Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

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CONTENTS

Diversity and endemism in the species-rich Ceropegieae (Apocynaceae) and *Euphorbia* in highlands and escarpments of Angola and Namibia

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ABSTRACT
We map the distribution of the species-rich groups Ceropegieae and *Euphorbia* in southwest tropical Africa (i.e., in Angola and Namibia). This shows that they are most diverse in the highland and escarpment areas of these countries, and in the coastal areas west of these highlands. Most of the endemic species occur here too. Several 'hotspots' within highlands and escarpments of Angola and Namibia (HEAN) are identified that are common to both groups. Diversity in both groups falls off rapidly in Angola north of Benguela. This diversity also tails off substantially on the Kalahari sands to the east of the escarpment (i.e., east of the HEAN), with some notable exceptions in Namibia in *Ceropegia*. In the Ceropegieae, many species occurring in these sandy regions are widespread in southern Africa. Areas covered by Kalahari sands are almost completely devoid of *Euphorbia*. Several lineages are identified in *Ceropegia* and *Euphorbia* that have diversified in and are endemic to the margins of the Namib Desert in Angola and Namibia (i.e., in and west of the HEAN). Apart from these endemic lineages, the species found in the HEAN (and more generally in Angola and Namibia) are mostly related to others occurring further east in southern Africa. Extreme examples of this are provided by closely related species pairs that occur on opposite sides of southern Africa. While the Asclepiadeae has significant numbers of geophytic herbs and few succulents, in the Ceropegieae and in *Euphorbia* succulents are particularly common. The proportion of succulents with greatly reduced leaves is also high, suggesting that this growth form is especially successful in the region of the HEAN and in the narrow coastal area west of it. These succulents are considered to have arisen within the last 8 million years.

Keywords: Angola, *Ceropegia*, Ceropegieae, distribution, diversity, endemic lineages, *Euphorbia*, growth forms, highland, Namibia, species pairs, succulents

INTRODUCTION

The Asclepiadoideae (which makes up most of the former Asclepiadaceae) is the most diverse subfamily of the Apocynaceae in southwestern tropical Africa; i.e., Angola and Namibia. The Asclepiadoideae consists of four tribes: Asclepiadeae, Ceropegieae, Fockeeae and Marsdenieae. Of these, the Asclepiadeae and Marsdenieae are cosmopolitan, although the latter is mainly tropical. The Fockeeae is restricted to sub-Saharan Africa and the southern Arabian Peninsula. The Ceropegieae is an exclusively Old World group that occurs mainly in the tropics, around the perimeter of the Indian Ocean, from South Africa to the northern parts of Australia. It is the most diverse of the four tribes in southwestern tropical Africa.

The Ceropegieae contains about 790 species, of which around 695 species are in the recently much expanded *Ceropegia* L. The genus *Ceropegia* now includes *Brachystelma* Sims with 139 species, the traditional members of *Ceropegia* with 202 species and the stem-succulents popularly known as the stapeliads with around 353 species (Bruyns *et al*. 2017). The remaining ~95 species of Ceropegieae belong to three early-divergent lineages, the Anisotominae (the most closely allied of these three lineages to *Ceropegia*), Leptadeniinae and the Heterostemminae (Rodda 2016, Meve *et al.* 2017, Bruyns *et al.* 2023). The distributions of these early-divergent lineages coincide with the rest of the tribe, except that they are absent from the temperate regions of southwestern South Africa, and northwest Africa in Morocco, Macaronesia and around the Mediterranean. Some species of Ceropegieae endemic to the highlands and escarpments of Angola and Namibia are shown in Figure 1.

Euphorbia L. (Euphorbiaceae) is another species-rich group in southwestern tropical Africa. *Euphorbia* consists of some 1,840 species (Yang *et al.* 2012, Dorsey *et al.* 2013, Peirson *et al.* 2013, Riina *et al.* 2013) and is divided into four subgenera (Bruyns *et al.* 2006). The relationships between these subgenera and their numbers of species in Angola and Namibia are shown in Figure 2. As in *Ceropegia*, *Euphorbia* is not a single radiation (i.e., a monophyletic entity, as stated by Frazão *et al.* (2020)) in either Angola or Namibia, but it is represented in each country by offshoots of many separate lineages. Taxonomy used for *Euphorbia* is that of Bruyns (2012, 2018), Bruyns and Berry (2019) and Bruyns *et al.* (2020), with some modifications as in Bruyns (2022).

In Angola and Namibia, the distributions of many species of plant are heavily influenced by the mountainous and hilly highlands and escarpments, where the broad range of altitude over a short horizontal distance gives rise to a great variety of distinct habitats and wide variation in rainfall. Another major influence is the narrow coastal belt taken up by the hyperarid Namib Desert. This desert is most arid between Port Nolloth in South Africa and Lucira in Angola and has been hyperarid for at least the last 20 million years (Pickford *et al.* 2014). On the eastern side of the region, the Kalahari sands provide a similarly strong influence on plant distributions; these sands extend from central South Africa to the basin of the Congo River, forming the largest continuous body of sand in the world, and have been present for the last 32,000 years at least (Lancaster 1989).

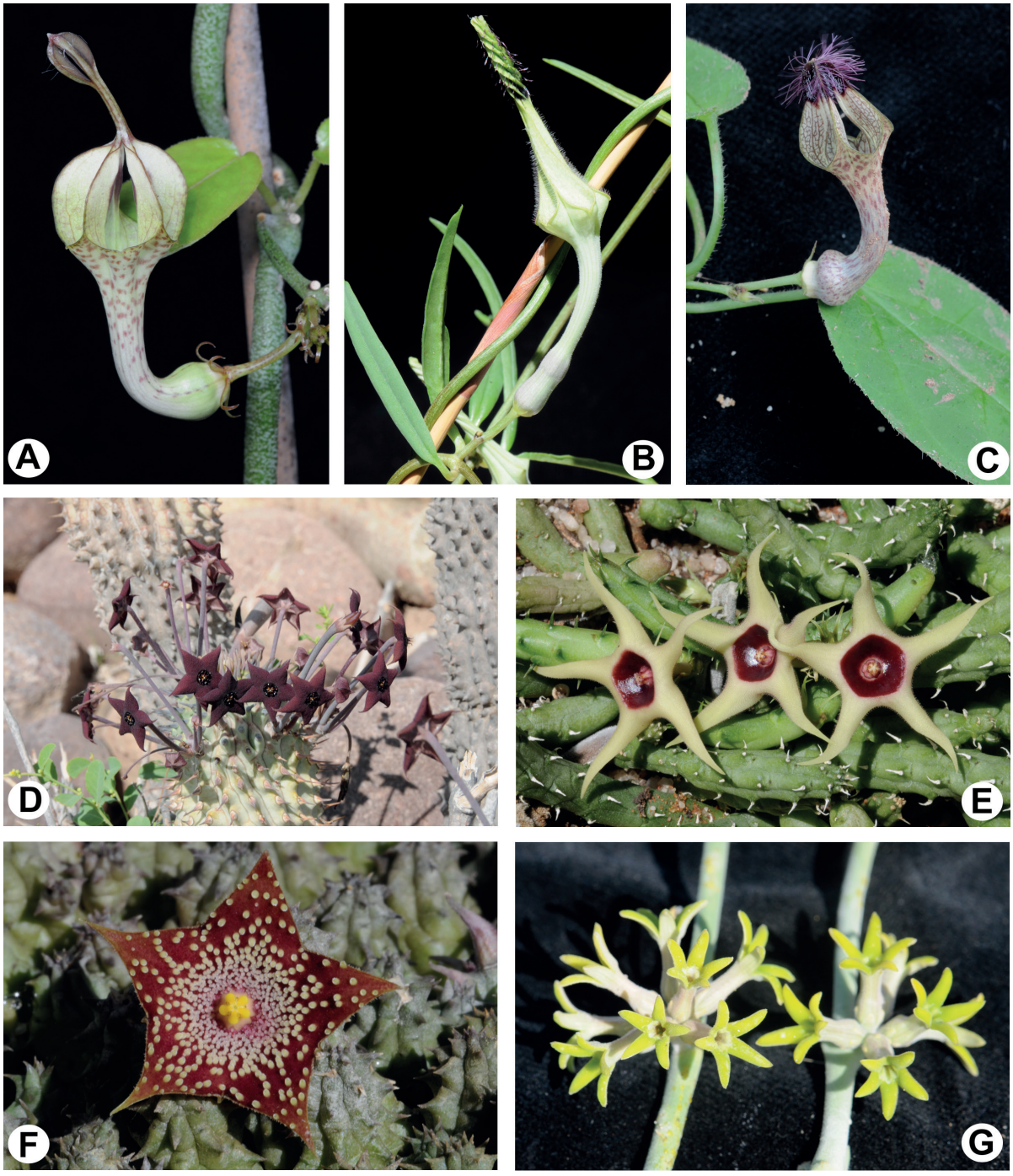

Figure 1: *Examples of species endemic to the highlands and escarpments of Angola and Namibia (HEAN) and the coastal plain west of it: A)* Ceropegia *cf.* haygarthii, *Bruyns 10444, west of Lubango, Angola; B)* Ceropegia terebriformis, *Bruyns 13289, near Caraculo, Angola; C)* Ceropegia volubilis, *Bruyns 14218, near Lucala, Angola; D)* Ceropegia mossamedensis, *near Caraculo, Angola; E)* Ceropegia angolensis, *Bruyns 10419, west of Lubango, Angola; F)* Ceropegia lopanthera, *Bruyns 10410, north of Moçâmedes, Angola; and G)* Leptadenia albida, *Bruyns 12830, near Solitaire, Namibia. Photos by P Bruyns.*

In this paper we investigate: (1) the diversity in the Ceropegieae and *Euphorbia* and the number of endemics present in Angola and Namibia; (2) how these two groups and their endemics are distributed in Angola and Namibia relative to the highlands and escarpments there; (3) how members of these two groups associated with the highlands and escarpments in Angola and Namibia (HEAN) are related to others in Africa, and whether there are any endemic lineages associated with the HEAN; and, finally, (4) which growth forms are most prevalent among these two groups and among their endemics in the HEAN.

MATERIALS AND METHODS

Data on the species of Apocynaceae occurring in Angola were extracted from Goyder (2008, 2009), supplemented by several additions to the Ceropegieae from records in the Natural History Museum Herbarium (BM), University of Cape Town Bolus Herbarium (BOL), University of Coimbra Herbarium (COI), Royal Botanic Gardens Herbarium (K), Jardim Botânico Tropical, Instituto de Investigação Científica Tropica Herbário (LISC), Instituto Superior de Ciencias da Educação (LUBA) and the South African National Biodiversity Institute (NBG) (Thiers 2020). Maps were drawn up from 334 records from these herbaria. Data on the species of Apocynaceae occurring in Namibia are from Bruyns (2014). This amounts to 1,392 specimens for the Ceropegieae. For *Euphorbia*, records from BM, BOL, COI, K, LISC, LUBA, NBG, the South African National Biodiversity Institute National Herbarium (PRE) and the National Herbarium of Namibia (WIND) were used to draw up the maps, which amounted to 439 specimens from Angola and 1,142 specimens from Namibia.

Appendices 1–5 list the species known from the respective regions. This adds to and refines those lists published in Goyder (2008) and Frazão *et al.* (2020) and provides a firm basis for the numbers given in Tables 1 and 2, Figures 2–4 and 6–7 and elsewhere in the text.

Phylogenetic trees shown are adapted and modified from previously published accounts, mainly from Bruyns *et al.* (2014, 2015) for *Ceropegia* (Figure 8) and from Bruyns *et al.* (2011) for *Euphorbia* (Figure 2). Other results are cited from as-yet unpublished data. All photographs are by P Bruyns.

