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Welwitschia mirabilis (Welwitschiaceae), male cone characters and a new subspecies

Abstract

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Based on the observation of male cones in plants of old stock of *Welwitschia mirabilis* cultivated in the Botanic Garden Berlin-Dahlem and documented in the garden herbarium, two groups can be distinguished. Plants of "group 1" are characterized by short peduncles and long, purplish brown male cones with widely overlapping bracts. Plants of "group 2" are regularly flowering about three weeks later and have usually longer peduncles but shorter male cones which are glaucous-green to salmon coloured and more "sculptured" due to different bract shape and less overlapping bracts. Tracking the incompletely documented origin of these accessions revealed that some of the over 50 years old plants were grown from seeds received from Coimbra originating from Angola and others from seeds received from Kirstenbosch originating from Namibia. Published illustrations of male cones provided only limited further evidence on cone characters. Examination of herbarium specimens of known origin showed that male cone characters fully agreeing with those of group 1 occur in material from Angola, whereas cone characters of plants of group 2 are typical for specimens from Namibia, particularly from the Swakop area. The differences suggest the existence of two subspecies. The controversial nomenclature of *W. bainesii* and the reasons for avoiding this epithet for the subspecies are briefly discussed. Instead the new combination *W. mirabilis* subsp. *namibiana* is validated. A lectotype is designated for the binomial *W. mirabilis*. As a further result, a total of three male cones with bracts arranged in verticils of three, instead of the regular two, were found among more than 3000 cones screened. One was found on a plant of group 1 grown at Berlin-Dahlem, one in a sample originally received from J. D. Hooker probably of Angolan origin, and one in a herbarium specimen from Namibia.

Introduction

Much has been written about *Welwitschia mirabilis* in the field and in cultivation. The welwitschias grown from seed in the Berlin-Dahlem Botanic Garden since 1946 have been mentioned repeatedly from the first flowering events onward by Gielsdorf (1953, 1956), Maas (1959), Herre (1959, 1960), Eckardt (1971), Langhammer & Schulze (1977), Leuenberger (1980, 1992, 1997), Schmidt (1997) and Barthlott & al. (1999). The successful cultivation was initiated by the late horticulturists K. Jentsch and H. Ehrke and have been continued by K. Swiatkowiak and his team (Leuenberger 1980: 262).

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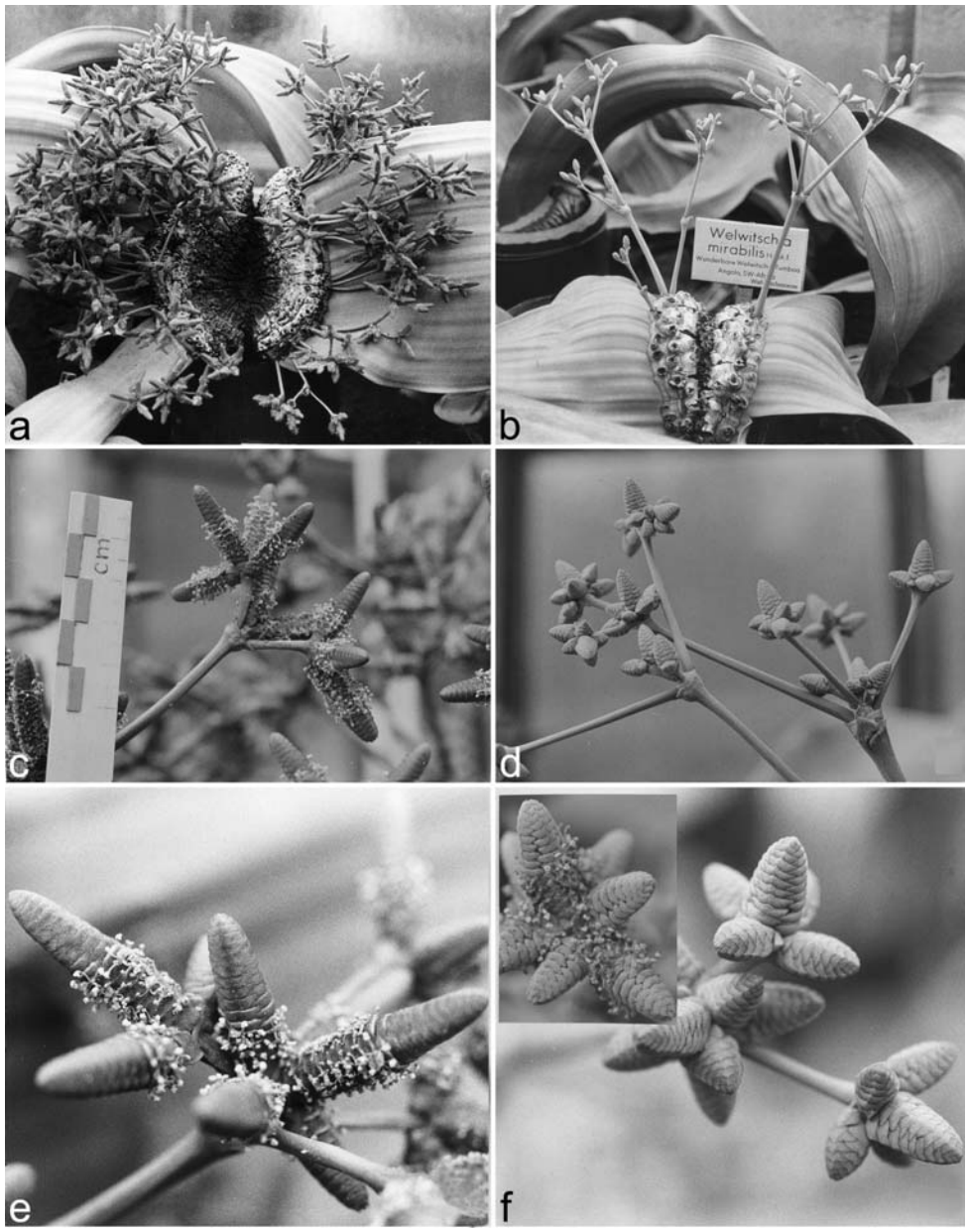


Fig. 1. *Welwitschia mirabilis,* cult. hort. Bot. Berol.; comparison of male flowering plants, inflorescences and male cones – a, c, e: group 1 (note the advanced stage of development); b, d, f: group 2 (inset in f showing cones at a stage of maturity comparable to that of Fig. 1e). – Photos a and e of plant no. 2; b of plant no. 6; c of plant no. 12; d and f of plant no. 3; all photographs by the author.

Published observations on the variation of *Welwitschia* refer particularly to vegetative features. Based on the observation of seedlings grown at Kirstenbosch, Van Jaarsveld (1990: 72) noted the "great genotypic variation of seedlings" from the Koigab river in north central

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Namibia. He concluded that "this variability is probably one of the reasons why *Welwitschia* is still common and such a highly successful plant". In Namibia, Willert (1993) found two whorls of leaves in about 5 % of all plants in the Brandberg area. Detailed studies on some populations exist. Eller & al. (1983) counted 113 male plants among 215 flowering welwitschias in a study area east of Swakopmund. The same population was monitored by Brinckmann & Willert (1987). Measurements of leaf growth made by Moisel were published by Walter & Breckle (1984, 1991). Whellan (1965) provided much information on the ecology and on populations of *Welwitschia* observed in 1963 between Moçamedes and Virei (Birei) in Angola, where he estimated the existence of several million plants in an area smaller than 1600 square kilometers, which is only about 2-3 % of the total range of the species. Wetschnig (1997) calculated the population size on the Welwitschiavlakte in Namibia to be 5000-6000 individuals. Both in Angola and in Namibia, large parts of its range are within national parks (IUCN/UNEP 1987). The species is not listed anymore among especially threatened species (Walters & Gillett 1998). Willert (1994) contributed important biological observations and ecological data from the field (see also Willert 2000). Wetschnig (1997) observed and documented bee pollination. Henschel & Seely (2000) reported about long-term ecological research on a far southern population near Gobabeb, Namibia. This work is complemented by a bibliography containing 297 papers on *Welwitschia* (Henschel & al. 2000).

Variation in cone characters, in contrast, does not appear to have caught the attention of authors doing research on *Welwitschia* or publishing reports from the field or notes on the cultivation. In pub- lications of J. D. Hooker (1862, 1863), W. J. Hooker (1863), Groenland (1863), McNab (1873), Dinter (1898), Anonymous (1898), Baum (1903), Sykes (1910), Takeda (1913), Markgraf (1926), Pearson (1929), Chamberlain (1934), Herre (1948, 1954), Hall (1950), Rodin (1953a-b, 1963), Jensen (1957), Martens (1961, 1971), Whellan (1965), Friedrich-Holzhammer & Roessler (1966), Verdoorn (1966), Kers (1967), Giess (1969), Benson (1970a-b), Horwood (1974), Zecher (1974), Martens (1977), Bornman (1977, 1978), Tijmens (1978), Eller & al. (1983), Willert (1985, 1993, 1994), Brinckmann & Willert (1987), Kedves (1987), Van Jaarsveld (1990, 1992), Kubitzki (1990), Leute & Wetschnig (1990), Kärnefelt (1994), Wetschnig (1997), Steyn & Smith (1999), Lombardi (2000), Schnabel (2000a-b) and Van Jaarsveld & Linder Smith (2001) no particular mention of variation of characters of inflorescences or male cones was made.

