieces of limestone and leaf-litter, *Euphorbia rubella* (subg. *Euphorbia*), Mt Achim, Harrar, Ethiopia, 29 Jan. 2015 (© PVB).



Fig. 1.16. Deciduous succulent leaves in the geophytic *Euphorbia acaulis* (subg. *Euphorbia*) among short grasses, leaf-litter and chunks of granite, PVB 11461, Nandi Hills near Bangalore, Karnataka, India, 16 Aug. 2009 (© PVB).



Fig. 1.17. Three plants of the geophytic *Euphorbia ecklonii* (subg. *Athymalus*) removed to show leaves radiating on surface of ground just above tuber, PVB 11162, Swellendam, South Africa, 22 Aug. 2008 (© PVB).

1.3.2 Shoots

Most of the southern African species of *Euphorbia* have fleshy shoots with persistent photosynthetic epidermis that may live and function for decades, where the development of bark is retarded or wholly prevented. The shoots may be cylindrical or distinctly angled. Species with angled shoots all belong to subg. *Euphorbia* and subg. *Athymalus* and are

not found in the other two subgenera, where succulent stems are always cylindrical (though they may sometimes be somewhat longitudinally ridged).



Fig. 1.18. Cylindrical branches in subg. *Athymalus* and subg. *Euphorbia*. A, *Euphorbia dregeana*, Harrasberg, Namaqualand, South Africa, 16 Jul. 1995. Right, *Euphorbia carunculifera*, NE of Namibe, Angola, 18 Mar. 2017 (© PVB).



Fig. 1.19. Angled branches: Left, in *Euphorbia pentagona* of subg. *Athymalus*, PVB 6892, Fort Beaufort, South Africa, Sept. 2019. Right, in *Euphorbia avasmontana* of subg. *Euphorbia*, PVB 12874, Otavi Mountains, Namibia, Sept. 2019 (© PVB).

A widespread type of cylindrical shoot in *Euphorbia* is the so-called ‘pencil-stemmed’ form. In these the plant consists of slender, cylindrical, photosynthetic branches that are usually erect and gathered together into a shrub, mostly also with reduced leaves. This has evolved in each of the four subgenera, sometimes even more than once and is an adaptation to semi-arid conditions that is found in several families.

So, in semi-arid parts of southern Africa it is not unusual to see representatives of *Cynanchum* (especially the former *Sarcostemma*, Apocynaceae), *Euphorbia* (sometimes from two different subgenera) and *Kleinia* (Asteraceae) growing socially, all exhibiting this growth-form and all looking quite similar vegetatively.



Fig. 1.20. Pencil-like branches of *Euphorbia lignosa* (subg. *Athymalus*) gathered into a dense low shrub, PVB 10067, East of Namusberg, Rosh Pinah, Namibia, 15 Jul. 2005. Behind this are several yellowish plants of *E. rhombifolia* (subg. *Chamaesyce*) also with pencil-like branches (© PVB).

Tuberculate shoots are common in succulent members of *Euphorbia*, mainly in subg. *Athymalus* and subg. *Euphorbia*. With increasing succulence and reduction of the leaf, the base of the leaf swells and raises the leaf out of the surface of the stem on a tubercle (sometimes referred to as a phyllopodium or podarium). These tubercles are often longitudinally elongated (as in *E. bubalina*) but may also be polygonal to nearly circular at their base.

In the highly succulent members of subg. *Athymalus* (in sect. *Anthacanthae*) tubercles cover the shoots (very spread



Fig. 1.21. Tuberculate branches of *Euphorbia hypogaea*, PVB 6684, Juriesfontein, Loxton distr., Great Karoo, South Africa, 8 Apr. 1996 (© PVB).