An endemic is defined here as a species that only occurs in the area concerned. Near-endemics, i.e., species with small numbers of records outside the area, such as *Cryptolepis decidua* (Planch. ex Benth.) N.E.Br. and *Raphionacme inconspicua* H.Huber of the Apocynaceae and *Euphorbia virosa* Willd. in *Euphorbia*, are not considered. This account is confined to species; subspecies and varieties are not considered.

For growth forms, many of the Asclepiadeae have been characterised as 'perennial herbs' with 'annual aerial stems' (e.g., Goyder (1998a) for *Pachycarpus*; Goyder (1998b) for *Stathmostelma*; and Goyder and Nicholas (2001) for some species of *Gomphocarpus*) or 'coming up after fires from narrow, tuberous, perennial rootstocks' for *Glossostelma* (Goyder 1995). These are plants that appear to retreat into their rootstock during the dry season. In our assessment of growth forms, they are included under 'geophytic herbs'.

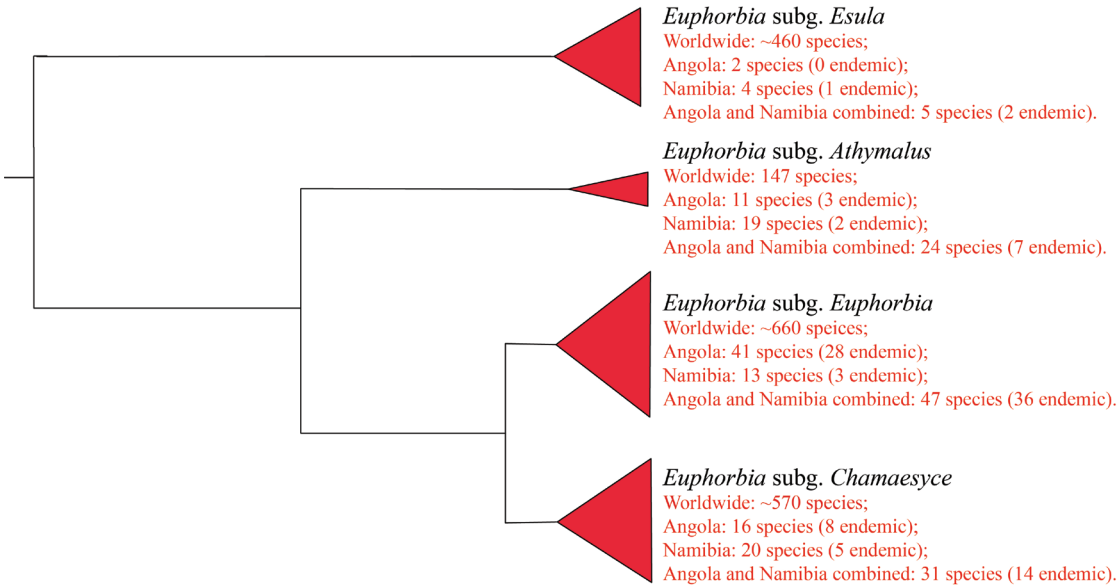

Figure 2: *Relationships between the four subgenera recognised in* Euphorbia *as derived from analysis of DNA data. The total number of species, the numbers of species in Angola and in Namibia and the number of endemics in Angola and Namibia combined are given for each subgenus. The vertical side of each triangle is proportional to the total number of species in the subgenus. Three species are not placed in this system (see Appendix 4).*

RESULTS

Our results are summarised below and in the maps (Figures 3–4 and 6–7). Table 1 provides statistics for numbers of species and endemics in the Apocynaceae and some of its subdivisions. Table 2 summarises information on several growth forms and the extent to which leaves are reduced to rudiments in these groups.

1. How diverse are these groups and how many endemics are there?

(i) Ceropegieae

The Apocynaceae *sensu stricto* (Table 1) is more than eight times as rich in species in Angola as in Namibia, but it is particularly poor in endemics. Of the subfamilies listed in Table 1, the Asclepiadoideae is by far the most diverse. In Angola the Asclepiadoideae (Table 1) makes up 50% of the family (and almost all the endemics), but in Namibia it makes up 86% of the family (and almost all the endemics). In the two countries combined, it makes up 62% of the family (and again almost all the endemics).

A comparison of the tribes that make up the Asclepiadoideae shows that the Ceropegieae is the most diverse. In Angola the Asclepiadeae comes a close second, since there the Asclepiadeae and Ceropegieae have roughly the same number of species. However, in Namibia, which is generally much drier, the Ceropegieae is nearly three times as diverse as the Asclepiadeae. The much higher number of stapeliads in Namibia (more than double that in Angola) contributes considerably to this difference (Appendices 1, 2 and 3). The number of Marsdenieae is small, underlining the generally poor representation of this tribe in Africa as a whole (most of its species occur in Australasia), and there is only one endemic species in Namibia. The Fockeeae is a small tribe altogether, with a total of nine species and no endemics in either Angola or Namibia (Bruyns & Klak 2006).

The Ceropegieae has three to four times as many endemics as any of the other tribes, even when Angola and Namibia combined is considered. That the percentage of *Ceropegia* (for example) endemic to the combined country area is significantly higher than the percentage in either country is due to the species that are endemic to the Kaokoveld, which straddles their common border.

(ii) *Euphorbia*

Euphorbia has a total of 70 species in Angola (Figure 2, Appendix 4) and 56 species in Namibia (Figure 2, Appendix 5). In total, 107 species occur in Angola and Namibia combined.

For Angola, 39 species (i.e., 56%; 61% according to Frazão *et al.* 2020) are endemic, whereas in Namibia only 11 (20%) are endemic. Of the 107 species in the two countries, 59 (55%) are endemic; i.e., more than half of them occur nowhere else.

This shows that in southwestern tropical Africa, while the diversity of *Euphorbia* and *Ceropegia* (for example) is similar, endemism is higher in *Euphorbia*.

2. Where are these groups most diverse and where do the endemics occur?

(a) Namibia

(i) Ceropegieae

The Ceropegieae is found over most of Namibia (Figure 3). However, diversity is concentrated in the highlands and escarpments, with areas of highest diversity around Grootfontein, Gobabis, Naukluft–Tiras, Rosh Pinah and the Groot Karasberge.

Table 1: *Numbers of species in the Apocynaceae and its subdivisions in Angola (adapted from Goyder 2008, 2009, Goyder* et al. *2018 and newer records in the appendices to this paper), in Namibia (data from Bruyns 2014) and in the two countries combined.*

	Angola			Namibia			Angola and Namibia		
	Total species	Endemic species	Endemic species %	Total species	Endemic species	Endemic species %	Total species	Endemic species	Endemic species %
Apocynaceae	235	24	10	153	20	12	326	58	18
Apocynaceae s.s.	88	1	1	10	0	0	92	2	2
Asclepiadoideae	119	21	18	131	17	13	202	51	25
Asclepiadeae	52	5	10	33	3	9	70	10	14
Ceropegieae	56	16	29	90	13	14	117	41	35
Ceropegia	52	15	29	88	13	15	113	39	35
'stapeliads'	24	8	33	59	11	19	68	26	38
Fockeeae	2	0	0	4	0	0	4	0	0
Marsdenieae	9	0	0	4	1	25	11	1	9
Periplocoideae	23	2	9	11	3	27	27	5	19
Secamonoideae	5	0	0	1	0	0	5	0	0

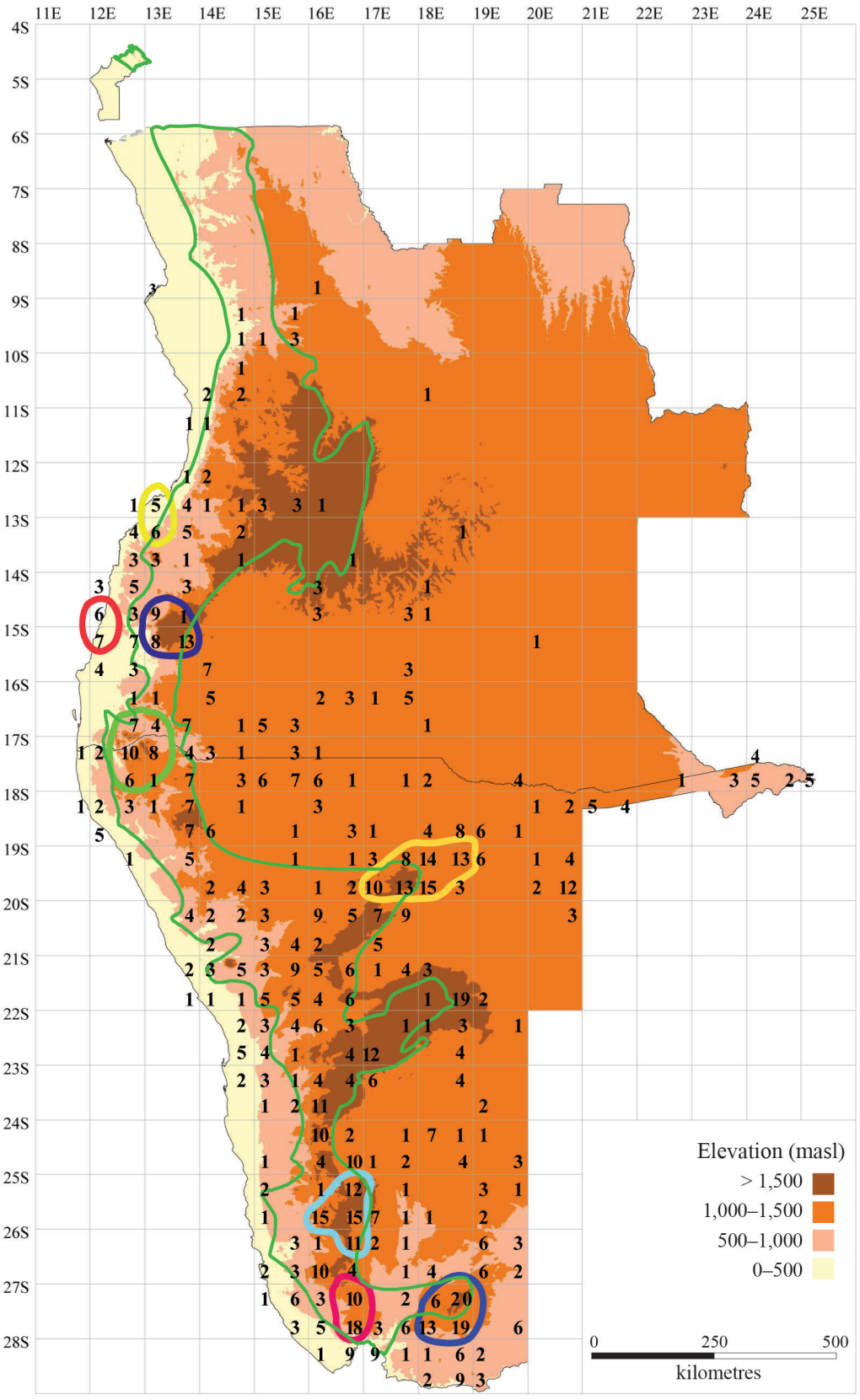

Figure 3: *Occurrence of Ceropegieae in Angola and Namibia (combined). Numbers indicate the numbers of species recorded per half-degree square. Centres of diversity are indicated, approximately, as follows: yellow = Benguela; red = Moçamedes; deep blue = Serra da Chela; thick green = Kaokoveld; orange-yellow = Otavi Mountains; turquoise = Naukluft–Tiras; pink = Namuskluft; and blue = Groot Karasberge. The thin green line indicates the zone of highlands and escarpments of Angola and Namibia.*