Carrière (1867) treated *Welwitschia bainesii* as second though still somewhat doubtful species besides *W. mirabilis*, stating as possible differences shorter trunks, four leaves and trichotomous panicles for *W. bainesii.* Eichler (1887) mentioned, in a footnote, an oral report by Pechuel-Lösche on plants in the "Hereroland" (N Namibia) with yellowish cones. Pearson (1929) interpreted these as mature seed cones.

Rodin (1963) studied particularly the anatomy of the male bracts based on a collection from Namibia. The very comprehensive anatomical and morphological study of Martens (1971: 73-168) provided most detailed information on flower characters, but the variation of cone and bract features was not addressed.

Berlin-Dahlem is one of the few gardens besides Kirstenbosch, where several plants of *Welwitschia mirabilis* can be observed in flower side-by-side. The old stock plants are over 50 years old and were all grown from seed. Numerous plants of second generation exist as well, and the first of these have flowered already. Thirteen plants in the *Welwitschia* house in the nursery, and two in the display glasshouse have trunk diameters between 15 and 45 cm and leaf widths between 16 and 61 cm. Of these, eight produce male cones, four have at least once produced female cones, three have not flowered yet. Surprisingly, the two old plants in the *Welwitscha* annex grown under more arid conditions, supposedly more appropriate in comparison with the natural habitat in Namibia, have only shown initial signs of inflorescence formation on the meristematic ridges, but have not developed peduncles and cones yet. This is possibly due to the lack of an underground heating system in this glasshouse. A constant soil temperature of c. 26 °C maintained in the glasshouse in the nursery has proved to be highly beneficial for successful growth and profuse flowering of our *W. mirabilis*. In 1995 the largest plants of the old stock of *W. mirabilis* were

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provided with individual numbers (1-13) to keep records and garden herbarium voucher specimens separate. The numbering of individuals has been recently extended to all 16 *Welwitschia* plants of the old stock for further monitoring.

Observations on male *Welwitschia* plants cultivated in Berlin-Dahlem

Mr Kurt Swiatkowiak, horticulturist working with the *Welwitschia* collection at Berlin-Dahlem since 1964, first observed differences in flowering period and male cone characters between individual plants among simultaneously flowering male welwitschias. His repeated observations on peduncle length, shape and colour of the male cones led the author to attempt a closer look some years ago. However, the lack of exact documentation of the origin of the plants of the old and presumably heterogeneous stock was taken as a major impediment for a systematic approach to such a study. Nevertheless, in 1993 the author consulted the first and preliminary observations with E. van Jaarsveld of the Kirstenbosch Botanic Garden, where numerous large plants of *Welwitschia mirabilis* originating from Namibia are cultivated (see also Van Jaarsveld 1990: 74[upper left], 2000). No observations suggesting particular differences between male cones of different plants of one accession or between plants of different origin had been made at Kirstenbosch (Van Jaarsveld, pers. comm. 1993). Only much later, an illustration of flowering male plants from Namibia by Van Jaarsveld (1992: 119), well compatible with those of group 2 at Berlin-Dahlem, came to the attention of the author. This was a further stimulus to search for more data by repeated observations, comparison with plants illustrated in literature and with herbarium material of known origin.

The observation suggested that the old stock at Berlin-Dahlem is composed of two groups of plants, denominated here as "group 1" and "group 2" (Tables 1 and 2) . Group 1 comprises plants no. 2, 8, 9, 11 and 12 (Fig. 1a, c, e, 2b, 3a, 4a, c, e, 5), group 2 consists of plants no. 3, 6 and 7 (Fig. 1b, d, f, 2c, 3b, 4b, d, f, 6). The five plants of group 1, including the three largest specimens, regularly produce their inflorescences about three weeks before the regularly flowering plants no. 3 and 6 of group 2. The differences in the length of the peduncles were first thought to be the most conspicuous feature, but this character alone does not permit to distinguish two clear-cut groups, as there is considerable overlap (Table 1).

The flowering period seems to be fairly constant. At full flowering stage of plants of group 1 (Fig. 1a, c, e), plants of group 2 only just start to flower (Fig. 1b, d, f). The inset in Fig. 1f shows a cone at a flowering stage comparable to that shown in Fig. 1e. It also demonstrates the importance of looking at comparable stages of development to appreciate the morphological differences in male cones.

Group 1 – The five plants of group 1 produce purplish brown male cones with rather smooth and thin, laterally very widely overlapping bracts with rather smooth surface and margin (Fig. 2b, 3a, 4a). Three of these plants flower regularly and profusely. Plant no. 8, an exceptional specimen

Table 1. Peduncle and branch lengths (in cm) in male inflorescences in six individuals of *Welwitschia mirabilis* cultivated at Berlin-Dahlem

	Welwitschia group 1				*Welwitschia* group 2	
	pl. no. 2	pl. no. 9	pl. no. 11	pl. no. 12	pl. no. 3	pl. no. 6
Secondary branches	0-2	0-2	0	0-7	0-5	0-7
Primary branches	2-9	2-7	2-5	2-9	7-9	6-9
Peduncle	5-9	2-11	3-10	7-11	10-15	6-14

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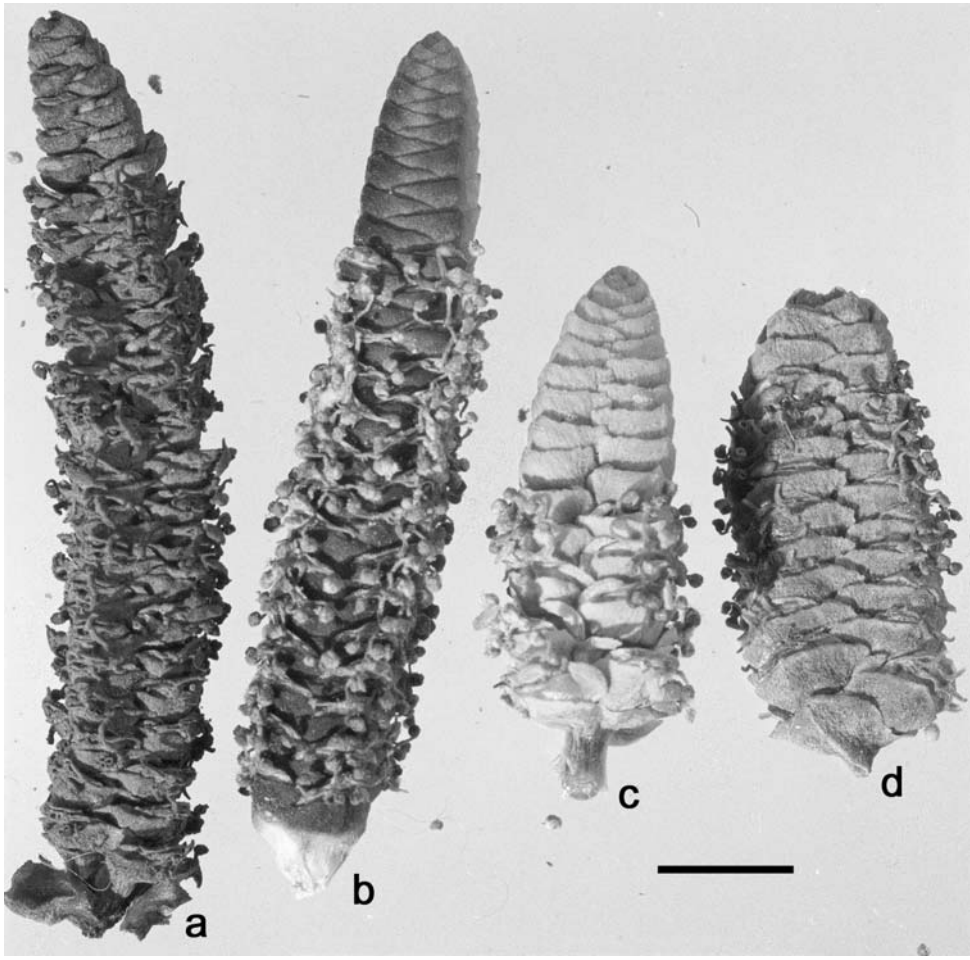


Fig. 2. *Welwitschia mirabilis,* comparison of male cones of cultivated and field-collected specimens – a-b: group 1; c-d: group 2; a: from *Brühl 44* (B) from Angola; b: from cult. plant no. 2; c: from cult. plant no. 6; d: from *Werdermann & Oberdieck 2428/2429* (B) from Namibia. – Scale 5 mm; photograph by M. Lüchow.

with one additional median leaf, only produced few inflorescences since 1991. In 2000, only two inflorescences not suitable for quantitative comparison were formed, but the plant clearly belongs to group 1.

In summer 2000, the number of inflorescences per plant ranged from 2 to 96. The largest plant (no. 12) produced 80 male inflorescences with most peduncles about 7 to 11 cm long and with a total of 2730 cones. From the shed inflorescences of this plant (partly kept in the garden herbarium, *Cubr 26183a*), a random selection of 315 male cones were measured. The broad variation of cone length (15-42 mm) in plant no. 12 is shown together with that of other plants of group 1 (Fig. 5). The inflorescences of no. 11 are possibly exceptional because this plant is currently growing in partial shade of a large leaf of a neighbouring plant. The cones are weaker and shorter, but on average still longer than those of plant no. 3, and equal the longer cones of plant no. 6 of group 2 (Fig. 5-6). Cone measurements of plant no. 12 (group 1) is taken as representative for comparison with field collected material (Fig. 7, 9). The cone length alone is not sufficient to distinguish between the two groups.