out in most species of subsect. *Pseudeuphorbia*, densely packed together in subsect. *Medusea* and others) and they are often spirally arranged along the stem and branches (as in *E. clandestina* and many others). In ser. *Meleuphorbia* they are fused vertically into angles along the stem and branches and here the individual tubercles are demarkated by a darkened outline if they are not still partly separated. The angles are mostly relatively low and mostly between four and eight per shoot, which is then square or polygonal in cross-section. They are most pronounced as slender, flattened (often undulating) wings with deep furrows separating them in *E. polygona*, where the shoots may be particularly stout (to 200 mm thick) and up to 20-angled (reaching nearly the same number in the not quite so stoutly branched *E. stellispina*) and here shoots are star-like in cross-section. Each tubercle is tipped by a leaf (often rudimentary and soon lost, leaving a small to prominent apical scar) and the axil of the leaf (from where sterile or fertile short-shoots may arise) remains against the

shoot. The angles along the shoots combined with spines lend the plants a distinctly cactoid appearance. In species with thicker shoots, such as *E. avasmontana*, more than half the thickness is occupied by soft, white pith, which is divided up into large inter-connected cavities separated by horizontal layers of tissue well supplied by latex (Pearson 1914: 43). Worsdell (1914) found that these spaces were created by groups of cells dissolving and that the cavities assist in the movement of gases within the shoot.

Tubercles bearing the leaves are universally present in sect. *Euphorbia*. They may be separate and vertically arranged into spirals (usually densely clustered on the shoots, as in *E. unicornis* and *E. unispina* (here very low) from tropical Africa), or partially fused into low spiralling rows (as in *E. neriifolia* from SE Asia). Most commonly they are laterally flattened and vertically fused into often slender and sometimes wavy angles along the shoots, where the individual tubercles are not distinguishable. Their



Fig. 1.22. Inside of branch showing pale pith with transverse cavities, *Euphorbia tetragona*, PVB 13531, west of Fort Beaufort, South Africa, 26 Oct. 2018 (© PVB).



Fig. 1.23. Branches with low tubercles near tips, but becoming almost smooth away from their tips, *Euphorbia unispina*, PVB 12604, east of Vom, Jos Plateau, Nigeria, 14 Sept. 2013 (© PVB).



Fig. 1.24. Tubercles on branches arranged into spiralling rows in *Euphorbia nerifolia*. Left, big shrub nearly 2.5 m tall during dry season, Shirwah, Maharashtra, India, 16 Mar. 2001. Right, stem of young plant with prominent tubercles, Trimbak, Maharashtra, India, Sept. 2019 (© PVB).



Fig. 1.25. Tubercles fused into prominent, continuous angles along branches, *Euphorbia eduardoi*, PVB 13410, south of Catengue, Angola, 13 Mar. 2017 (© PVB).

approximate centre is indicated by a (usually) minute leaf which is surrounded by a patch of hard, brown to grey, rigid surface, the ‘spine-shield’ and is subtended by two spines. Two more spines often develop in the stipular position at the bases of the margins of the minute leaf and the upper end of the tubercle is indicated by a small hemispherical axillary bud.

In sect. *Euphorbia* the number of angles starts off at two in tiny plants, corresponding to the two cotyledons. If this two-angled stage persists, a flat-stemmed seedling arises (as in the SE Asian *E. antiquorum*). Usually as the seedling elongates new angles are introduced with the terminal bud giving rise to three or four tubercles rather than two. This often happens immediately after the first pair of leaves after the cotyledons so that usually within 20 mm of the cotyledons the stem is 3- or 4-angled. Some species have six or more angles on the branches, but this is a relatively rare phenomenon that evolved more than once and is confined to certain lineages. This is usually achieved by, say, whorls of three leaflets or tubercles being shifted to alternate with the previous whorl of three and being joined only to the next whorl up which is in that position and not joined to the whorl immediately above it (Troll 1935–7). This leads to an increase from three angles to six in such a case. In the taller tree-forming species this takes place in the trunk (and occasional forks in it, as in *E. grandidens*) but mostly not in the branches. Many of these trunks gradually become cylindri-



Fig. 1.26. New angles on stem beginning by adding a new row of tubercles in sect. *Athymalus* and sect. *Euphorbia*. **A**, stem changing from 4- to 5-angled, ± 40 mm thick, *Euphorbia eduardoi*, (subg. *Euphorbia*) PVB 13410, south of Catengue, Angola, 13 Mar. 2017. **B**, changing from 4- to 8-angled, ± 40 mm thick, *Euphorbia polygona*, (subg. *Athymalus*) east of Joubertina, South Africa, 11 Nov. 2018 (© PVB).

cal through swelling of the tissue between the angles (by secondary thickening with wood). They also gradually lose their spines and the green epidermis is progressively replaced with thick grey to brown bark.