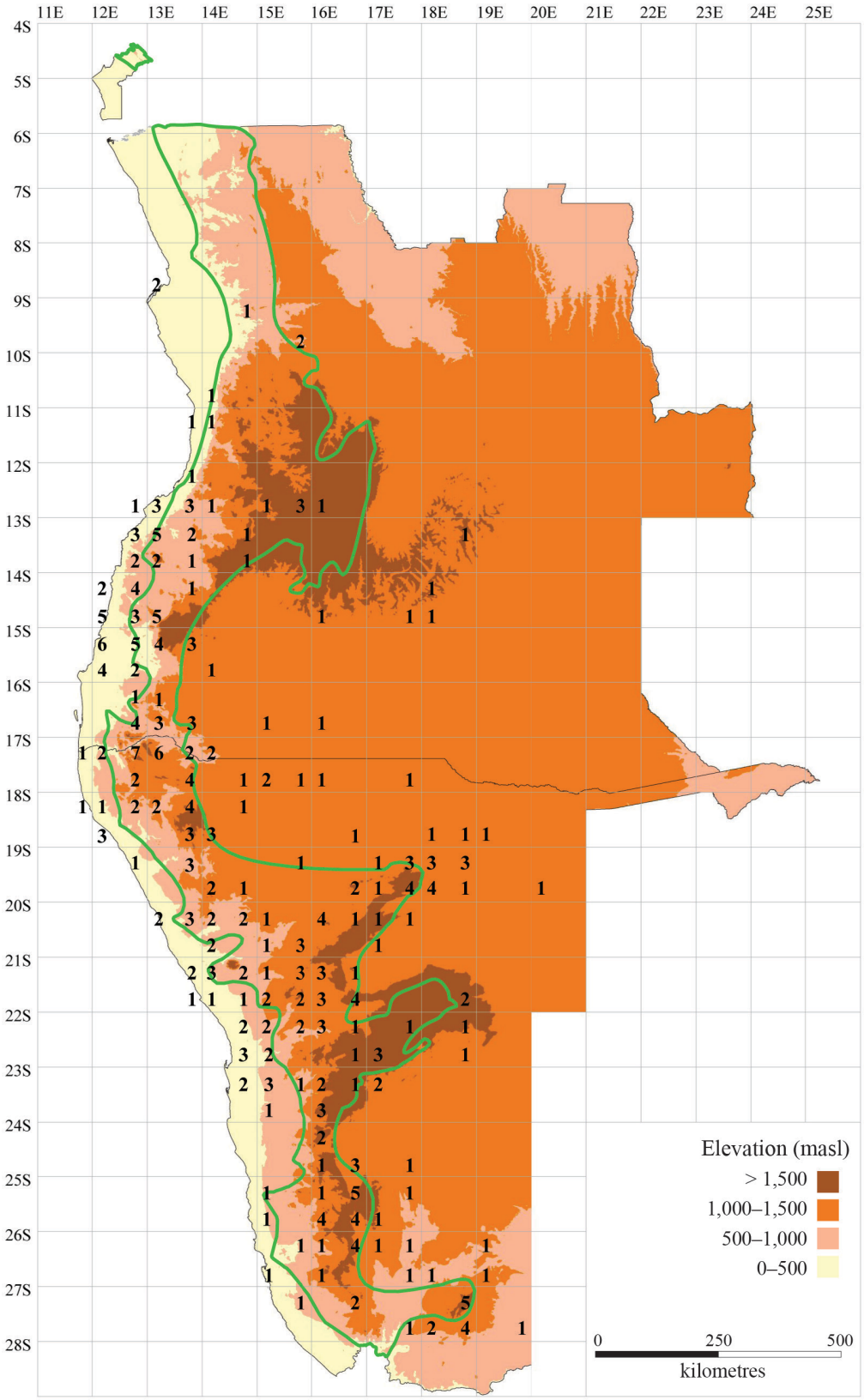

Figure 4: *Diversity of endemic Ceropegieae in Angola and Namibia (combined). Numbers of endemic species to Angola and Namibia are recorded in each half-degree square. The thin green line indicates the zone of highlands and escarpments of Angola and Namibia.*

Endemic species (Figure 4) are mainly associated with the more arid parts of the country and are closely associated with the highlands and escarpment, where endemics are most numerous in the Kaokoveld, Naukluft–Tiras and in the Groot Karasberge. With respect to endemics, Rosh Pinah falls away, as most of the species here are common to the neighbouring arid winter-rainfall parts of South Africa. In Namibia there are far fewer endemics in the most arid coastal zones than in the semi-arid parts. This corresponds closely to the conclusions of Simmons *et al.* (1998: Figure 1a) for all plants in Namibia. Inselbergs (such as the Brandberg and the Groot Karasberge) are not known to harbour any endemics in the Ceropegieae (nor in the Apocynaceae, more generally, or in *Euphorbia*).

The number of endemics in the Kalahari sands east of these highlands is extremely low. Thus, for example, in the square 1920D there is fairly high diversity (12 species; Figure 3), but none of the species is endemic to Namibia (0 species; Figure 4). Species occurring in the Kalahari sands are mostly widely distributed in southern Africa, and a typical example of their wide distribution is shown in Figure 5 for *Ceropegia lugardiae*. The same holds true for southern Namibia, where most of the species are also found in neighbouring South Africa. This is particularly clear in the Groot Karasberge (2718B, 2718D), where diversity is the highest in Namibia (closely followed by the Rosh Pinah area, 2716D), but the number of endemics is lower than in the Kaokoveld (though here species endemic to Angola and Namibia combined contribute to keeping this number high).

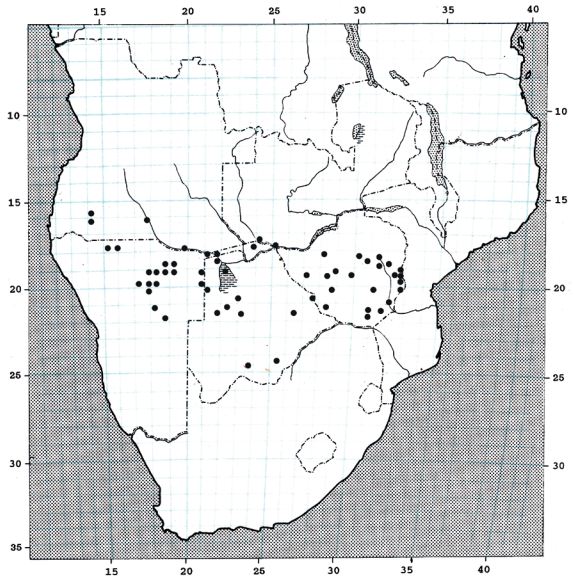

Figure 5: *The distribution of* Ceropegia lugardiae*, a typical species of the drier parts of the Kalahari sands. Here, the concept of this species does not follow Goyder* et al. *(2012), but rather of Bruyns (2014), with its distribution restricted to Angola, Botswana, Namibia and Zimbabwe.*

(ii) *Euphorbia*

Euphorbia presents a similar picture to *Ceropegia*. It is most diverse along and west of the HEAN (Figure 6) in the Kaokoveld–Orupembe area in the extreme north, and Rosh Pinah and the Groot Karasberge in the southern part of the country. Diversity in the Groot Karasberge (2718B, 2178D) is considerably exceeded by that in the Rosh Pinah area (2716D) which receives winter rainfall.

Endemics are extremely few. They are mostly concentrated in the Kaokoveld and are almost completely absent in the south (Figure 7). In particular, the very diverse areas of the Groot Karasberge (where most of the species recorded also occur further east and south in South Africa) and the Rosh Pinah area (where most occur further south in South Africa) have no endemics.

(b) Angola

(i) Ceropegieae

Records are scanty for the Ceropegieae in Angola (Figure 3) and more collecting is required to obtain a clearer picture of the distribution of many of the species. However, although there are still several species awaiting description, further collecting is unlikely to change the fact that the diversity in Ceropegieae in Angola is substantially lower than in Namibia. There is a very strong decrease in numbers northwards as the rainfall increases and the steepness of the escarpment decreases.

In Angola the concentration of the Ceropegieae along and west of the highlands and escarpments is more striking than in Namibia (Figure 3). The Ceropegieae is most diverse in the Serra da Chela (around Lubango, in the squares 1413C, 1513A, 1513B). It is also diverse around Moçamedes, around Lucira (all three on the western side of the country, within the HEAN or west of it).

Endemics (Figure 4) are mainly concentrated along the highlands and escarpments of Angola and west of it, especially in the Serra da Chela, in the Moçamedes area and around Iona. These areas are primarily semiarid, covered with scrub (often very open mopane scrub) and open savanna. Several endemic species occur in the Serra da Chela, perhaps partly reflecting higher collecting activity. The endemics are found in shallow, nutrient-poor soils overlaying sandstones and a few of them are associated with the extensive *Brachystegia* woodland that extends eastwards from here onto Kalahari sands. This is the preferred habitat of the *Ceropegia umbraticola* group (Stopp 1964; with some endemic species) and the rare endemic *Orthanthera gossweileri* (Goyder *et al.* 2018). The major, more isolated inselbergs of Angola have not been investigated in sufficient detail to know whether any endemics occur there.

(ii) *Euphorbia*

Euphorbia in Angola is mainly confined to the highland and escarpment areas and areas west of these. The Serra da Chela is diverse in *Euphorbia* (Figure 6), but it is equalled by the diversity on the northern edge of the Namib Desert around Benguela and is exceeded in the much drier area around Moçamedes (1512A, 1512C). There is also notable diversity in the mountains around Iona. Except for a few geophytic species, there are virtually no records of *Euphorbia* in the vast regions east of the highlands and escarpments in Angola covered by Kalahari sands and *Brachystegia* woodland.

Unlike in Namibia, many of these *Euphorbia* species are endemic. Most of the endemics are found in or west of the highlands and escarpments of Angola, especially in the Serra da Chela, in the Moçamedes area and around Benguela (Figure 7). There are almost no endemics east of the highlands and escarpments in Angola.

Figures 3–4 and 6–7 show that, in Angola, the patterns found in the Ceropegieae are closely followed in *Euphorbia*. One major difference is that *Euphorbia* is almost absent from all regions covered by Kalahari sands and is almost restricted to the highlands and escarpments and to the Namib Desert to the west of these.

3. Which growth forms are most common among these two groups and among the endemics?

The growth forms of the Apocynaceae and *Euphorbia* are discussed below and summarised in Table 2.

(i) Apocynaceae

In the Apocynaceae there are no annuals known in Africa south of the equator.

(a) Apocynaceae *sensu stricto*

Geophytes in the Apocynaceae *sensu stricto*, are unknown. Succulents are also uncommon and are found in *Adenium* Roem. & Schultes and *Pachypodium* Lindl. Of the two endemic species (out of the 92 species of Apocynaceae s.s. in Angola and Namibia combined, Table 1), one is the spiny succulent tree *Pachypodium lealii* (the other is the non-succulent *Landolphia gossweileri*). *Pachypodium* comprises 21 species (Burge *et al.* 2013), with 16 species in Madagascar and five in southern Africa; all are succulent. Two of the five southern African species of *Pachypodium* are spiny succulent trees and both are associated with the escarpment zone in Namibia and Angola (i.e., the HEAN), though only one is endemic to it. (The other, *P. namaquanum* Welw., occurs from southern Namibia into the extremely arid adjacent valley of the Orange River in South Africa.) So in the Apocynaceae *sensu stricto*, four out of 92 species in southwestern tropical Africa are succulent, while 50% of the endemics are succulents.