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Table 2. Male cone characters of *Welwitschia* plants cultivated at Berlin-Dahlem (see also Fig. 1-6).

Characters	Group 1: plants no. 2, 8, 9, 11, 12; measurements from no. 2, 9, 11 and 12	Group 2: plants no. 3, 6, 7; measurements from no. 3 and 6
Flowering	early July to mid August	late July to late September
Shedding of male inflorescences	late August	December to January
Number of male inflorescences	2-96	2-7
Peduncle length [cm] (only well developed inflorescences with several cones)	(3-)6-1	(6-)9-15
Cone length [mm]	(11-)22-45	10-30
Cone colour	purplish brown (green when shaded)	glaucous-green to glaucous-salmon (green when shaded)
Cone surface	rather smooth	sculptured
Wax on peduncles, bracts and floral bracts	absent to the naked eye	usually conspicuous at least at the base of the cones
Bract pairs, position	overlapping to c. 2 mm	overlapping to c. 1 mm
Bract pairs, shape	deeply cupular	saucer-shaped
Bracts, outer surface	smooth	slightly rugose
Apex of bracts	not pronounced	pronounced, slightly keeled
Bract margin	smooth to slightly erose, not angled	usually erose, angled
Fusion zone of bracts	2.5 mm high	1 mm high
Upper margin of fusion zone	0.5-1 mm broad	2-3 mm broad

Another feature of the group 1 plants not recorded hitherto is the abundant presence of a pigment, probably anthocyan, in the epidermis of the bracts of the cones. The pigment is soluble and reddish brown in alcoholic solution. The reddish brownish colour of the cones is visible in numerous illustrations, as discussed below.

Group 2 – Our three plants with glaucous-green male cones and more sculptured surface (plants no. 3, 6 and 7) produce on average fewer inflorescences with longer peduncles but shorter cones ranging between 10 and 26 mm length (Fig. 1b, 2c). A diagram with cone measurements of two plants of group 2 is shown in Fig. 6. Inflorescences of plant no. 7 were observed and photographed in 1993 and coincide perfectly with plants no. 3 and 6.

The male cones of all three plants are pale greenish grey when young but turn salmon coloured with a glaucous hue at maturity, caused by a wax cover which is particularly conspicuous on the basal bracts but sometimes extends to the whole cone. The presence of wax on the leaf epidermis of *Welwitschia* was illustrated by Barthlott & Ehler (1977) and mentioned for specimens from Namibia by Wilhelmi & Barthlott (1997), whereas wax on the cones has not been specifically mentioned. In Fig. 4d, f the presence of a dense cover of tubular wax on bracts of plant no. 3 is shown in comparison with the scattered wax tubes on bracts of the group 1 plant no. 2 (Fig. 4c, e). Male cones of group 2 of the cultivated specimens do not (or at least not markedly) release pigment when preserved in alcohol. The colour of the cones alone may not be conclusive, however. It varies to some degree on the same plant and on the sun-exposed and shaded side of individual cones. Cones of group 2 vary between glaucous green and salmon coloured. Both the wax and the pigment characters need further study in comparison with material from the field.

Bract shapes in groups 1 and 2 – The most conspicuous and constant difference is in the shape and fusion zone of the bracts. In the plants of group 1 the bract pair forms a deep cup, the fusion

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Fig. 3. *Welwitschia mirabilis,* comparison of tips of male cones in lateral view (upper row), of dissected pairs of bract scales of the same in lateral view and viewed from above (lower two rows) – a: of plant no. 2; b: of plant no. 6. – Scale 2 mm; photographs by M. Lüchow & G. Kuhlmann.

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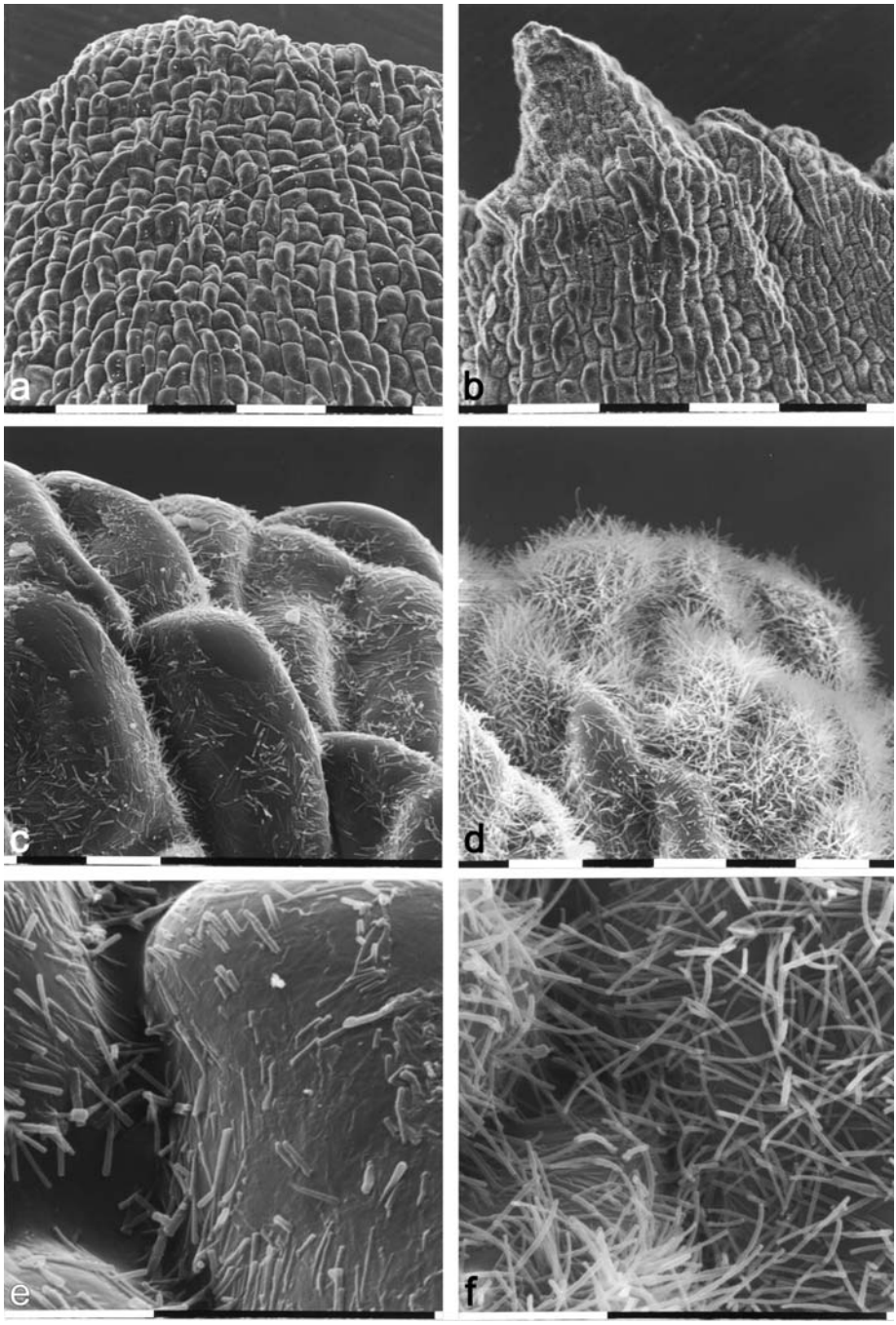


Fig. 4. *Welwitschia mirabilis,* scanning electron micrographs of epidermal features of male cone bracts – a-b: tips of bract scales of male cones; c-d: epidermis of bract margin near tip; e-f: wax secretions on male cone bracts. – a, c, e of group 1 (plant no. 2); b, d, f of group 2 (plant no. 3). – Scale 0.1 mm (a-b); 10 µm (c-f); photographs by M. Lüchow.

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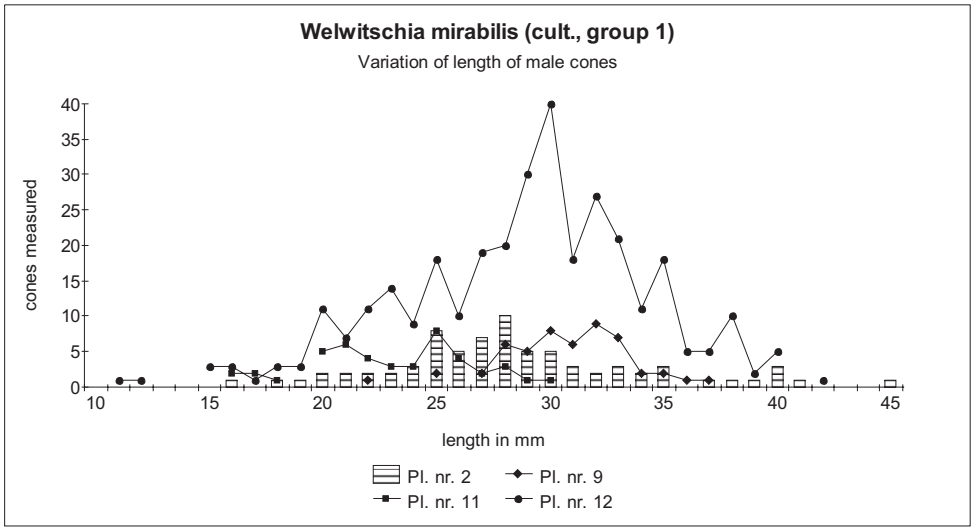