Angled shoots are not unique to *Euphorbia* (though they are not found elsewhere in the Euphorbiaceae) and are present in stem-succulents in several other families. They are especially widespread in the Cactaceae, where they are only absent in some of the ‘basal lineages’ such as the Pereskioideae and some members of the Opuntioideae. Angled shoots are found in several distinct lineages in the Asclepiadoideae of the Apocynaceae, they also occur in the Geraniaceae, Vitaceae and in a few Cucurbitaceae in Madagascar (Troll 1935–7; Rauh 1967; Mauseth 2004b). Generally, they are associated with the increased photosynthetic activity of the shoots replacing that of the reduced leaves. Angles also increase the surface area of the shoots and they add strength to these structures in the larger species, helping them to survive dry periods without collapsing. In succulents in *Euphorbia*, which lack cortical bundles to transport substances across the cortex (Mauseth 2004b), the angles also reduce the distance between the epidermis and the transporting tissue.



Fig. 1.27. Bark, which has replaced green, photosynthetic tissue, formed on cylindrical trunk ± 20 cm thick, *Euphorbia confinalis* ssp. *confinalis*, PVB 12061, eastern Soutpansberg, South Africa, 4 Nov. 2011 (© PVB).

The surfaces of the branches are mostly smooth but, especially in sect. *Articulofruticosae*, there are several with variously papillate, ridged, warty or convoluted surfaces. Those of *E. muricata* and *E. verruculosa* are shown here. Similarly convoluted surfaces were also observed in *E. restituta* of subg. *Athymalus*. All these are species of the arid west coast of southern Africa where fog from the sea adds to the precipitation and these complex surfaces may assist in absorbing this moisture.