Table 2: *Numbers of the Asclepiadeae, Ceropegieae, Fockeeae, Periplocoideae and* Euphorbia *in Angola, Namibia and in the two countries combined exhibiting various growth forms.*

	Annual		Geophytic		Succulent		Succulent with reduced leaves*	
	Total species	Endemic species	Total species	Endemic species	Total species	Endemic species	Total species	Endemic species
Asclepiadeae								
Angola	0	0	38	4	2	0	1	0
Namibia	0	0	12	0	4	0	3	0
Angola + Namibia	0	0	42	5	4	1	3	0
Ceropegieae								
Angola	0	0	24	7	31	9	24	8
Namibia	0	0	26	2	67	11	59	11
Angola + Namibia	0	0	41	12	77	28	68	27
Fockeeae								
Angola + Namibia	0	0	3	0	4	0	0	0
Periplocoideae								
Angola	0	0	11	1	0	0	0	0
Namibia	0	0	6	2	0	0	0	0
Angola + Namibia	0	0	13	3	0	0	0	0
Euphorbia								
Angola	12	5	12	8**	48	29	30	21
Namibia	10	3	1	1	41	7	34	6
Angola + Namibia	19	9	13	9**	76	43	55	34

* Leaves are rudimentary or each is reduced to a spine.

** The three unplaced endemic species (Appendix 4) are probably geophytic herbs, but this is not certain and they are omitted from these numbers.

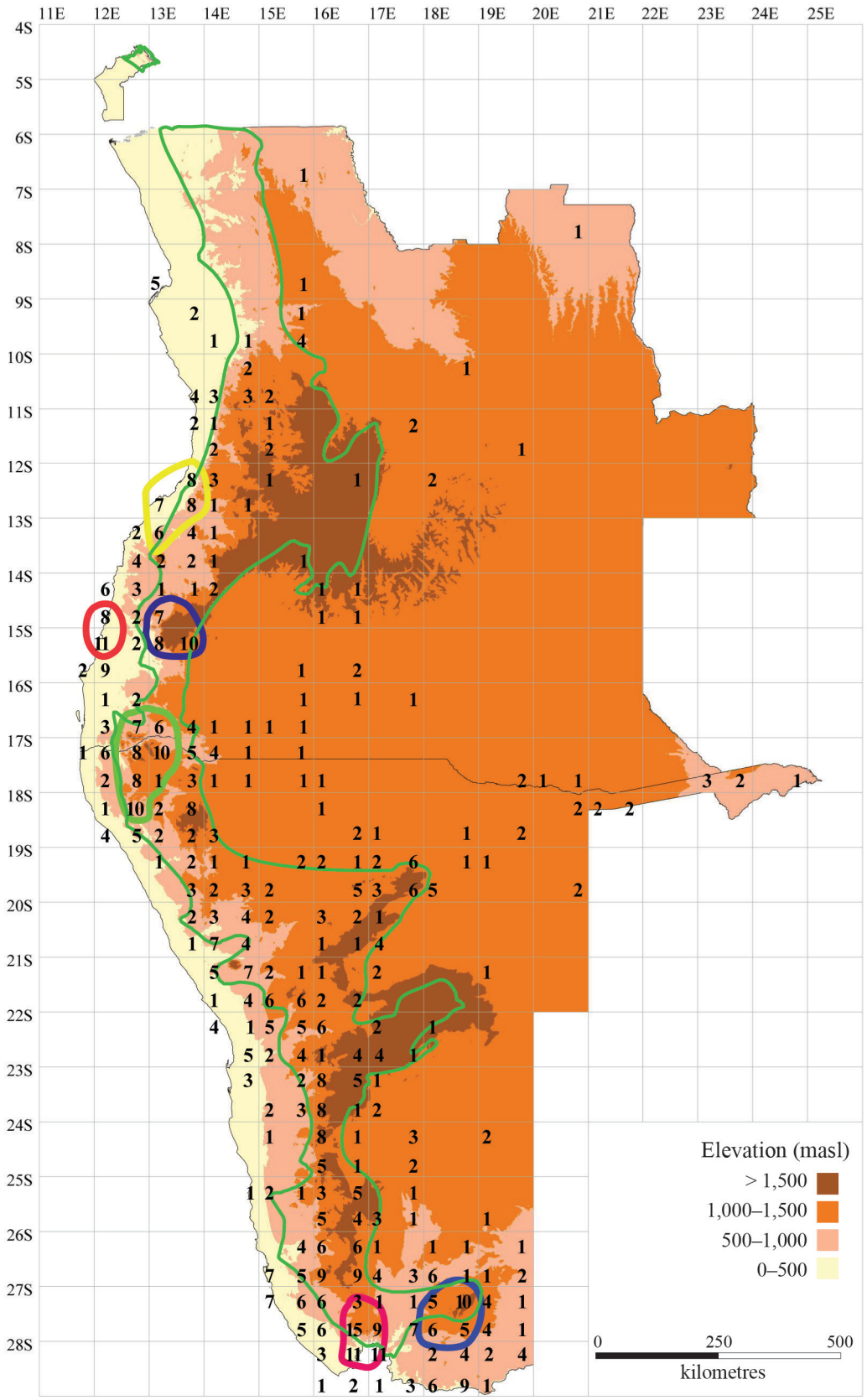

Figure 6: *Occurrence of* Euphorbia *in Angola and Namibia (combined). Numbers indicate the numbers of species recorded per half-degree square. Centres of diversity are indicated, approximately, as follows: pale yellow = Benguela; red = Moçamedes; deep blue = Serra da Chela; thick green = Kaokoveld; pink = Namuskluft; and blue = Groot Karasberge. (Here the Otavi Mountains and Naukluft–Tiras are absent.) The thin green line indicates the zone of highlands and escarpments of Angola and Namibia.*

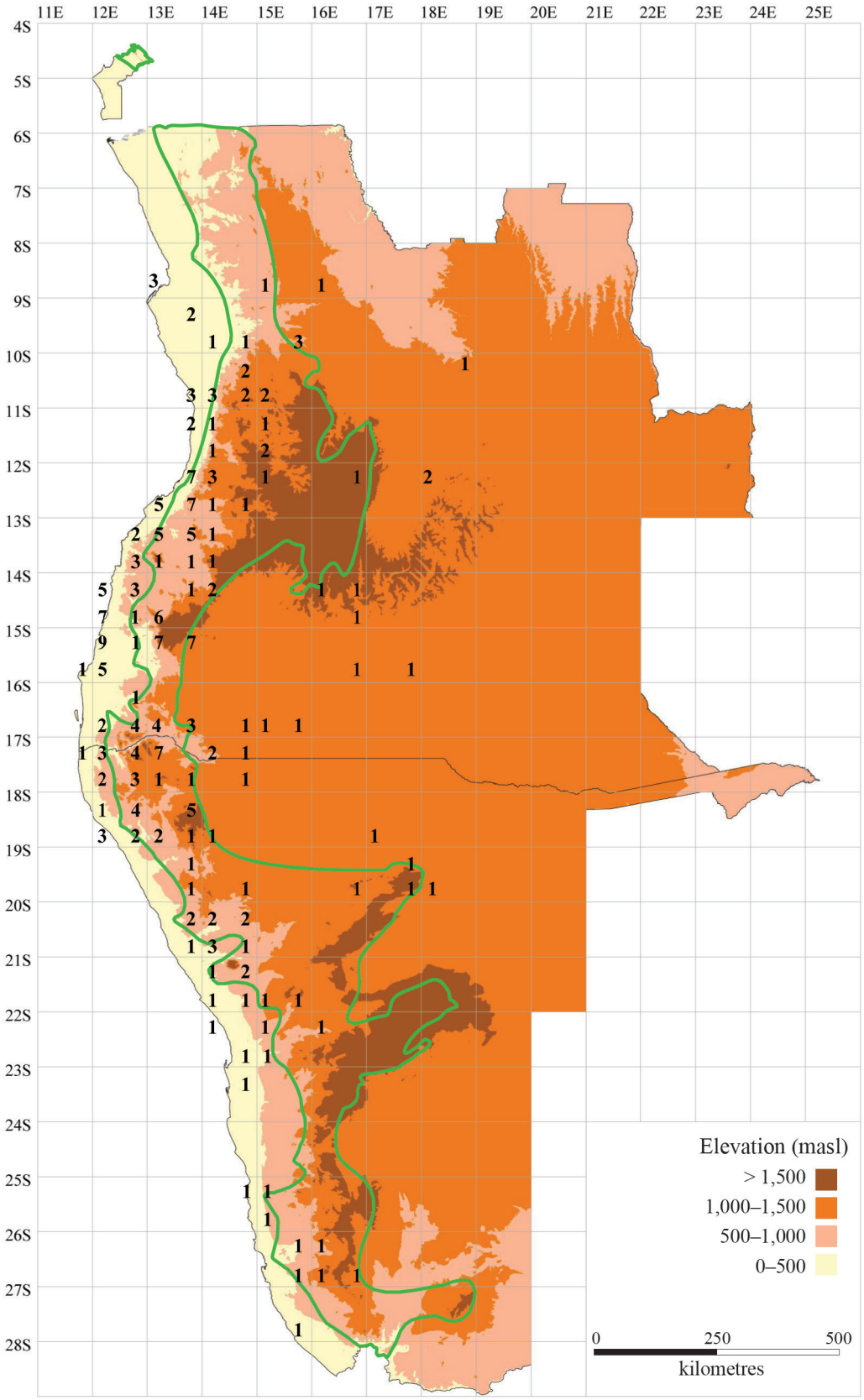

Figure 7: *Diversity of endemic* Euphorbia *in Angola and Namibia (combined). Numbers of endemic species to Angola and Namibia are recorded in each half-degree square. The thin green line indicates the zone of highlands and escarpments of Angola and Namibia.*

(b) Asclepiadeae
Geophytes are especially common in the Asclepiadeae (Table 2), where they make up over half (60%) of the 70 species in Angola and Namibia combined. There are very few endemic geophytes (only 6% of the total).

Succulents, on the other hand, are rare in the Asclepiadeae. Here only 6% of the 70 species found in Angola and Namibia combined are succulent and only one of them is endemic.

(c) Ceropegieae
Geophytes make up less than half (35%) of the 117 species of the Ceropegieae (Appendix 1), though they still form a significant proportion for Angola and Namibia combined. Of these 41 geophytic species, 29% are endemic.

In the Ceropegieae, the earlier diverging lineages are all non-succulent plants with well-developed leaves. An example is provided by the widespread, arid-adapted lineage of nine species of the subtribe Leptadeniineae, which is mainly found from the deserts and semi-deserts of NW India to the Sahel in West Africa (Bruyns *et al.* 2023). This lineage is represented in Angola and Namibia by the three species, *Leptadenia albida* (endemic to the Namib Desert of Angola and Namibia); *L. jasminiflora* (widespread in Kalahari sands from Zambia to South Africa) and *L. gossweileri* (an Angolan endemic from near Menongue).

A significant 66% of the 117 species of the Ceropegieae in Angola and Namibia are succulent. Succulents with reduced leaves (rudimentary or reduced to spines) are also the most common growth form, making up 58% of the 117 species of Ceropegieae in Angola and Namibia combined. Of these 77 succulent species, 35% are endemic.

(ii) *Euphorbia*

Annuals (Table 2) make up 18% of the 107 species of *Euphorbia* in Angola and Namibia combined. Geophytes make up 12% of these 107 species.