Fig. 5. *Welwitschia mirabilis,* diagram showing variation of cone length in cultivated plants of group 1 (no. 2, 9, 11 and 12).

zone is higher and only slightly differentiated, hence the wide overlapping of the bract pairs (Fig. 1e, 2b, 3a). The cones of group 2 have a more "sculptured" aspect (Fig. 1f, 2c, 3b). The bracts are slightly keeled, the surface is slightly rugose, and the margin is not smooth but slightly erose (Fig. 4b). The bracts are less overlapping laterally and the exposed margin is angled. In dissected or broken cones, the difference is more apparent (Fig. 3). In the plants of group 2 the fusion zone is much shorter than the main body of the bract. The bract pair is saucer-shaped in lateral view. At the fusion zone, the bracts thus overlap to a lesser degree with the upper bract pair. The differ-

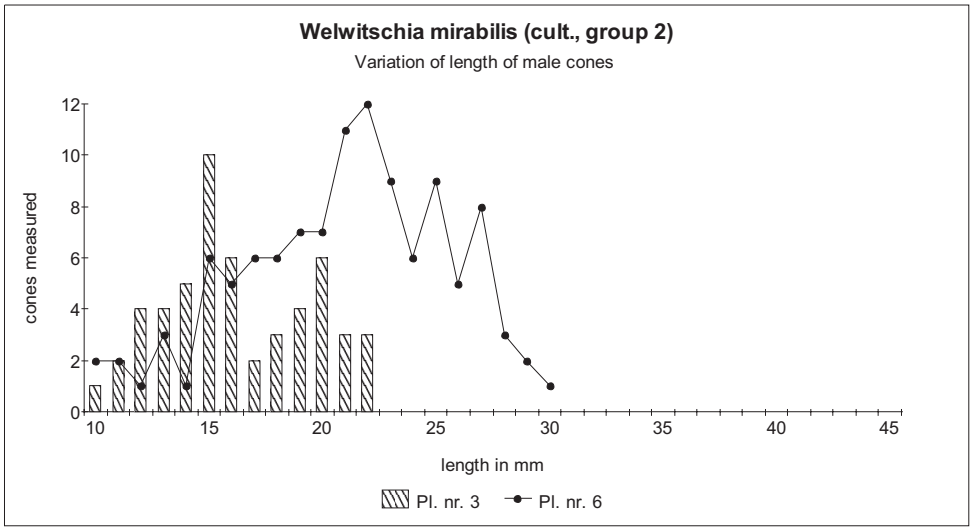


Fig. 6. *Welwitschia mirabilis,* diagram showing variation of cone length in plants of group 2 (no. 3 and 6).

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ence is clearly visible both in fresh material and in herbarium specimens. This has not been noted in literature and, as will be shown below, the details described here are not conspicuous in most published illustrations. In the vast majority of papers cited above, probably only material from Namibia was examined. Often the exact origin of the material is not specified.

Differences in female cones may exist too. Three female plants at Berlin-Dahlem (no. 1, 4 and 13) produced cones without conspicuous wax and with the apex of the scales not keeled at all. These probably belong to group 1. One plant (no. 5) flowered for the first time in 1999, later in the year than the three plants probably belonging to group 1, but simultaneously with male plants of group 2. It produced peduncles and cones with a conspicuous wax cover and the bracts have a slightly more pronounced apex. More material is needed to ascertain that these differences are representative. Female cones appear to be pigmented in all plants.

The origin of the Berlin-Dahlem *Welwitschia* plants

A specimen-based accession system did not exist at Berlin-Dahlem from the time of the first *Welwitschia* sowings until 1979 (Leuenberger 1981) and little information on the early accessions is available. Gielsdorf (1953), however, stated that, following the loss of plants during World War II, the first *Welwitschia* plants of the old stock were grown in Berlin-Dahlem from seed in 1946. In a later report, he stated that the first plants flowered in 1955, probably for the first time in Germany, and that the seed had been received upon request from the University of Coimbra, Portugal (Gielsdorf 1956). A corresponding sample of three male cones in a dried out jar, dated 3 July 1955 from "B.G. Berlin" without further data is preserved in the spirit collection at Berlin-Dahlem. Pilger (1953a-c), Mildbraed (1953) and Mattick (1956, 1958) did not mention the Berlin welwitschias in their reports on the garden.

According to unpublished information given to the author years ago by the late deputy technical director Erhard Borges, seeds were received in 1946 also from Kirstenbosch Botanic Garden. In this context, it may be noted that the oldest plants at Kirstenbosch date back to sowings of 1949 (Van Jaarsveld 1990). Accession lists at Berlin-Dahlem were checked in order to find more detailed evidence on the seed origin but only few lists documenting species (but rarely accessions) in the temperate house section between 1951 and 1959 could be located. Unfortunately, no lists or card files documenting accessions or sowings of *Welwitschia mirabilis* were found in a search among the relevant accession files with Mr Hartmut Loose, horticultural head of the temperate house section.

Seed lists of putative providers were checked for further information. The Index Seminum of Coimbra lists seed of *Welwitschia mirabilis* without details of origin for the years 1944, 1945, 1950 and 1951. The cover picture of the index of the year 1944 is a photograph of male *W. mirabilis* (with very short peduncles!) with the indication "in arenosis deserti Mossamedis". According to information received from Coimbra (J. Paiva, A. Tavares, pers. comm.), the origin of the seed was Moçamedes, Angola but only the last one of these seed lists is kept in the library at Berlin-Dahlem and it does not contain any annotations on seeds ordered by Berlin-Dahlem. Seed lists received from c. 1960 onward contain such annotations.

The information that *Welwitschia* seed was received both from Coimbra in 1946 and from Kirstenbosch in 1946 or later provides evidence that the old stock of *Welwitschia* at Berlin-Dahlem is composed of plants of at least two provenances, some of seed from Angola (via Coimbra) and some from Namibia (via Kirstenbosch).

According to lists and card files, seeds of *Welwitschia* were later received also from "Belem-Lisboa in 1968/69". Seed of *Welwitschia* was distributed from Lisboa through the Index Seminum of the Agricultural Garden and Museum of Lisboa (1968), but no details on this accession are available. Another record of 1968 at Berlin-Dahlem simply states "Nova Lisboa, Angola" and appears to refer to field collected seed received from Angola. The only specimen of this accession was lost in 1988. Also one later accession grown from seed received in 1972 from H. Herre, Stellenbosch, was lost only recently. Both plants were grown in pots and had not flow-

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ered yet, even though it is meanwhile known that *Welwitschia* plants can flower as early as 2 ½ years after germination (Van Jaarsveld 1992). Earlier experiences about flowering in cultivation state a range between three to four and 20 years (Herre 1948, Gielsdorf 1956, Eckardt 1971, Van Jaarsveld 1990, Triebner 1938). Song (1980: 69) reported "coning signs" even on seedlings one year and two months old. The youngest plants producing flowers at Berlin-Dahlem were 9-10 years old.

The first flowering of a male plant at Berlin-Dahlem is documented by a photograph taken by a local photographer (Hahn, unpublished, dated 1954). Remarkably, the same photograph appeared without indication of origin in Graf (1963: 1002). The plant can be identified as no. 2 because of the shape of the rim of the drain pipe tube in which the plant is still growing today. The first flowering of a female plant at Berlin-Dahlem was in summer 1968 (Eckardt 1971). In the same year, plants no. 1 and 2 were documented by a series of unpublished b/w photographs by E. Dieckmann. Further photographs exist of plants no. 8, 9, and 12 froms 1969 to 1976 and the plants of the old stock were photographed individually by the author in 1993 and again in 2000.

Published illustrations of male cones of *Welwitschia*

Published illustrations and descriptions were analysed for possible evidence of geographical, infra- or interpopulational variation in male cone characters. However, many of the published illustrations do not show sufficient details or are difficult to compare because of the halftone resolution, and the quality of early colour photographs in print is also often insufficient for this purpose. In descriptions, morphological data relevant to our question are scarce, if provided at all. Only the colour of the cones is usually mentioned.

In the very detailed and profusely illustrated original account on *Welwitschia,* J. D. Hooker (1863: t. 6(1-2)) figured young male cones collected by Welwitsch in Angola, stated to be from Cape Negro (14°S). Due to the juvenile stage they are not easy to compare and resemble the equally young stages shown in Fig. 1d, f. The female cones were explicitely illustrated "chiefly from Mr Baines' specimens", i.e., from material from further south in the Namib desert (today Namibia).

The colour plate in the Botanical Magazine (W. J. Hooker 1863: t. 5368, 5369) is copied from J. D. Hooker (1863). The male cones illustrated are the same as in the first work. They are green and stated to be young, "immediately previous to expanding". The description, however, notes "cones scarlet", which may refer to the female cones shown in the illustrations. If it refers also to the male cones, this could be significant. J. D. Hooker (1863) mentioned and illustrated material of Welwitsch and of Monteiro from Angola, of Andersson and of Baines from the southernmost part of the range in Namibia ("Damaraland ... about Walvisch Bay, or between the 22nd and 23rd degree of S. lat."). Later illustrations are thus of interest.