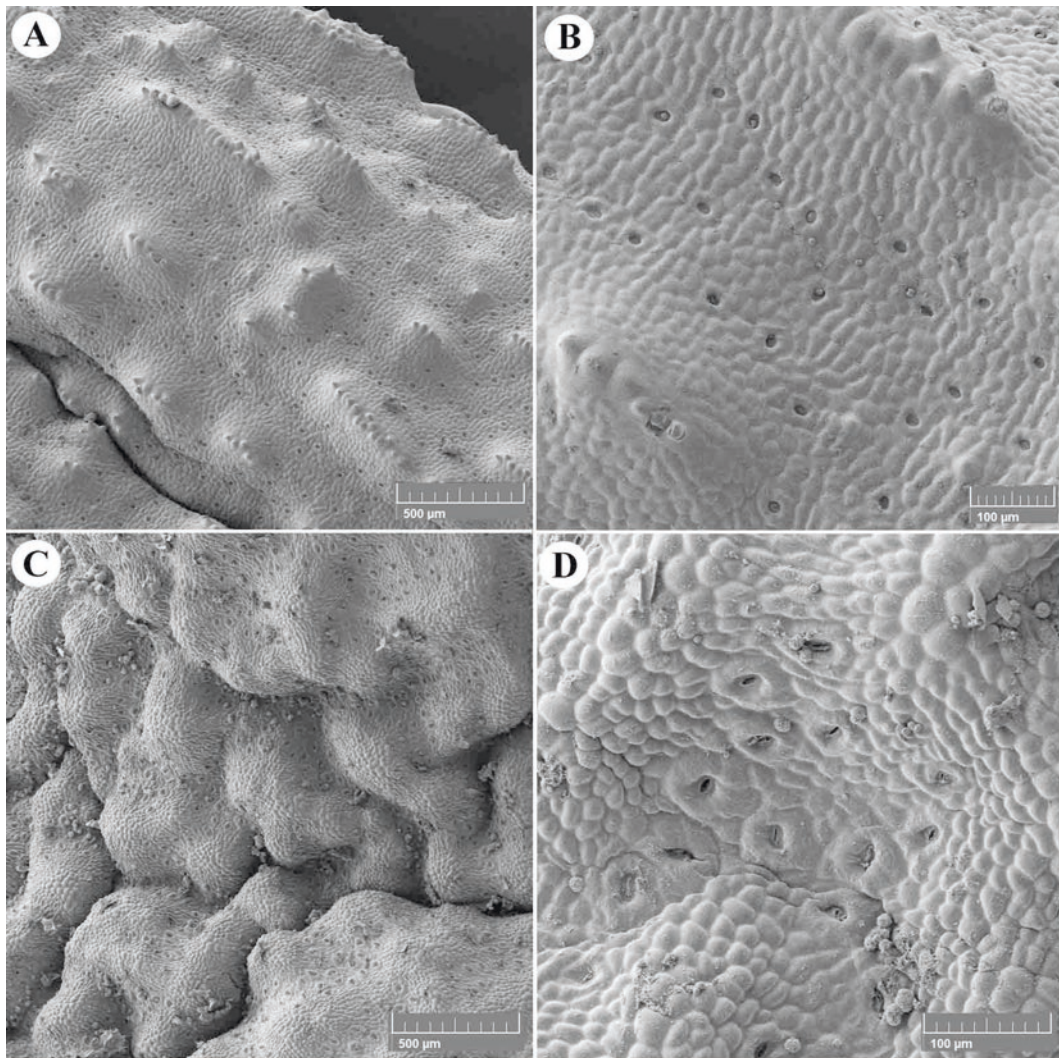


Fig. 1.28. Surfaces of branches viewed with SEM: **A, B**, *Euphorbia muricata*, PVB 6026, road to Kalkgat, NE of Vanrhynsdorp, South Africa; **C, D**, *Euphorbia verruculosa*, PVB 12542, Lüderitz, Namibia (© PVB).

1.3.3 Spines

Often inaccurately referred to as ‘the cacti of the Old World’, *Euphorbia* has many spiny members. In subg.

Chamaesyce only *E. spinea* is spiny and here the spines are formed by the branch-tips drying out rapidly to form a hard and sharp spike (*E. espinosa* and *E. guerichiana* were also said to become spiny at the branch-tips, e.g. Yang et al.



Fig. 1.29. Spikes formed by the tips of the shoots have arisen many times independently in *Euphorbia*. Left, in *E. spinea* of subg. *Chamaesyce*, PVB 13499, just west of Alheit, near Kakamas, South Africa, 23 May 2018. Middle, in *E. cuneata* of subg. *Athymalus*, Teita Hills, Kenya, 6 Oct. 2015. Right, in *E. lignosa*, also of subg. *Athymalus*, PVB 12836, east of Wlotzkabaken, Namibia, 21 Dec. 2014 (© PVB).

2012: 776–7 but this is unknown in both species in habitat and it is not mentioned in either White et al. 1941 or Carter & Leach 2001: 390–1, so it is discounted here). In subg. *Esula* spines are absent. There are many spiny species in subg. *Athymalus* and also many in subg. *Euphorbia*. In subg. *Athymalus* spines are derived from hardened and sharp shoot-tips or special slender and sharp-tipped short-shoots that arise in the axils of tubercles and are particu-

larly prominent in subsect. *Florispiniae*. These short-shoots are morphologically different from the other shoots: they are much more slender, non-succulent and taper to a fine tip, they bear only vestigial tubercles and tiny leaf-rudiments and dry out quickly to harden into a rigid spike. As they are morphologically very similar to short-shoots bearing cyathia, they are often referred to as ‘sterile peduncles’ (e.g. White et al. 1941).



Fig. 1.30. Spikes formed by axillary short-shoots. Left, dense armature of spines, one per leaf-axil, in *Euphorbia ferox* ssp. *ferox*, PVB 11946, south of Steytlerville, South Africa, 7 Jun. 2011. Right, more densely clustered spines, several per leaf-axil, in *Euphorbia polygona*, PVB 12727, Toorwaterpoort, South Africa, 27 May 2014 (© PVB).

The spiny members of subg. *Euphorbia* are all succulent and they are confined to the Old World in Africa and Madagascar, the Arabian Peninsula and in SE Asia from Pakistan to China. They are typically tropical and subtropical but a few species venture into temperate zones in Morocco, in the Himalaya of SE Asia and in South Africa. In South Africa they are found as far south as 33° around Port Elizabeth and Calitzdorp. In southern Africa all members of subg. *Euphorbia* are spiny except the four species of sect. *Tirucalli* (where spines are only known in *E. stenoclada* from Madagascar and are formed by the rigid tips of the shoots drying into spikes, as in *E. spinea*).