In *Euphorbia*, most of the ~1,840 species are not succulent. This is true especially of the subgenera *Chamaesyce* and *Esula* in the northern hemisphere. In the predominantly southern African subgenus *Athymalus*, most of the species are succulent, and in subgenus *Euphorbia* all the African members are succulent. However, even in subgenus *Athymalus*, the earlier-diverging lineages are non-succulent. Examples in Angola and Namibia are provided by non-succulent, deciduous tree-like species (such as *Euphorbia currorii* and *E. matabelensis* in subgenus *Athymalus*, *E. espinosa* and *E. guerichiana* in subgenus *Chamaesyce*) that are mainly associated with the edge of the Namib Desert.

In numbers of species, subgenus *Athymalus* and subgenus *Euphorbia* dominate in southern Africa generally. This is also true in Angola and Namibia (Figure 2). Consequently, most species of *Euphorbia* are succulent in Angola (where 48 out of 70 are succulent, Appendix 4) and in Namibia (where 41 out of 56 are succulent, Appendix 5). Across Angola and Namibia, of the 107 species of *Euphorbia*, 76 (or 71%) are succulent, while among the 59 endemics, 43 (or 73%) are succulent. Those with reduced leaves (55 out of 107) make up 51% of the total. Of these 55 species with reduced leaves, 62% are endemic.

DISCUSSION

1. To which species are those in and west of the HEAN related?

In the Crassulaceae, the species of *Crassula* in the Serra da Chela of SW Angola are closely allied to others in the eastern parts of South Africa. A species of *Umbilicus*, also found in the Serra da Chela, is closely related to others from further north in Africa (Bruyns *et al.* 2019), more specifically to plants from Kenya (H.Schaefer pers. comm.). In the Crassulaceae, therefore, plants have arrived in hospitable parts of SW Angola from further north in Africa (for *Umbilicus*) and from further SE in Africa (for *Crassula*). This pattern is repeated in the Ceropegieae and in *Euphorbia*.

(i) Ceropegieae
Species belonging to the traditional concept of *Ceropegia*, such as *C. haygarthii* and *C. lugardiae* or *C. stenoloba* are all members of lineages that are widespread on the eastern flank of Africa from South Africa to northeastern Africa and the Arabian Peninsula. Here the endemic members (Figure 8) are scattered among others of wider occurrence but there are no lineages endemic to the HEAN or west of it in the Namib Desert. On the other hand, all sampled members of the 'stapeliads' (now also included in *Ceropegia*) in Angola and Namibia have their closest relatives in southern Africa (Bruyns *et al.* 2014). However, no major radiations exist in either Angola or Namibia. The largest known endemic radiation consists of *C. oculatoides*, *C. urceolata*, *C. calosticta* and *C. similior*, a unique well-supported lineage (Figure 8) within section *Huernia* that has speciated in Angola and tropical Namibia, probably along the eastern margins of the Namib Desert. Other members of section *Huernia* that were sampled are not closely related and they belong to other southern African lineages. In section *Stapelia*, the Angolan species are nested among others from Namibia and the western side of South Africa, suggesting that they too have speciated northwards along the edges of the Namib Desert. The same is true of parts of section *Hoodia* and section *Larryleachia*.

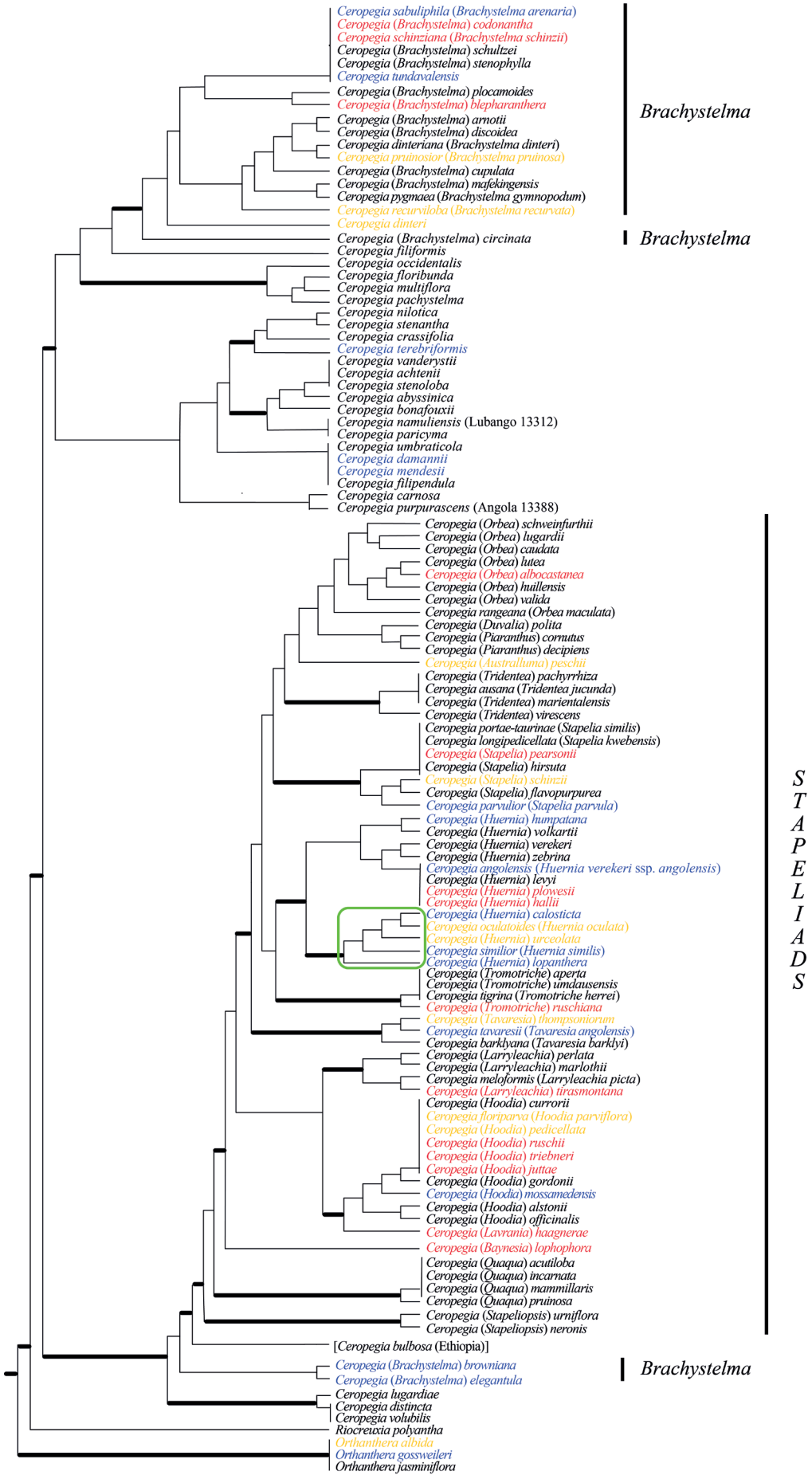

Figure 8: *Relationships among the Namibian and Angolan members of the Ceropegieae.* *[Caption continued on next page]*

Figure 8: *[Caption continued from previous page] Here all known species are listed from Bruyns (2014) and Goyder (2008), and also includes newer records. Angolan endemics are indicated in blue, Namibian endemics in red and species that are only endemic to Angola and Namibia, combined, in beige. The cladogram is adapted from Bruyns* et al. *(2014, 2015) and additional unpublished data. Former genera for the stapeliads and other familiar generic names (such as* Brachystelma*) are given in brackets. Important to observe here is the manner in which the stapeliads are nested deep within* Ceropegia*, where their closest relative is* Ceropegia bulbosa *(from outside our area, but nevertheless indicated here). Also important is the nesting of the erect, tuberous* Ceropegia dinteri *among the former species of* Brachystelma *and the two fusiform-rooted species of* Brachystelma *that have an entirely different position to the other species of* Brachystelma *with tubers. Species with a vertical line to their left have not been sequenced and their position is assumed from morphological features. Thickened branches are well supported (with bootstrap percentage > 80). The unique clade endemic to Angola and Namibia (combined) is ringed in green.*

(ii) *Euphorbia*

Relationships in *Euphorbia* are similar (unpublished results, not shown). *Euphorbia sapinii* De Wild. and *E. teke* Schweinf. ex Pax, both recorded only in northern Angola, are related to others from West Africa and represent the furthest south that these groups penetrate. Most of the species found in Angola have their closest relatives further southeast in southern Africa. All of the small spiny members of 'sect. *Tetracanthae*' (Leach 1976) are related to others from eastern South Africa but they do not form a lineage. The only lineage of *Euphorbia* that has diversified to any degree in Angola and Namibia (combined) is one made up of *E. atrocarmesina*, *E. cannellii*, *E. dekindtii*, *E. dispersa*, *E. ingenticapsa*, *E. otavibergensis*, *E. otjingandu*, *E. semperflorens*, *E. strangulata* and *E. virosa*. This lineage has diversified along the entire length of the HEAN, with all except *E. virosa* endemic to it. *Euphorbia virosa* occurs outside the HEAN, only in South Africa in the adjacent, extremely arid valley of the Orange River (Bruyns 2022: Figure 5.357).

2. Disjunct species pairs

Our results show unexpectedly that closely related species may be found on opposite sides of the subcontinent. This is the case with the closely related pair of species of *Ceropegia* section *Australluma* (Bruyns *et al.* 2014), namely *Ceropegia peschii* and *C. ubomboensis* (I.Verd.) Bruyns (the latter found along and east of the Lebombo Mountains in Mozambique, South Africa and Zimbabwe; Figure 9).

This case is closely mirrored In *Euphorbia* (unpublished data) by the respective distributions of the two very closely related species, *E. candelabrum* Welw., a prominent feature of the western coastal plain of Angola (west of the HEAN; Bruyns & Berry 2019) and *E. confinalis*, mainly found along the Lebombo Mountains in Mozambique, South Africa and Zimbabwe (Figures 10 and 11). Another example is provided by the spatially very isolated *E. faucicola* (from a remote rocky area along a tributary of the Cubango River in southeastern Angola) which is the closest known relative of *E. cooperi*, a species that is widespread from South Africa to Tanzania.

3. Succulence in the HEAN and succulence in the Cape Floral Kingdom

Not all lineages that have diversified in and west of the HEAN are succulent. For example, the entirely non-succulent *Euphorbia* section *Tenellae* has species in the driest parts of the west coast (*E. claytonioides*, *E. phylloclada*) and others at 2,000 m in the Serra da Chela (*E. parifolia*), so that it too has been able to exploit the niches offered by the HEAN. Nevertheless, the presence of succulents is sufficiently striking that it bears comparison with other areas where succulents are common.