A detailed drawing of male and female cones of material received from Dinter from SW Africa was published in an article in the Gardener's Chronicle (Anonymous 1898). The plant is without exact origin, but in the case of Dinter undoubtedly from Namibia. The drawing clearly shows sculptured male cones with angled bract margins, just like those of the tardily flowering welwitschias of group 2 at Berlin-Dahlem. The habitat photograph on the cover of the Index Seminum of Coimbra 1944, in contrast, shows large plants with very short male inflorescences agreeing with plants of group 1.

Rodin (1963) illustrated material of male plants from Namibia. The fused cone bracts are shown in transverse section. The inflorescence and the cones agree perfectly with our plants of group 2. The illustration of Giess (1969: 36) of plants in Namibia shows also cones of pale colour with clearly sculptured bracts.

Matos (1970), illustrating the *Welwitschia* habitat in the Iona National Park in Angola, provided no details of flower cones. Horwood (1974), who visited the area of Moçamedes in Angola illustrated very short inflorescences and dark and lustrous male cones. However, the details are difficult to assess further due to the lack of resolution. Schulze & Schulze (1976) illustrated habi-

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tat and habit of *Welwitschia* in the Namib without details of male cones. Bornman (1978) illustrated Namibian *Welwitschia* plants with pale salmon coloured to notably glaucous male cones. A colour photograph by Tijmens (1978) shows a plant with rather long and glaucous peduncles.

The most detailed photographic account is based on cultivated specimen in the greenhouse of the California State University at Fullerton published by Song (1980). Good colour and several b/w photographs of male cones were provided, but they lack details on the origin of each specimen. According to the text, the collection contains plants grown from seeds from Angola and Namibia. The plants from Angola were reported "being the more rapid growers" (Song 1980: 68). The colour of the peduncles and cones was specifically addressed: "The color of the stem and strobili ranges from a dark green tinged with red to a deep brick red from the time of emergence to maturity" (Song 1980: 70). One individual was reported to have slightly glaucous stem and strobili. The peduncle length and the details of the bracts agree remarkably with our tardily flowering specimens. The flowering time indicated by Song (20 July to 9 September) also agrees with our observations on group 2. All male plants illustrated were probably of Namibian origin.

A drawing by Craven & Marais (1986) is too sketchy to be interpreted. Van Jaarsveld (1990) illustrated a male plant in habitat at Springbokwasser, N Namibia. It shows definitely pale cones, but the resolution of the photographs does not allow to say much about the texture. Nevertheless, this is an indication of the presence of pale cones outside the region of the most frequently visited populations in the southernmost part of the range. The photograph of Breitenbach (1992: 214) shows young female rather than male cones.

The best illustration for comparison is that of Van Jaarsveld (1992: 119). It is a colour photograph of a 5½ year old plant at Kirstenbosch grown from seed collected at Koigab (in the Skeleton Coast Park in north central Namibia) and shows male inflorescences with cones exactly like the pale-flowered plants at Berlin-Dahlem. Schultze-Motel (1992) also illustrated plants with conspicuously glaucous male cones in the Namib desert near Swakopmund. Knotters (1996) illustrated a male plant in the Petrified Forest in Namibia with short peduncles and rather long but glaucous cones, possibly a significant record. The good colour photographs of Wetschnig (1997: 161, 164, 167) from the Welwitschiavlakte near Swakopmund in Namibia show clearly glaucous cones with bract shape and wax typical of the southern group. Van Jaarsveld (1998) illustrated only the female cones in close-ups.

Schnabel (2000a) provided numerous good colour illustrations of plants in the habitat in Namibia. A photograph on p. 32, of a male plant, without indication of locality, shows glaucous cones, but another photograph on p. 35 of a plant in the Petrified Forest in north central Namibia shows a plant with reddish brown and rather long male cones. Again, resolution of the photographs is not sufficient for comparison of details.

Miscellaneous photographs recently published on websites have not provided conclusive further evidence (for a comprehensive link, see Earle 1999). A photograph (Pratorius, undated) showing dark salmon-red to brownish male cones is of interest because, at first sight, it seems to be intermediate. However, the presence of wax and the bract shape point rather to the kind with sculptured scales of Namibian origin. According to Wilson (pers. comm.) it was in fact from Namibia, but no details on ist origin are known. The photograph by Schoepke (undated) from Namibia neither allows to assess morphological details. A photograph of a plant in cultivation without origin (Anonymous, undated) has dark reddish brown cones similar to our plants of group 1.

As a conclusion, the illustrations in the Gardeners Chronicle (Anonymous 1898), those of Giess (1969), Bornman (1978), Van Jaarsveld (1992), Schultze-Motel (1992) and most clearly of Wetschnig (1997) show that plants with glaucous, sculptured cones can be geographically located in the southern part of the species' range in Namibia. There is no particular evidence of variation, except for the photographs of Knotters (1996), Schnabel (2000a) and Pratorius (undated), which suggest that within Namibia plants with long but pale cones and plants with dark salmon to reddish brownish cones occur. One might assume that the occurrence of plants with markedly differing cone features within one population would have been detected by some of the numerous observers.

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The published photographs or other illustrations give no conclusive indication on the geographical origin of plants with brownish male cones such as those of group 1 at Berlin-Dahlem. Unfortunately, no illustrations of *Welwitschia* plants from the native habitat in Angola showing sufficient details could be located so far. This is mainly due to fact that the area has been largely inaccessible to botanists over the past two decades.

The interpretation of our observations on cultivated plants and the comparison with the illustrations thus indicate a possible geographical pattern or gradient in the cone features discussed here. To produce evidence, exact data on the origin of each specimen illustrated and cultivated are needed.

Comparison with herbarium material of known origin

The eight old stock plants with male cones cultivated at Berlin-Dahlem were compared with material with male cones from throughout the range of *Welwitschia mirabilis.* The specimens studied are cited below.

The only specimen with male cones in the Berlin-Dahlem herbarium originating from Angola *(Brühl 44)* is very similar to plants of group 1 (Fig. 2a-b). Also material from Angola of *Monteiro* at Kew and of *Duparquet* at Paris, available for study only at a late stage of this survey, fits perfectly with group 1. Peduncles are 2-12 cm long, secondary branches usually lacking, but if present, very short (to 2 cm). Cone size and bract features coincide with group 1. Variation of cone length in the three specimens is shown in a diagram (Fig. 7).

On the contrary, male cones of plants from Namibia, particularly those of collections of *Dinter, Engler* and *Werdermann & Oberdieck* cited below from the area east of Swakopmund, agree perfectly with cones of group 2 (Fig. 2c-d). The same applies to collections from further north *(Rodin 8900, Giess 3867, 3867, Merxmüller 1447)*. Cone length of representative samples is shown in a diagram (Fig. 8). The herbarium material is not sufficient to comment conclusively on the peduncle and branch length. Peduncle length varies in herbarium material of the southern group. Comparison with published illustrations does not indicate that the southern group has consistently longer peduncles. However, secondary branches are frequent and conspicuous, 2-6 cm long. *Dinter 6792* from the Swakop area in Namibia, the most accessible and frequently visited site, is noteworthy because it agrees perfectly with cultivated plants of group 2. Male cone characters of group 2 agree very well with material from Namibia.

Measurements of cone length of two cultivated specimens of unknown origin together with field collected specimens of known origin (Fig. 9) show a good correlation of cone size of our largest plant (no. 12) with the Angolan specimen of *Duparquet,* and a good correlation of the cone size of plant no. 3 with a Namibian sample from the Swakop area *(Dinter 6792)*.

It is noteworthy that the northernmost specimen available, *Merxmüller 1447* from the Kaokoveld in Namibia, has very clearly sculptured cones with wax at the base but bracts with a rather high fusion zone (Fig. 10a). This does not yet support the hypothesis of a gradient of cone features from north to south, but calls for further examination of variation based on a broader selection of samples covering the whole geographical range. Comparison with other, e.g., climatic and other ecological data may be appropriate as well.

The northernmost specimens available from Namibia, i.e., from the Outjo West and Kaokoveld districts, agree basically with those of (the southern) group 2, though with one exception: a specimen from the Petrified Forest *(Giess 3228)* has very long male cones (33-45 mm) agreeing in length with those of group 1 (Fig. 10b). The bracts with a relatively high fusion zone almost approach those of group 1, but in the general aspect of the bracts with the erose margin and the wax cover, the sample still fits better with group 2. This suggests that the photographs published by Knotters (1996) and Schnabel (2000a) from the same area in the Outjo West district may also show plants not clearly falling into either group 1 or 2. The populations in this region need further study.