In sect. *Euphorbia* each leaf is usually surrounded by a hardened, brown to grey ‘spine-shield’ which covers the tip of the tubercle and may extend downwards towards the leaf below. In some species the shields fuse to form a continuous hard margin along the angle, while in others the shields remain separate. Two stout ‘dorsal spines’ are situated slightly behind each leaf on the spine-shield (one spine in the case of some species, such as *E. unicornis* and *E. unispina*, more rarely with one spine forked towards its apex, as in *E. glochidiata* or *E. marrupana*). Two much smaller gland-like to scale-like or spine-like structures (usually referred to as

prickles) are found on the spine-shield near the base of the margin of each leaf. When they are similar in shape and in size to the dorsal spines, the spine-shield then has four spines surrounding each leaf. The interpretation of the structures on the spine-shield has varied in the literature: Berger (1906: 6) referred to the dorsal spines as thorns or stipular thorns and Troll (1935–7: 900) also called them stipular thorns but Brown (1911: 471; 1915: 223–4) pointed out that, because they are located behind the leaf, they could not be of stipular origin, though he admitted that he was not quite sure what they were; White et al. (1941: 20–21) repeated that their origin was ‘not definitely understood’ and that they were often referred to as ‘stipular outgrowths’. Dyer (1957), not wanting to enter into complex morphological arguments, preferred to refer to them as ‘stipular spines’ and in Dorsey et al. (2013: 313) they were again referred to a ‘stipular spines’ (see also Uhlarz 1978: 56). Ontogenetic investigations (Shah and Jani 1964; Uhlarz 1974) showed that the smaller structures at the base of the leaf-margins arise when the leaf blade begins to develop in the apical bud (of the shoot) and keep pace with the leaf to reach their full size quickly. Only once these are fully developed do the meristematic zones giving rise to the dorsal spines begin to swell