The remarkable dominance of succulents in the arid and semi-arid parts of the winter-rainfall Cape Flora in southern Namibia and western South Africa is well known (Manning & Goldblatt 2012, Snijman 2013). This dominance is particularly a consequence of the high diversity of leaf-succulents in the families Aizoaceae and Crassulaceae in the Cape Flora. For

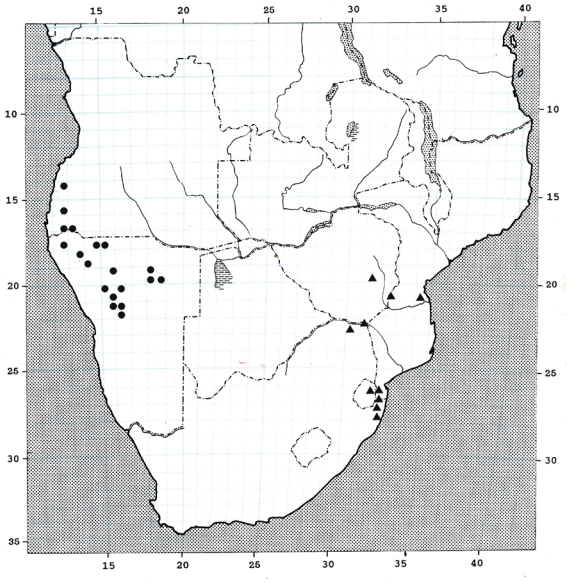

Figure 9: *An example of the distribution of a closely related species pair of* Ceropegia*,* C. peschii *(•) and* C. ubomboensis *(▲), which are found on opposite sides of southern Africa.*

example, the Aizoaceae is the largest family in the 'Succulent Karoo' (Snijman 2013) and is the fifth-largest family in the 'Core Cape Flora' (Manning & Goldblatt 2012). It is less well known that *Ceropegia* and *Euphorbia* (along with *Aloe* L.) are also diverse in this winter-rainfall region. A striking subdominance of succulents continues for the length of Namibia and extends into Angola as far as the Benguela District, after which it fades away northwards as rainfall increases and as the escarpment becomes less steep and rocky. Nevertheless, it reappears occasionally further to the north on isolated, locally dry, rocky areas, such as in the hills at Pungo Andongo. The relatively high percentage of succulent species in *Ceropegia* and *Euphorbia* in the HEAN suggests that this could be a continuation of the dominance of succulents in the arid and semi-arid parts of the winter-rainfall region in southern Namibia and western South Africa. However, here the leaf-succulent families Aizoaceae and Crassulaceae are almost absent. Furthermore, the lineages in *Ceropegia* and *Euphorbia* that provide their diversity in the Cape Flora are mostly different to those that supply the diversity in Angola and Namibia (and in the HEAN more particularly); i.e., these groups of succulents in different areas have different origins.

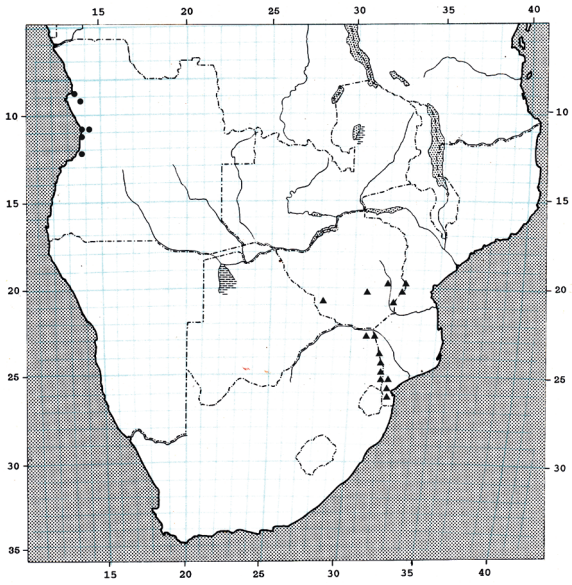

Figure 10: *An example of the distribution of a very closely related species pair of* Euphorbia, E. candelabrum *(•) and* E. confinalis *(▲), which are found on opposite sides of southern Africa.*

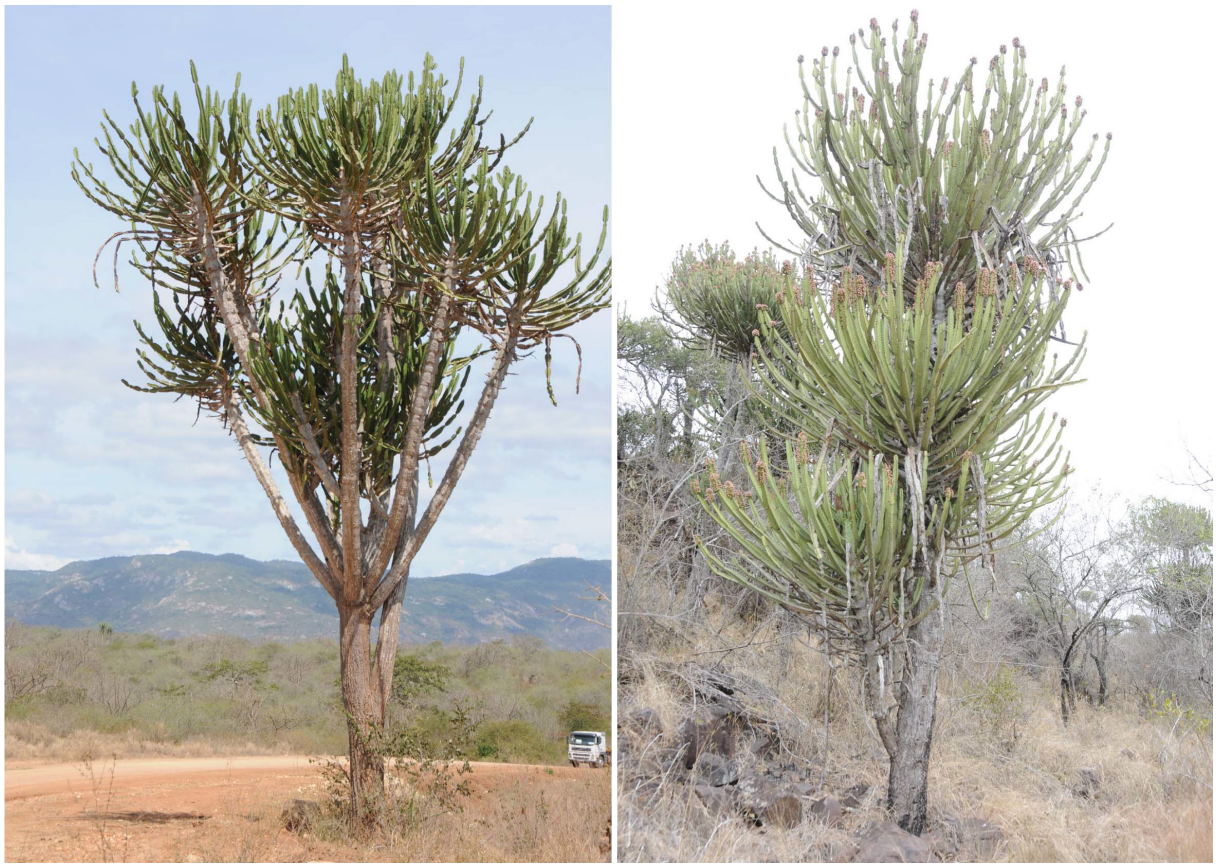

Figure 11: *Two very closely related species from opposite sides of southern Africa. Left:* Euphorbia candelabrum *east of Egito Praia, Lobito District, Angola, at the western foot of the highlands with the escarpment in the background. Right:* E. confinalis, *PVB 11764, near Komatipoort, western slopes of Lebombo Mountains, South Africa. Photos by P Bruyns.*

4. Ages of lineages

Most of the diversity and most endemics in the Ceropegieae and *Euphorbia* of Angola and Namibia are associated with their highlands and escarpments. They are mostly succulent, indicating that succulent lineages have been favoured in this region. Generally, succulents are a relatively recent development in the groups where they are found (Arakaki *et al.* 2011, Bruyns *et al.* 2011 for *Euphorbia*; Bruyns *et al.* 2015 for *Ceropegia*). This suggests that at least the succulent endemics in this region originated within the last 8 million years (Arakaki *et al.* 2011) and are unlikely to have evolved during the early aridification of the Namib which occurred 20 mya or earlier (Pickford *et al.* 2014).

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Appendix 1: *Endemic species of Apocynaceae s.s. and all species of Asclepiadoideae, Periplocoideae and Secamonoideae that are known in Angola (partly from Goyder 2008, 2009, Goyder* et al. *2018, Venter 2009 and other herbarium records), and their placement in sections (for* Ceropegia*). Growth form and nature of the leaves of each species are also given.*

Taxon	Section	Growth form	Leaf
Apocynaceae s.s.			
Landolphia gossweileri (Stapf) Pichon*		rhizomatous subshrub	with blade
Asclepiadoideae			
Asclepiadeae			
Asclepias ameliae S.Moore		geophytic herb	with blade
A. aurea (Schltr.) Schltr.		geophytic herb	with blade
A. foliosa (K.Schum.) Hiern		geophytic herb	with blade
A. minor (S.Moore) Goyder		geophytic herb	with blade
A. palustris (K.Schum.) Schltr.		geophytic herb	with blade
A. randii S.Moore		geophytic herb	with blade
A. schumanniana Hiern		geophytic herb	with blade
Aspidoglossum masaicum (N.E.Br.) Kupicha		geophytic herb	with blade
Cynanchum adalinae (K.Schum.) K.Schum.		climber	with blade
C. ethiopicum Liede & Khanum		climber	with blade
C. polyanthum K.Schum.		climber	with blade
C. schistoglossum Schltr.		climber	with blade
C. viminale (L.) Bassi ex L. (incl. *Sarcostemma welwitschii* Hiern)		succulent	rudimentary
Glossostelma angolense Schltr.*		geophytic herb	with blade
G. cabrae (De Wild.) Goyder		geophytic herb	with blade
G. carsonii (N.E.Br.) Bullock		geophytic herb	with blade
G. ceciliae (N.E.Br.) Goyder		geophytic herb	with blade
G. erectum (De Wild.) Goyder		geophytic herb	with blade
G. lisianthoides (Decne.) Bullock		geophytic herb	with blade
G. spathulatum (K.Schum.) Bullock		geophytic herb	with blade
G. xysmalobioides (S.Moore) Bullock*		geophytic herb	with blade
Gomphocarpus fruticosus (L.) W.T.Aiton		shrub	with blade
G. munonquensis (S.Moore) Goyder & Nicholas		geophytic herb	with blade
G. praticola (S.Moore) Goyder & Nicholas		geophytic herb	with blade
G. semiamplectens K.Schum.		geophytic herb	with blade
G. semilunatus A.Rich.		shrub	with blade
G. swynnertonii (S.Moore) Goyder & Nicholas		geophytic herb	with blade
G. tomentosus Burch.		shrub	with blade
Kanahia laniflora (Forssk.) R.Br.		shrub	with blade
Pachycarpus bisacculatus (Oliv.) Goyder		geophytic herb	with blade
P. firmus (N.E.Br.) Goyder		geophytic herb	with blade
P. lineolatus (Decne.) Bullock		geophytic herb	with blade
Pergularia daemia (Forssk.) Chiov.		climber	with blade
Schizoglossum angolense Schltr. & Rendle*		geophytic herb	with blade
S. graminifolium C.Norman*		geophytic herb	with blade
S. saccatum Bruyns		geophytic herb	with blade
Schizostephanus gossweileri (S.Moore) Liede		succulent scrambler	with blade
Stathmostelma fornicatum (N.E.Br.) Bullock		geophytic herb	with blade
S. incarnatum K.Schum.*		geophytic herb	with blade
S. welwitschii Britten & Rendle		geophytic herb	with blade
Xysmalobium andongense Hiern		geophytic herb	with blade
X. clavatum S.Moore		geophytic herb	with blade
X. holubii Scott-Elliot		geophytic herb	with blade
X. kaessneri S.Moore		geophytic herb	with blade
X. rhomboideum N.E.Br.		geophytic herb	with blade
X. sessile (Decne.) Decne.		geophytic herb	with blade
X. stocksii N.E.Br.		geophytic herb	with blade
X. undulatum (L.) W.T.Aiton		geophytic herb	with blade
Vincetoxicum caffrum (Meisn.) Kunze		geophytic herb	with blade
V. congolanum (Baill.) Liede & Meve		climber	with blade
V. conspicuum (N.E.Br.) Liede & Meve		climber	with blade
V. sylvaticum (Decne.) Kunze		climber	with blade