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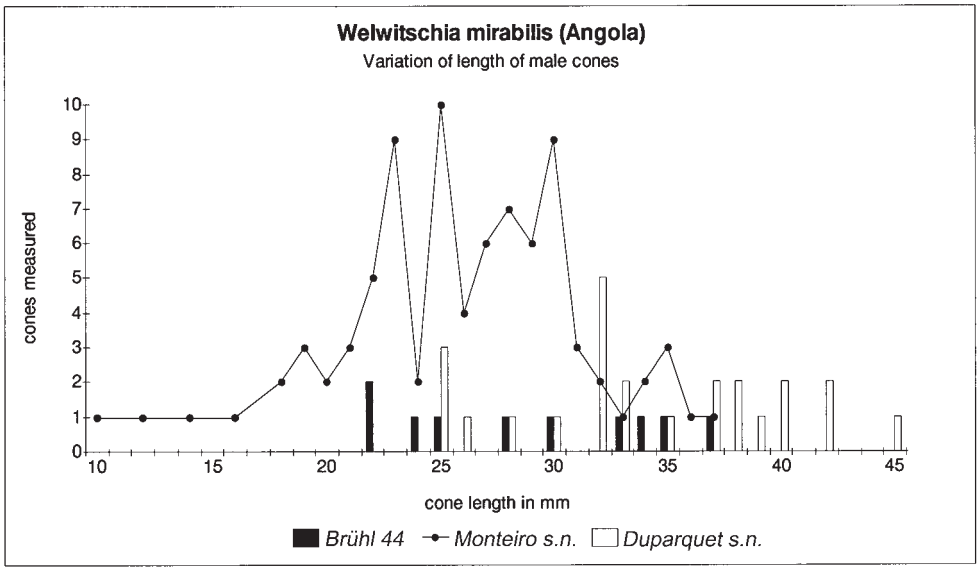


Fig. 7. *Welwitschia mirabilis,* diagram of variation of cone length in samples from Angola *(W. mirabilis* subsp. *mirabilis).*

Finally, a historical sample probably originating from Angola merits mention here. It was located in a small jar in the spirit collection at Berlin-Dahlem, labelled *"ded. Hook. fil."* without further information (Fig. 11a). It contains rather young male cones measuring c. 17-30 mm agreeing well in morphological details with group 1 (Fig. 11b). This material may thus be from the Angolan specimen of Welwitsch mentioned in the protologue (J. D. Hooker 1862) or of

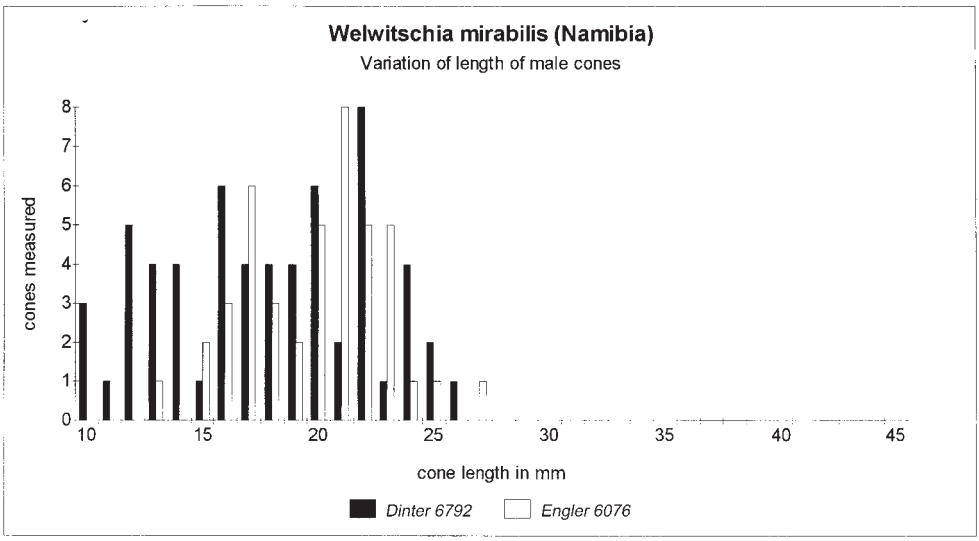


Fig. 8. *Welwitschia mirabilis,* diagram of variation of cone length in samples from Namibia *(W. mirabilis* subsp. *namibiana).*

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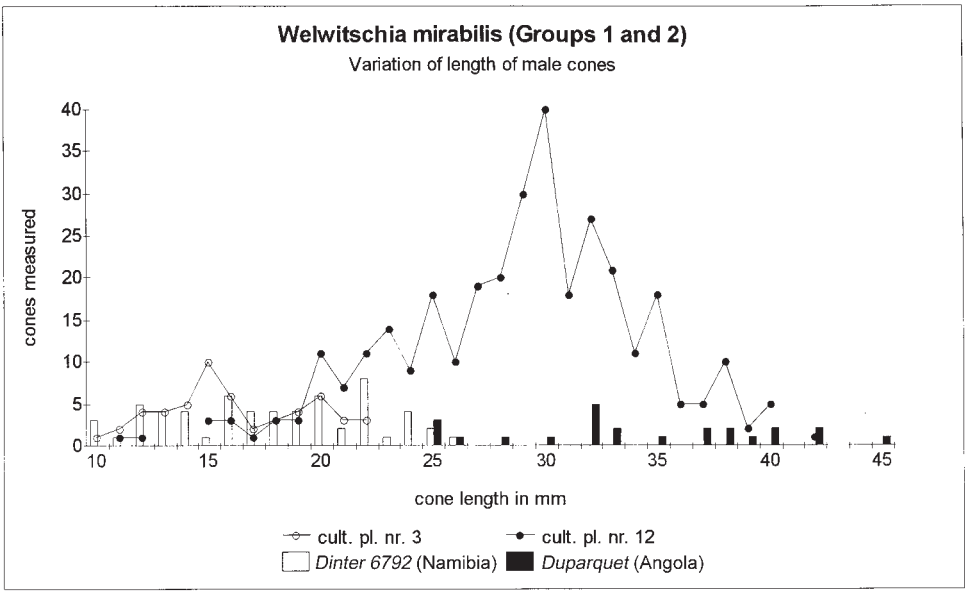


Fig. 9. *Welwitschia mirabilis,* diagram of variation of cone length in representative cultivated plants of groups 1 and 2 (lines) compared to that in two field-collected specimens of known geographical origin (columns).

Monteiro cited in J. D. Hooker (1863). Hooker (1863: 4) mentioned a bottle of cones preserved in spirit received from Monteiro. This could be an indication on the origin of the sample at Berlin. The comparison of this material with a Monteiro herbarium specimen at Kew (K), and the information that the Welwitsch material is not well preserved (A. Farjon, pers. comm.) support this interpretation.

Conclusions

From morphological features first observed on the old Berlin-Dahlem stock of *Welwitschia mirabilis* and corroborated by comparison with material of known origin from Angola and Namibia, it can be concluded that plants with brownish, smooth cones occur in the northernmost part of the range, in Angola, whereas plants with pale and glaucous, more sculptured cones grow in the southern part of the range, in Namibia. It appears that the differences in male cones between plants from Angola and Namibia were not recognized hitherto because the first illustration published by J. D. Hooker (1863: t. 6(1-2)), very often reproduced in later publications on *Welwitschia,* shows rather young stages of development of the male cones. In young cones prior to flowering, the features discussed above are less conspicuous, also because the cone length is more similar. In medium to advanced flowering stages, the details of the bract shape of the Angolan plants are sometimes obscured by the slightly protruding flower buds. The buds are narrower and more conspicuous than the bract margin itself and thus make the cones look superficially more similar to the bract pattern of the Namibian plants.

The morphological differences observed and the geographical distribution pattern suggest the recognition of two distinguishable subspecific entities. Further investigation based on additional herbarium material particularly from Angola, field studies on variation of cone characters, and molecular backing up of the morphological evidence seem worthwhile.

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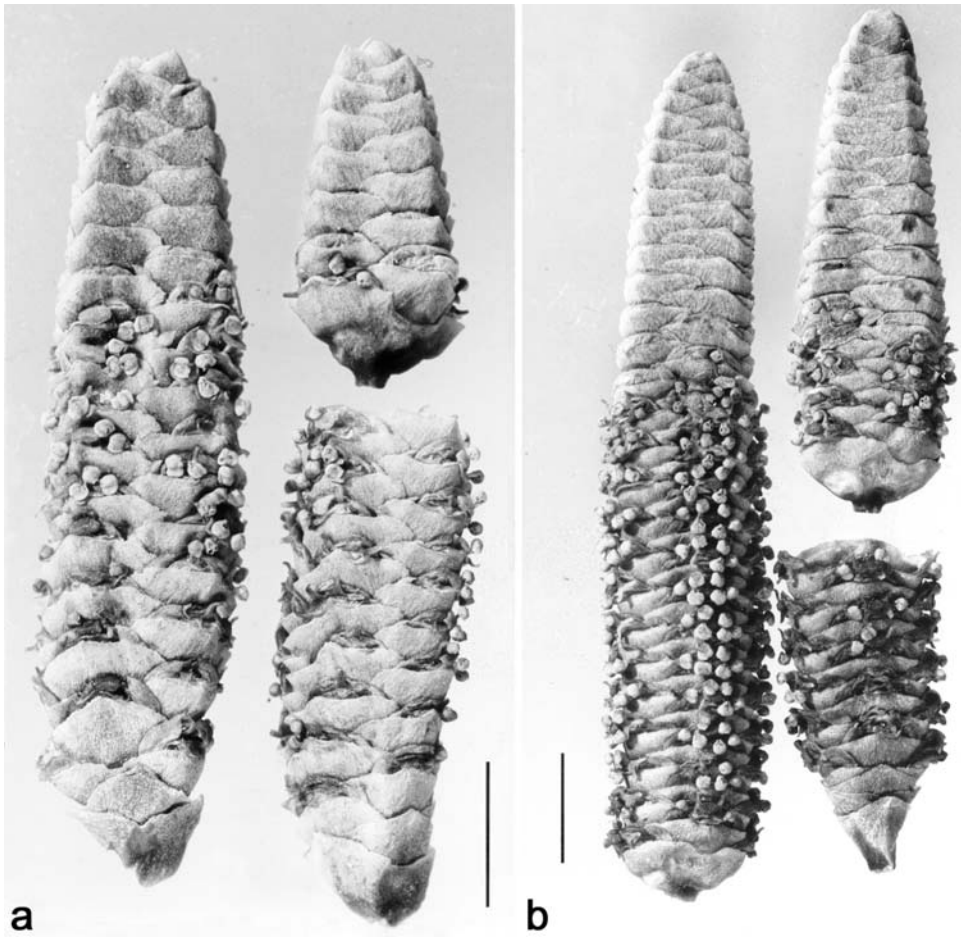


Fig. 10. *Welwitschia mirabilis,* male cones of specimens from Namibia with bract shapes corresponding to those of group 2, but with rather high fusion zone of bracts – a: cones of *Merxmüller 1447* from the Kaokoveld; b: long male cones of *Giess 3228* from the Petrified Forest. – Scale 5 mm; photographs by M. Lüchow & G. Kuhlmann.