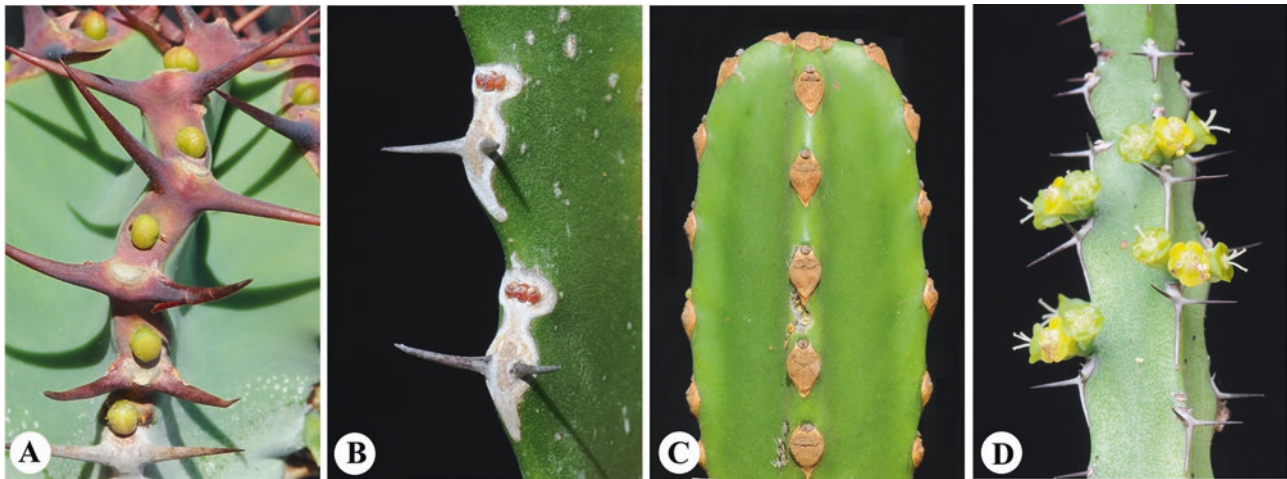


Fig. 1.31. Shape and degree of vertical fusion of spine-shields. **A**, spine-shields fused together into tough, continuous \pm uniformly broad margin along the angles (at first pinkish brown hardening to grey), *Euphorbia virosa*, PVB 13523, north of Pella near Orange River, South Africa, 29 May 2018. **B**, spine-shields (here almost white) remaining separate along margin of the angles, broader around axillary bud (with red primordia of synflorescences) and around spines, *Euphorbia triangularis*, PVB 9407, near Bathurst, South Africa, 24 Apr. 2016. **C**, spine-shields separate, \pm elliptical, spines absent here, from branch out of reach of grazers, on large tree-like species, *Euphorbia tetragona*, PVB 13531, west of Fort Beaufort, South Africa, 26 Oct. 2018. **D**, spine-shields separate, very slender beneath spines and slightly broader around axillary buds and spines, *Euphorbia cataractarum*, PVB 9599, Zambia (© PVB).

near the dorsal base of the tiny leaf. After the leaf has left the apical bud, the dorsal spines develop, reaching their full size in many cases only after the leaf has dried up and fallen off. Since the smaller structures arise very early in the development of the leaf, as they are positioned near the base of the leaf-margins and since they are present at every leaf on a plant, they are interpreted as stipules. As the dorsal spine or spines arise later and also well behind the ‘stipular region’ at the base of the leaf-margins, they are not part of any stipular ‘complex’ but are considered to be dorsal emergences of the leaf-base (Uhlarz 1974). Unlike stipular structures, these dorsal spines are not constant in their presence or shape on the plant: in several species they are present (often in very robust form) in the young plant but, as it ages, smaller and smaller dorsal spines are produced and eventually there are none below each leaf-base (as in many of the tree-like species, Fig. 1.31); in those species with just one dorsal thorn, this uniqueness may vary on the plant. For example, in the Nigerian *E. unispina* two dorsal spines are present below each leaf-base in young plants with a gradual transition via lateral fusion to a single dorsal spine per leaf-base as the plant matures (Rauh et al. 1969: 217, fig. 9; Uhlarz 1974: 43). In the Moçambican *E. marrupana*, on a single plant some leaf-bases have two dorsal spines, others have only one spine which is forked below its apex and yet others have only one unforked spine (Fig. 6.82 and 6.85, vol. 2).

In a few species further small prickles may project alongside the axillary bud. These are most notable in *E. grandicornis*, where they can reach 7 mm long, but they also occur in *E. barnardii*, *E. restricta*, *E. pseudocactus* and occasionally in *E. knobelii*. Their origin is uncertain, but it is possible that



Fig. 1.32. Spines changing from paired (lower right) to solitary (centre) in young seedling \pm 2 cm tall of *Euphorbia unispina*, PVB 12604, east of Vom, Jos Plateau, Nigeria, 14 Sept. 2013 (© PVB).

the small bracts that initially shelter the axillary bud may each have a single dorsal spine-like outgrowth or may have stipular prickles.

In sect. *Monadenium* tiny prickles are present as rudimentary stipules alongside the bases of the leaf-margins in *E. lugardiae* (Uhlarz 1978: 52). In certain species from tropical Africa these prickles may be much larger. There may be also a dorsal spine below the leaf as well as complex spiny outgrowths raised on papillae in a row below between the leaves. Bally (1961: 63) referred to the spines in such species as *Euphorbia guentheri* (*M. guentheri*) and *E. neospinescens* (*M. spinescens*) as ‘three sharp prickles’, so did not distinguish the dorsal spines from the stipular prickles. Uhlarz



Fig. 1.33. Spines around the leaves in sect. *Monadenium*. **A**, leaves with small flattened stipular scales and no spines (branch \pm 10 mm thick), *Euphorbia bisellenbeckii*, PVB 12763a, N. Kenya. **B**, each leaf-scar with single spine below it (branch \pm 10 mm thick), *Euphorbia torrei*, PVB 9701, north of Nantulo, northern Moçambique. **C**, each leaf-scar with three spines, one below and two alongside scar (branch \pm 10 mm thick), *Euphorbia biselegans*, PVB 8733, Tanzania. **D**, each leaf-scar with several spine-tipped teeth in row below it and sometimes somewhat fused, with pair of much smaller irregular stipular spines alongside it (branch \pm 20 mm thick), *Euphorbia magnifica*, PVB 9647, south of Mpwapwa, Tanzania (© PVB).