Taxon	Section	Growth form	Leaf
Ceropegieae			
Ceropegia abyssinica Decne.	*Laguncula*	geophytic climber	with blade
C. achtenii De Wild.	*Laguncula*	geophytic climber	with blade
C. angolensis (L.C.Leach) Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. barklyana Bruyns	*Tavaresia*	dwarf succulent	spine
C. bonafouxii K.Schum.	*Laguncula*	geophytic climber	with blade
C. browniana (S.Moore) Bruyns*	*Stenatae*	geophytic herb	with blade
C. calosticta (Bruyns) Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. caudata (N.E.Br.) Bruyns	*Orbea*	dwarf succulent	rudimentary
C. currorii (N.E.Br.) Bruyns	*Hoodia*	succulent shrub	spine
C. damannii Stopp*	*Umbraticolae*	geophytic herb	with blade
C. dinteri Schltr.	*Chamaesiphon*	geophytic herb	with blade
C. dinteriana Bruyns (=*Brachystelma dinteri* Schltr.)	*Chamaesiphon*	geophytic herb	with blade
C. elegantula (S.Moore) Bruyns*	*Stenatae*	geophytic herb	with blade
C. filipendula K.Schum.	*Umbraticolae*	geophytic herb	with blade
C. floriparva Bruyns	*Hoodia*	succulent shrub	spine
C. haygarthii Schltr	*Phalaena*	slender succulent climber	with blade
C. huillensis (Hiern) Bruyns	*Orbea*	dwarf succulent	rudimentary
C. humpatana (Bruyns) Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. longipedicellata (A.Berger) Bruyns	*Stapelia*	dwarf succulent	rudimentary
C. lopanthera (Bruyns) Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. lugardiae N.E.Br.	*Phalaena*	slender succulent climber	with blade
C. lutea (N.E.Br.) Bruyns	*Orbea*	dwarf succulent	rudimentary
C. mendesii Stopp*	*Umbraticolae*	geophytic herb	with blade
C. mossamedensis (L.C.Leach) Bruyns*	*Hoodia*	dwarf succulent	spine
C. multiflora Baker	*Ceropegiella*	geophytic succulent climber	with blade
C. namuliensis Bruyns	*Laguncula*	geophytic climber	with blade
C. nilotica Kotschy	*Calopegia*	geophytic succulent climber	with blade
C. oculatoides Bruyns	*Huernia*	dwarf succulent	rudimentary
C. parvulior Bruyns*	*Stapelia*	dwarf succulent	rudimentary
C. pedicellata (Schinz) Bruyns	*Hoodia*	dwarf succulent	spine
C. peschii (Nel) Bruyns	*Australluma*	dwarf succulent	rudimentary
C. plocamoides (Oliv.) Bruyns	*Chamaesiphon*	geophytic herb	with blade
C. polita (N.E.Br.) Bruyns	*Duvalia*	dwarf succulent	rudimentary
C. pruinosior Bruyns	*Chamaesiphon*	geophytic herb	with blade
C. purpurascens K.Schum.	*Pseudoceropegiella*	geophytic climber	with blade
C. pygmaea Schinz	*Chamaesiphon*	geophytic herb	with blade
C. racemosa N.E.Br.)**	*Carnosae*	slender climber	with blade
C. rangeana (Dinter & A.Berger) Bruyns	*Orbea*	dwarf succulent	rudimentary
C. recurviloba Bruyns	*Chamaesiphon*	geophytic herb	with blade
C. sabuliphila Bruyns*	*Chamaesiphon*	geophytic herb	with blade
C. schinzii (A.Berger & Schltr.) Bruyns	*Stapelia*	dwarf succulent	rudimentary
C. similior Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. stenantha K.Schum.	*Calopegia*	geophytic succulent climber	with blade
C. tavaresii Welw. ex Bruyns*	*Tavaresia*	dwarf succulent	spine
C. terebriformis Bester*	*Callopegia*	geophytic succulent climber	with blade
C. thompsoniorum	*Tavaresia*	dwarf succulent	spine
C. tundavalensis Bruyns*	*Chamaesiphon*	geophytic herb	with blade
C. umbraticola K.Schum.	*Umbraticolae*	geophytic herb	with blade
C. urceolata (L.C.Leach) Bruyns	*Huernia*	dwarf succulent	rudimentary
C. vanderystii De Wild.	*Laguncula*	geophytic climber	with blade
C. volkartii (Peitsch. ex Werderm. & Peitsch.) Bruyns	*Huernia*	dwarf succulent	rudimentary
C. volubilis N.E.Br.	*Phalaena*	slender succulent climber	with blade
Leptadenia albida (Schinz) Bruyns		shrub	with blade
L. gossweileri (C.Norman) Bruyns*		creeping herb	with blade
L. jasminiflora (Burch. ex Decne.) Bruyns		creeping herb	with blade
Riocreuxia polyantha Schltr.		slender climber	with blade

Taxon	Section	Growth form	Leaf
Fockeeae			
Fockea angustifolia K.Schum.		geophytic climber	with blade
F. multiflora K.Schum.		massive climber	with blade
Marsdenieae			
Gymnema sylvestre (Retz.) R.Br. ex Schult.		climber	with blade
Marsdenia abyssinica (Hochst.) Schltr.		climber	with blade
M. angolensis N.E.Br.		climber	with blade
M. crinita		climber	with blade
M. latifolia (Benth.) K.Schum.		climber	with blade
M. macrantha (Klotzsch) Schltr.		climber	with blade
M. magniflora P.T.Li		climber	with blade
M. schimperi Decne.		climber	with blade
Telosma africana (N.E.Br.) N.E.Br.		climber	with blade
Periplocoideae			
Batesanthus parviflorus C.Norman		climber	with blade
Cryptolepis decidua (Planch. ex Benth.) N.E.Br.		shrub	with blade
C. gossweileri S.Moore*		climber	with blade
C. microphylla Baill.		climber	with blade
C. nigrescens (Wennberg) L.Joubert & Bruyns		climber	with blade
C. oblongifolia (Meisn.) Schltr.		climber	with blade
C. producta N.E.Br.		climber	with blade
C. sanguinolenta (Lindl.) Schltr.		climber	with blade
Mondia whitei (Hook.f.) Skeels		climber	with blade
Raphionacme angolensis (Baill.) N.E.Br.*		geophytic herb	with blade
R. globosa K.Schum.		geophytic herb	with blade
R. inconspicua H.Huber		geophytic herb	with blade
R. lanceolata Schinz		geophytic herb	with blade
R. linearis K.Schum.		geophytic herb	with blade
R. madiensis S.Moore		geophytic herb	with blade
R. michelii De Wild.		geophytic herb	with blade
R. monteiroae (Oliv.) N.E.Br.		geophytic herb	with blade
R. utilis N.E.Br. & Stapf		geophytic herb	with blade
R. velutina Schltr.		geophytic herb	with blade
R. welwitschii Schltr. & Rendle		geophytic herb	with blade
Tacazzea apiculata Oliv.		climber	with blade
T. pedicellata K.Schum.		climber	with blade
T. rosmarinifolia (Decne.) N.E.Br.		climber	with blade
Secamonoideae			
Secamone africana (Oliv.) Bullock		climber	with blade
S. brevipes (Benth.) Klack.		climber	with blade
S. dewevrei De Wild.		climber	with blade
S. erythradenia K.Schum.		climber	with blade
S. punctulata Decne.		climber	with blade

* Endemic to Angola.

** The NE-African *Ceropegia affinis* Vatke, included among the Angolan species by Goyder (2008), is omitted here. This follows Huber (1957), who placed the collection cited by Goyder (2008) under *C. racemosa* N.E.Br.

Appendix 2: *Species of Apocynaceae that are endemic to Namibia, and their placement in sections (for* Ceropegia*). Their growth form and the nature of their leaves are also given.*

Family and species	Section	Growth form	Leaf
Asclepiadoideae			
Asclepiadeae			
Microloma hereroense Wanntorp		twining herb	with blade
M. penicillatum Schltr.		shrub	with blade
Vincetoxicum fleckii (Schltr.) Meve & Liede*		shrub	with blade
Ceropegieae			
Ceropegia albocastanea (Marloth) Bruyns	sect. *Orbea*	dwarf succulent	rudimentary
C. blepharanthera (H.Huber) Bruyns**	sect. *Chamaesiphon*	geophytic herb	with blade
C. codonantha (Bruyns) Bruyns	sect. *Chamaesiphon*	geophytic herb	with blade
C. haagnerae (Plowes) Bruyns	sect. *Lavrania*	dwarf succulent	rudimentary
C. hallii (E.&B.M.Lamb) Bruyns	sect. *Huernia*	dwarf succulent	rudimentary
C. juttae (Dinter) Bruyns	sect. *Hoodia*	succulent shrub	spine
C. lophophora (Bruyns) Bruyns	sect. *Baynesia*	dwarf succulent	rudimentary
C. pearsonii (N.E.Br.) Bruyns	sect. *Stapelia*	dwarf succulent	rudimentary
C. plowesii (L.C.Leach) Bruyns	sect. *Huernia*	dwarf succulent	rudimentary
C. ruschiana (Dinter) Bruyns	sect. *Tromotriche*	dwarf succulent	rudimentary
C. ruschii (Dinter) Bruyns	sect. *Hoodia*	succulent shrub	spine
C. tirasmontana (Plowes) Bruyns	sect. *Hoodia*	succulent shrub	rudimentary
C. triebneri (Nel) Bruyns	sect. *Hoodia*	succulent shrub	spine
Marsdenieae			
Stigmatorhynchus hereroensis Schltr.***		shrub	with blade
Periplocoideae			
Ectadium rotundifolium (H.Huber) Venter & Kotze		shrub	with blade
Raphionacme haeneliae Venter & R.L.Verh.		geophytic herb	with blade
R. namibiana Venter & R.L.Verh.		geophytic herb	with blade

* Sometimes stated to occur in Somalia as well (Thulin 2006), but here this is assumed to be a parallel development.
** The citation of Angola in Bruyns (2014) referred to material subsequently described as *C. tundavalensis*.
***A species very similar to this is also known in Somalia and eastern Ethiopia (Thulin 2006), but here this is also assumed to be a parallel development.

Appendix 3: *Species of Apocynaceae that are endemic only to Angola and Namibia (combined), and their placement in sections (for* Ceropegia*). Their growth form and the nature of their leaves are also given.*

Taxon	Section	Growth form	Leaf
Apocynaceae s.s.			
Pachypodium lealii Welw.		tree	with blade
Asclepiadoideae			
Asclepiadeae			
Schizoglossum saccatum		geophytic herb	with blade
Schizostephanus gossweileri		trailing succulent shrub	with blade
Ceropegieae			
*Ceropegia currorii**	*Hoodia*	succulent shrub	spine
C. dinteri	*Chamaesiphon*	geophytic herb	with blade
C. floriparva	*Hoodia*	succulent shrub	spine
C. oculatoides	*Huernia*	dwarf succulent	rudimentary
C. pedicellata	*Hoodia*	succulent shrub	spine
C. peschii	*Australluma*	dwarf succulent	rudimentary
C. pruinosior	*Chamaesiphon*	geophytic herb	with blade
C. recurviloba	*Chamaesiphon*	geophytic herb	with blade
C. schinzii	*Stapelia*	dwarf succulent	rudimentary
C. thompsoniorum	*Tavaresia*	dwarf succulent	spine
C. urceolata	*Huernia*	dwarf succulent	rudimentary
Leptadenia albida		shrub	with blade

* Previously considered to consist of two subspecies, one occurring in Angola and Namibia combined and the other in Botswana, South Africa and Zimbabwe; new molecular results suggest the second is unrelated to *C. currorii*, so here we use the traditional concept of '*Hoodia currorii*'.