The case may be taken as an example of the potential importance of careful specimen-based documentation and observation of plants in living collections. It also demonstrates the remarkable potential and importance of appropriately documented living collections in botanical gardens for biodiversity studies in general.

Taxonomy and nomenclature

Welwitschia mirabilis Hook. f. as the binomial with priority over the formerly common name *W. bainesii* has been used by Markgraf (1926), Widder (1960), Friedrich-Holzhammer & Roessler (1966), Benson (1970b) and Anonymous (1975). Verdoorn (1966), in contrast, recognized *W. bainesii* with *W. mirabilis* as synonym and cited type specimens for both names. The binomial *W. mirabilis,* and implicitely the name of the genus, were validly published by J. D. Hooker (1862) and listed as such in ING by Farr & al. (1979), in NCU by Greuter & al. (1993) and in the most re-

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Fig. 11. *Welwitschia mirabilis* subsp. *mirabilis,* collection labelled "*ded. Hook. fil.*" in the spirit collection at Berlin-Dahlem (probably collected by Monteiro) – a: jar with label containing sample of male cones; b: part of contents. The cone with verticils of three bracts is marked by arrows; photographs by M. Lüchow & G. Kuhlmann.

cent family treatment by Steyn & Smith (1999). Index Kewensis (Jackson 1894-95) attributed *Welwitschia* to J. D. Hooker (1862), *W. mirabilis* erroneously to J. D. Hooker (1863), and *W. bainesii* to Carrière (1867).

The name published by J. D. Hooker (1862) is based exclusively on plants observed by Welwitsch in Angola, between "Mossamedes and Cabo Negro". Steyn & Smith (1999) cite a *Welwitsch* specimen from Cabo Negro, Angola, at Kew as syntype, which implies the presence of more than one Welwitsch collection connected with the protologue. The far more detailed, formal treatment of the new genus *Welwitschia* by J. D. Hooker (1863) is based on material of four different collectors (Welwitsch, Monteiro, Andersson and Baines) from distant collection localities.

For the southern entity treated below as subspecies, the controversial name *W. bainesii* is available at species level. The earliest names, *Tumboa bainesii* J. D. Hooker (1861) and (with this orthography) *Toumboa bainesii* Naudin (1862), were only provisional names. Both authors stated clearly that this would be the name if the plant proved to be distinct from that discovered by Welwitsch. Few year later, Carrière (1867) formally published *W. bainesii* as second name within the genus. In the observations on *W. mirabilis,* Carrière (1867: 783) rather ambiguously mentioned that there were, if not two species, at least "plusieurs formes" (several forms) of *Welwitschia*. He added that these observations seemed to him of quite strong value to make a second species, which he actually published on the same page under the subtitle "doubtful species" as

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second name in the same typography: "2. *Welwitschia bainesii*". He based it on Naudin (1862), cited from the same source a description (including four leaves as distinctive character) and the indication of origin "Dammara, vers le 23e degré (lat. austr.)". On the following page, Carrière (1862: 784) further added a restrictive observation, which is contradictory and could raise doubts on the acceptance of the name *W. bainesii*. The observation reads (translated): "If the case is confirmed, and if there really are two forms of *Welwitschia,* the one discovered by M. T. Baines will be *W. mirabilis* Hook.; the other, which has only two leaves, will be *W. bainesii* Carr.". The switched attribution of the names and leaf characters are evidently a slip of the pen, which may have contributed to the later confusion on the correct name of the only species accepted by later authors.

As a consequence, contradictory opinions on the status of the name *W. bainesii* exist. It was accepted as validly published synonym by Benson (1970b), whereas Steyn & Smith (1999) considered it to be only a provisional name. The provisions of the ICBN, Art. 34.1 (Greuter & al. 2000) would seem to support the validity of the name but also leave room for arguments against, depending on the emphasis one should give Art. 34.1a or 34.1b. If definitely valid, the epithet could be used for the taxon treated here at subspecific level because the material of group 2 clearly falls within the geographical range of this taxon. However, to circumnavigate possible nomenclatural traps and torrents, it seems more advisable to propose a new name based on a different type with extant male cones.

Key to subspecies of *Welwitschia mirabilis*

1. Male cones smooth, purplish brown (rarely green when shaded), without evident wax cover; longer peduncles usually c. 5-11 cm long, secondary branches to 2 cm long; longest male cones 30-45 mm long; bract pairs overlapping c. 2 mm; bract scales more than ¾ connate, margin of bracts smooth; Angola . . . . . *W. mirabilis* subsp. *mirabilis*
– Male cones sculptured, glaucous green to salmon, with evident wax cover; longer peduncles c. 7-15 cm long, secondary branches to 7 cm long; longest male cones 20-30 mm long; bract pairs overlapping c. 1 mm; bract scales 1/3 to 2/3 connate, margin of bracts slightly erose; Namibia . . . . . *W. mirabilis* subsp. *namibiana*

Welwitschia mirabilis Hook. f. subsp. ***mirabilis***
≡ *Welwitschia mirabilis* Hook. f. in Gard. Chron. 1862: 71. 1862. – Lectotype (designated here): Angola, Cabo Negro, 4.9.1859 (♀), *Welwitsch* (K; isolectotypes LISU [photo], PRE [photo]).

Note. – The isolectotype material at LISU has an original Welwitsch label without number and with the collection data: "... inter = Rio Caroca et Praia da Amelia 3 et 4 Septbr. leg. *Welwi*". A second, partially printed label, filled in by Welwitsch's handwriting on the same sheet says: "Welw. Iter Angolense. (Reg. littoralis interior) (Distr. Mossamedes) No. 1223. *Welwitschia mirabilis* Hook. f. Habit. freq. et gregaria in alta planitie petroso-sabulosa ad ?ireit?. 350 ped. elevat. inter Cabo negro et Mossamedes. c. fl. et fr. Sept. 1859 leg. *Dr. Welwitsch*".

Ic. – Fig. 1a, c, e, 2a, b, 3a, 4a, c, e, 5, 7, 11, 12a, b; other representative illustration: Horwood 1974: 260, fig. 29.

Specimens studied
ANGOLA: "20 min. Autofahrt auf der Strasse von Mossamedes nach Porto Alexandre", 20 m, 31.10.1922 (♀ & ♂), *Brühl 44* (B and B alc, ♂ cones only in alcohol); Mossamedes, 1871 (♂), *Duparquet* (P); "Iter Angolense", 5.7.1878 (♀), *Welwitsch 1223* (P); "Loanda, recvd. June 1863" (♀ & ♂), *Monteiro* (K, photo B); Mossamedes, 1.3.1923 (♂), *Pimentel Teixeira* (LISU alc); sine *loc., 1.1930 (*♀), *Simeon* (H) .
WITHOUT LOCALITY: sine coll., s. d., (♂ cones only), "ded. Hooker fil." (B alc).
SPECIMENS OF CULTIVATED PLANTS: Hort. Berol., without origin, (pl. no. 1, ♀), 11.1993 (fl),

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Cubr 32130 (B); 19.7.1995 (fl), *Cubr 34117* (B); [pl. no. 2(?) ♂], 3.7.1955, sine coll. (B alc); (pl. no. 2, ♂), 15.10.1987 (fl), *Schwerdtfeger 15035* (B); (pl. no. 8, ♂), 19.9.2000 (fl), *Cubr* 38209 (B); (pl. no. 9, ♂), 19.9.2000 (fl), *Cubr 38210* (B); (pl. no. 11, ♂), 19.9.2000 (fl), *Cubr 38211* (B); (pl. no. 12, ♂), 19.9.2000 (fl), *Cubr 26183a* (B); Hort. Berol., [pl. no. 2 or 12? ♂], 14.6.1959, *Domke* (HBG).

Welwitschia mirabilis subsp. ***namibiana*** Leuenberger, **subsp. nova**
Holotype: Namibia, "Damarabezirk, Namib oberhalb Kan-Tal bis Pforte", 700 m, 4.4.1913 (♂), *Engler 6076* (B).
= *Welwitschia bainesii* Carr., Traité Gén. Conif., ed. 2.: 783. 1867 (controversial name, validly published according to Benson 1970b, but a nom. prov. only according to Steyn & Smith 1999).

A *Welwitschia mirabilis* subsp. *mirabilis* differt strobilis masculis brevioribus, 10-33 mm longis, basaliter vel omnino cereis, viridibus vel glauco-viridibus ad salmoneis, bracteis minus alte (1/3 ad 2/3) in cupulam patelliformis non cyathiformis connatis, lateraliter ad 1 mm (non 2 mm) superpositis, margine leviter erosis, parte connata membranacea breviore (1mm) et latiore (2-3 mm).