(1975b) showed that the spines below the leaf in sect. *Monadenium* are homologous to the dorsal spines in sect. *Euphorbia*. The presence of dorsal spines that are not stipular in both sect. *Euphorbia* and sect. *Monadenium* corroborates the close relationship between these two groups that was later revealed by DNA-data. This shows also that, even morphologically, sect. *Euphorbia* is not as isolated within *Euphorbia* as Gilbert (1995) suggested.

1.3.4 Leaves

In *Euphorbia*, leaves are generally prominent. However, in southern Africa leafy plants such as in *E. transvaalensis* are



Fig. 1.34. Leafy shrub of *Euphorbia transvaalensis*, PVB 12089, south of Ellisras, South Africa, 28 Dec. 2011 (© PVB).

the exception: only eight species of sect. *Esula* and 14 members of subg. *Chamaesyce* are herbaceous. The remaining species are more or less succulent and in most of them the leaves are reduced to minute rudiments.

Succulent leaves are uncommon generally in *Euphorbia* except in subg. *Euphorbia* where they are usually combined with fleshy green shoots so that photosynthesis takes place both in the shoots and in the leaves (a rare phenomenon among succulents generally, Mauseth 2004b). Some Madagascan species such as *E. elliotii* (sect. *Denisophorbia*) bear succulent leaves, but these are evergreen and the shoots are not photosynthetic. Succulent leaves are typical of sect. *Monadenium* (as in *E. lugardiae*) and may reach 150 mm long or more (even larger in *E. neoarborescens*), but they are always deciduous. Members of sect. *Euphorbia* also have succulent leaves, but these are mostly reduced to tiny rudiments that are only visible around the terminal bud when it is actively growing. Nevertheless, prominent, fleshy, deciduous leaves occur in SE Asian species such as *E. caducifolia* and *E. nivulia* (also in the closely allied geophytic *E. acaulis* and its relatives), in several West African species and in the south tropical African geophytes related to *E. decidua* (Leach 1976b). *Euphorbia ampliphylla* from tropical Africa bears prominent, fleshy, deciduous leaves 10 cm long or more and its close relative in southern Africa, *E. ingens*, also has prominent leaves on young plants, though these rarely exceed 8 cm long. However, in *E. ingens* (unlike in *E. ampliphylla*), the leaves decrease in size as the plant ages and in mature trees they are reduced to minute, scale-like rudiments on the new shoots.



Fig. 1.35. The prominent succulent deciduous leaves in the shade-loving *Euphorbia neocannellii*, PVB 13413, east of Catengue, Angola, 13 Mar. 2017 (© PVB).

1.3.5 Stipules

Stipular structures in *Euphorbia* may take the form of thorns or small rudiments or may be absent (Uhlarz 1974; 1975a; 1978) and are not elaborate as in some members of *Jatropha*. In *Euphorbia* they are of irregular occurrence among groups of related species: a good example is sect. *Articulofruticosae*, where fairly prominent gland-like stipules are present only in *E. burmanni* (examined in detail by Uhlarz 1975a), *E. exilis* and *E. suffulta* out of the 15 species in this section, while in sect. *Tirucalli* they are found in three of the four species in southern Africa (being absent in *E. gregaria*). Nevertheless, in species where they are found, their occurrence is very regular. Stipules are absent in all members of subg. *Esula* (Riina et al. 2013), they are occasional in subg. *Athymalus* and subg. *Chamaesyce* in southern Africa and are almost always present (though small but variable in shape in different species) in subg. *Euphorbia* among the structures around the leaf-rudiments on the spine-shields.



Fig. 1.36. Leaf-rudiments on growing branches in members of sect. *Euphorbia*. **A**, leaflets ± 5 mm broad around the terminal bud in *Euphorbia radyeri*, PVB 10539, 3 km towards Matjiesvlei, west of Calitzdorp, South Africa, 5 Oct. 2008. **B**, ± 4 mm broad in *Euphorbia triangularis*, PVB 9407, near Bathurst, South Africa, 24 Apr. 2016. **C**, small scale-like leaflets ± 2 mm long in *Euphorbia grandidens*, PVB 6870a, Springs, NE of Uitenhage, South Africa, 16 Jul. 2018 (© PVB).