Appendix 4: *Species of* Euphorbia *found in Angola, and their placement in the sections and subsections of the four subgenera. Their growth form and the nature of their leaves are also given.*

Taxon	Section or subsection***	Growth form	Leaf
Subgenus *Athymalus*			
E. benthamii Hiern	sect. *Crotonoides*	annual herb	with blade
E. caperonioides R.A.Dyer & P.G.Mey.**	sect. *Crotonoides*	annual herb	with blade
E. sarmentosa Welw. ex Pax*	sect. *Crotonoides*	annual herb	with blade
E. trichadenia Pax	subsect. *Dactylanthes*	geophytic herb	with blade
E. currorii N.E.Br.**	sect. *Lyciopsis*	small non-succulent tree	with blade
E. acalyphoides Hochst.	sect. *Pseudacalypha*	annual herb	with blade
E. gariepina E.Mey. ex Boiss.	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. indurescens L.C.Leach*	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. lignosa Marloth	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. monteiroi Hook.f.	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. linearibracteata L.C.Leach*	sect. unknown	geophytic herb	with blade
Subgenus *Chamaesyce*[1]			
E. arabicoides N.E.Br.*	sect. *Anisophyllum*	annual herb	with blade
E. granulata Forssk.	sect. *Anisophyllum*	annual herb	with blade
E. loandensis N.E.Br.*	sect. *Anisophyllum*	annual herb	with blade
E. mossamedensis N.E.Br.*	sect. *Anisophyllum*	annual herb	with blade
E. subterminalis N.E.Br.*	sect. *Anisophyllum*	annual herb	with blade
E. zambesiana Benth.	sect. *Anisophyllum*	perennial herb	with blade
E. negromontana N.E.Br.**	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. espinosa Pax	sect. *Espinosae*	small non-succulent tree	with blade
E. guerichiana Pax	sect. *Espinosae*	small non-succulent tree	with blade
E. transvaalensis Schltr.	sect. *Frondosae*	succulent shrub	with blade
E. agowensis Hochst. ex Boiss. (*E. pearsonii* N.E.Br.)	sect. *Scatorhizae*	perennial herb	with blade
E. claytonioides Pax*	sect. *Tenellae*	perennial herb	with blade
E. glanduligera Pax	sect. *Tenellae*	annual herb	with blade
E. macra Hiern*	sect. *Tenellae*	geophytic herb	with blade
E. parifolia N.E.Br.*	sect. *Tenellae*	geophytic herb	with blade
E. radiifera L.C.Leach*	sect. *Tenellae*	geophytic herb	with blade
Subgenus *Esula*[2]			
E. berotica N.E.Br.**	subsect. *Africanae*	succulent shrub	rudimentary
E. cyparissioides Pax	sect. *Esula*	perennial herb	with blade
Subgenus *Euphorbia*			
E. atrocarmesina L.C.Leach*	sect. *Euphorbia*	succulent shrub to tree	rudimentary
E. brevis N.E.Br.*	sect. *Euphorbia*	geophytic succulent	with blade
E. candelabrum Welw.*	sect. *Euphorbia*	succulent tree	rudimentary
E. cannellii L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. dekindtii Pax*	sect. *Euphorbia*	succulent shrub	rudimentary
E. desmondii Keay & Milne-Redh.	sect. *Euphorbia*	succulent tree	with blade
E. dispersa L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. eduardoi L.C.Leach**	sect. *Euphorbia*	succulent tree	rudimentary
E. faucicola L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. gracilicaulis L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. hiernii Croizat*	sect. *Euphorbia*	succulent tree	with blade
E. imitata N.E.Br.*	sect. *Euphorbia*	geophytic succulent	with blade
E. ingens E.Mey. ex Boiss.	sect. *Euphorbia*	succulent tree	rudimentary
E. ingenticapsa L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. mwinilungensis L.C.Leach	sect. *Euphorbia*	geophytic succulent	with blade
E. oligoclada L.C.Leach*	sect. *Euphorbia*	geophytic succulent	with blade
E. opuntioides Welw. ex Hiern*	sect. *Euphorbia*	succulent shrub	rudimentary
E. otjipembana L.C.Leach**	sect. *Euphorbia*	succulent shrub	rudimentary
E. parviceps L.C.Leach*	sect. *Euphorbia*	succulent tree	rudimentary
E. semperflorens L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. strangulata N.E.Br.*	sect. *Euphorbia*	succulent shrub	rudimentary
E. teixeirae L.C.Leach*	sect. *Euphorbia*	succulent tree	rudimentary
E. teke Schweinf. ex Pax	sect. *Euphorbia*	succulent tree	with blade

Taxon	Section or subsection***	Growth form	Leaf
E. vallaris L.C.Leach*	sect. *Euphorbia*	succulent tree	rudimentary
E. virosa Willd.	sect. *Euphorbia*	succulent shrub	rudimentary
E. coerulans Pax*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrublet	rudimentary
E. cuneneana L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. demissa L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. nubigena L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. otjipembana L.C.Leach**	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. sapinii De Wild.	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	with blade
E. scitula L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. subsalsa Hiern**	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. neoangolensis Bruyns*	sect. *Monadenium*	geophytic succulent	with blade
E. neocannellii Bruyns*	sect. *Monadenium*	succulent shrub	with blade
E. neogossweileri Bruyns*	sect. *Monadenium*	succulent shrub	with blade
E. orobanchoides (P.R.O.Bally) Bruyns	sect. *Monadenium*	geophytic succulent	with blade
E. pseudosimplex Bruyns	sect. *Monadenium*	geophytic succulent	with blade
E. carunculifera L.C.Leach*	sect. *Tirucalli*	succulent shrub	rudimentary
E. congestiflora L.C.Leach**	sect. *Tirucalli*	succulent shrub	rudimentary
E. damarana L.C.Leach**	sect. *Tirucalli*	succulent shrub	rudimentary
E. neochamaeclada Bruyns*	sect. *Tirucalli*	succulent shrub	rudimentary

* Endemic to Angola.
** Endemic only to Angola and Namibia combined.
*** The three Angolan endemic species *E. asclepiadea* Milne-Redh., *E. carinifolia* N.E.Br. and *E. tuberifera* N.E.Br. are unplaced in this system.
[1]*Euphorbia parva* N.E.Br belongs to *E. indica* Lam., according to a note by S. Carter on the type specimen (there referred to *E. hypericifolia* L.), but see Carter and Leach (2001: 347). Both *E. indica* and *E. hypericifolia* are introduced weeds so are not listed here.
[2] The specimen *Welwitsch 286* (LISU) was included, doubtfully, by Hiern (1900: 952) under *E. genistoides*, a species from the Western Cape Province of South Africa, but Brown (1911: 542) included this specimen under *E. cyparissioides*, which is more probable and is followed here.

Appendix 5: *Species of* Euphorbia *found in Namibia and their placement in the sections and subsections of the four subgenera. Their growth form and the nature of their leaves are also given.*

Taxon	Section or subsection	Growth form	Leaf
Subgenus *Athymalus*			
E. benthamii	sect. *Crotonoides*	annual herb	with blade
*E. caperonioides***	sect. *Crotonoides*	annual herb	with blade
E. crotonoides	sect. *Crotonoides*	annual herb	with blade
*E. insarmentosa**	sect. *Crotonoides*	annual herb	with blade
*E. currorii***	sect. *Lyciopsis*	small non-succulent tree	with blade
E. matabelensis Pax	sect. *Lyciopsis*	small non-succulent tree	with blade
E. braunsii N.E.Br.	subsect. *Medusea*	succulent shrub	rudimentary
E. caput-medusae L.	subsect. *Medusea*	succulent shrub	rudimentary
E. crassipes Marloth	subsect. *Medusea*	succulent shrub	rudimentary
E. duseimata R.A.Dyer	subsect. *Medusea*	succulent shrub	rudimentary
E. friedrichiae Dinter	subsect. *Medusea*	succulent shrub	rudimentary
E. melanohydrata Nel	subsect. *Medusea*	succulent shrub	rudimentary
E. namibensis Marloth*	subsect. *Medusea*	succulent shrub	rudimentary
E. celata R.A.Dyer	subsect. *Pseudeuphorbium*	dwarf succulent shrub	rudimentary
E. dregeana E.Mey. ex Boiss.	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. gariepina	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. hamata (Haw.) Sweet	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. lignosa	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. monteiroi	subsect. *Pseudeuphorbium*	succulent shrub	with blade
Subgenus *Chamaesyce*			
E. chamaesycoides B.Nord.*	sect. *Anisophyllum*	annual herb	with blade
E. inaequilatera Sond.	sect. *Anisophyllum*	annual herb	with blade
E. neopolycnemoides Pax & K.Hoffm.	sect. *Anisophyllum*	annual herb	with blade
E. pergracilis P.G.Mey.*	sect. *Anisophyllum*	annual herb	with blade
E. burmanni E.Mey. ex Boiss.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. ephedroides E.Mey. ex Boiss.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. giessii L.C.Leach*	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. herrei A.C.White *et al.*	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. juttae Dinter	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. negromontana N.E.Br.**	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. rhombifolia Boiss.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. spartaria N.E.Br.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. stapelioides Boiss.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. verruculosa Marloth*	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. espinosa	sect. *Espinosae*	small non-succulent tree	with blade
E. guerichiana	sect. *Espinosae*	small non-succulent tree	with blade
E. leistneri R.Archer*	sect. *Frondosae*	succulent shrub	with blade
E. transvaalensis	sect. *Frondosae*	succulent shrub	with blade
E. glanduligera	sect. *Tenellae*	annual herb	with blade
E. phylloclada Boiss.	sect. *Tenellae*	annual herb	with blade
Subgenus *Esula*			
*E. berotica***	subsect. *Africanae*	succulent shrub	rudimentary
E. mauritanica L.	subsect. *Africanae*	succulent shrub	rudimentary
E. stolonifera Marloth ex A.C.White *et al.*	subsect. *Africanae*	succulent shrub	rudimentary
E. corneliae Bruyns*	sect. *Esula*	geophytic herb	with blade
Subgenus *Euphorbia*			
E. avasmontana Marloth	sect. *Euphorbia*	succulent shrub	rudimentary
*E. eduardoi***	sect. *Euphorbia*	succulent tree	rudimentary
E. ingens	sect. *Euphorbia*	succulent tree	rudimentary
E. otavibergensis Bruyns*	sect. *Euphorbia*	succulent shrub	rudimentary
E. otjingandu Swanepoel*	sect. *Euphorbia*	succulent shrub	rudimentary
E. virosa	sect. *Euphorbia*	succulent shrub	rudimentary
E. kaokoensis (A.C.White *et al.*) L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
*E. otjipembana***	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
*E. subsalsa***	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary

Taxon	Section or subsection	Growth form	Leaf
*E. congestiflora***	sect. *Tirucalli*	succulent shrub	rudimentary
*E. damarana***	sect. *Tirucalli*	succulent shrub	rudimentary
E. gregaria Marloth	sect. *Tirucalli*	succulent shrub	rudimentary
E. gummifera Boiss.	sect. *Tirucalli*	succulent shrub	rudimentary

* Endemic to Namibia.
** Endemic only to Angola and Namibia combined.