Ic. – Fig. 1b, d, f, 2c, d, 3b, 4b, d, f, 6, 8, 10, 12c; other representative illustrations: Song 1980: 30, fig. 1, 70, fig. 15, 71, fig. 17-19; Van Jaarsveld 1990: 74, 1992: 119; Van Jaarsveld & Linder Smith 2001: 2, t. 2161; Wetschnig 1997: 161, fig. 4, 164, fig. 6, 167, fig. 10.

Etymology. – The name refers to the Namibian range of the taxon.

Additional specimens examined
NAMIBIA: WITHOUT EXACT LOCALITY: "SW-Afrika", 1937 (♂), *Kühn* (HBG); "W-Afrika", 1881 (♂), *Kuntze* (B); "S-Africa, Namib", 1903 (♀ & ♂), *Schultze* (B alc); "SW-Africa", 1952 (♀ & ♂), *Schweickerdt* (B); "Südwestafrika", 1922 (♀), *Lotz* (B). — KAOKOVELD: Kaokoveld, Haob, 23.9.1929 (♂), *Range 13* (HBG); between Otjikongo and Sanitatas, 28.1.1958 (♀ & ♂), *Merxmüller 1447* (M); Sechomib River valley, 1966 (♀ & ♂), *Soini* (H 1056381). — OUTJO WEST: 9 mi. W of Farm Wereldend, 12.11.1961 (♀ & ♂), *Giess 3867* (M); 14 mi W of Welwitschia, Farm Versteende Woud, 3.1.1961 (♀ & ♂), *Giess 3228* (M); Petrified Forest, c. 20 mi W of Welwitschia, 12.11.1961 (♀ & ♂), *Giess 3857* (M). — SWAKOPMUND: On road from Brandberg to Cape Cross, c. 5 mi from the atlantic Ocean, 2.2.1973 (♂), *Rodin 8900* (M); Walfischbai, (st), *Nachtigal* (B); Welwitschia-Flat, 1974 (♀), *Bislich* (B); Svakopmund, 1935 (♀ & ♂), *Ojonen* (H 1503985); 72 km östl. Swakopmund, 22.12.1933 (♀ & ♂), *Dinter 6792* (B, HBG); Welwitschiafläche, 10.3.1935 (♀ & ♂), *Dinter 6792* [sic!] (B); 72 km E of Swakopmund, 3.1935 (♀ & ♂), *Dinter* (B, with photos and notes on exceptional growth rate); near Swakopmund, 8.3.1959 (♀ & ♂), *Werdermann & Oberdieck 2428 & 2429* (B); 14 mi. ESE Swakopmund, 7.3.1959 (♀), *Oberdieck* (B); zwischen Otimbingue u. Swakopmund, 13.1.1921 (♂), *Fischer* (HBG); Walvisbai bei Swakopmund (♂), *Jensen* (HBG); "seit 1956 gesammelte Pfl." (♀ & ♂), *Jensen* (HBG).
SPECIMENS OF CULTIVATED PLANTS: Hort. Berol., without origin, (pl. no. 3, ♂), 4.10.1993 (fl), *Cubr 31875* (B); (pl. no. 5, ♀), 1.3.2000 (fl), *Cubr 38190* (B); (pl. no. 6, ♂), 9.10.2000 (fl), *Cubr 38246* (B); (pl. no. 7, ♂), 19.7.1993 (fl), (only foto 182/22) (B).

Additional note on aberrant bract arrangement

J. D. Hooker (1863) described the bract scales as quadrifariously arranged on the cones. During the comparison of numerous male cones in the course of this study, aberrant male cones with bracts arranged in verticils of three were found in three samples (Fig. 11, 12). This has not been mentioned for cones of *Welwitschia,* which normally have two bracts following the opposite, decussate plan (Biswas & Johri 1997, Kubitzki 1990). Verticils of three leaves are common in the foliage, scale leaves and bracts of other gymnosperms like *Ephedraceae* and *Cupressaceae* and occur in male cones of some *Cupressaceae* like *Callitris* and *Fitzroya*. As to the vegetative

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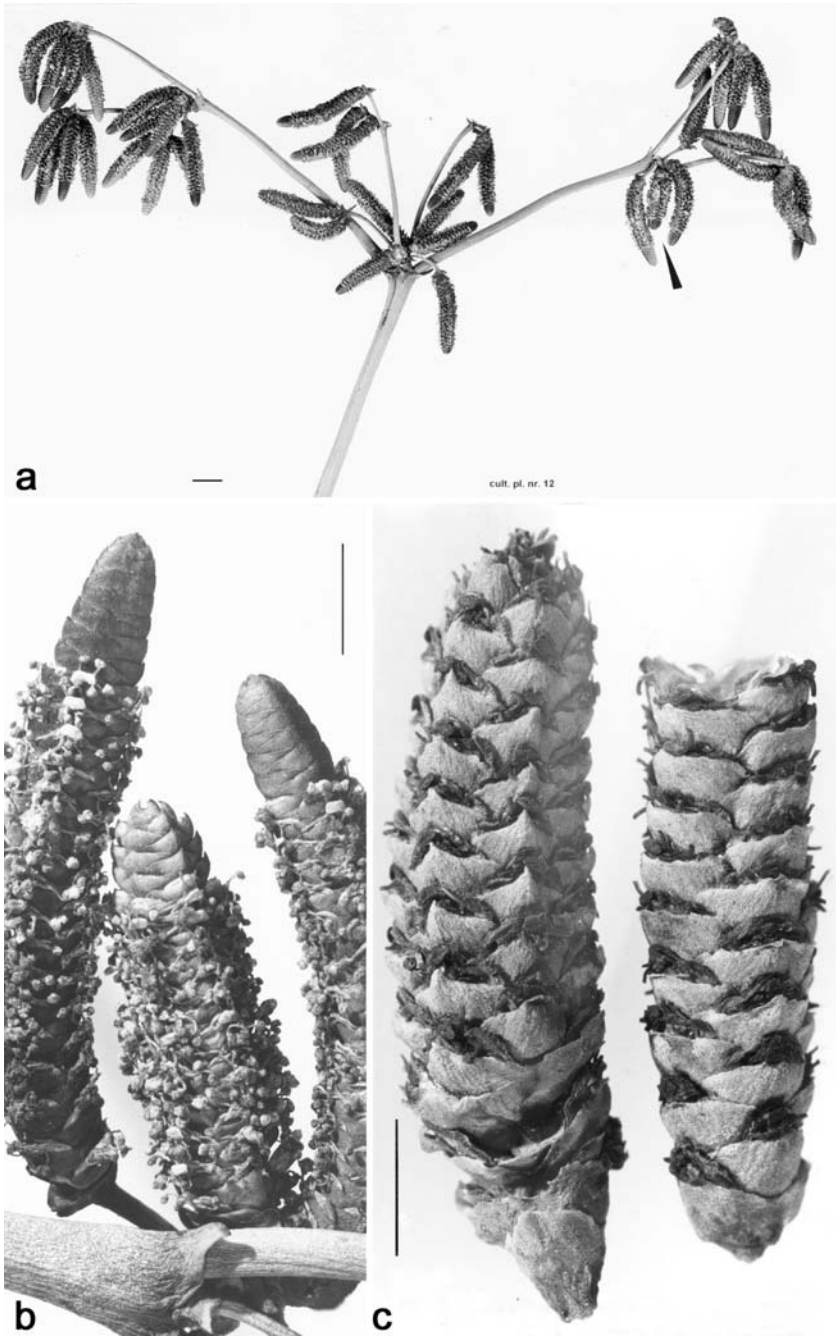


Fig. 12. *Welwitschia mirabilis,* aberrant bract arrangement with verticils of three bracts in male cones – a: *W. mirabilis* subsp. *mirabilis,* inflorescence of plant no. 12, cult. hort. Berol., *Cubr 26183a,* aberrant cone marked by arrow; b: close-up of the same; c: *W. mirabilis* subsp. *namibiana,* cones of *Schweickerdt* (B), the left one with bracts arranged in verticils of three, the right one quadrifarious (tip broken off). – Scale 1 cm (a); 5 mm (b, c); photographs by M. Lüchow & G. Kuhlmann.

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organs of *Welwitschia,* aberrant seedlings with three cotyledons and three foliage leaves have been reported by Van Jaarsveld (1990).

A single cone with verticils of three bracts was first observed in summer 2000 among the c. 2700 cones of plant no. 12 *(Welwitschia mirabilis* subsp. *mirabilis)* at Berlin-Dahlem (Fig. 12a-b). At first sight, it seemed to differ particularly by the more apiculate bracts and the sculptured aspect, recalling the cones of plants of Namibian origin. However, a closer examination revealed that the difference was caused mainly by the presence of six orthostichies instead of four. In the aberrant cone, only the lowermost bracts are slightly irregular, and the lowest flowering verticil has male flowers of unequal size. The rest of the cone is regularly hexagonal in transsection, not bluntly tetragonous as in the two accompanying cones (Fig. 12b).

Remarkably, the second case of a male cone with verticils of three bracts was observed in the material of *W. mirabilis* subsp. *mirabilis* in the spirit collection received from J. D. Hooker and preserved in alcohol. The small glass jar contains more than 70 male cones, nearly all young and with flower buds only. One differs both in shape and also in its advanced flowering stage. It is a cone with six fully developed rows of scales and flowers (Fig. 11b, marked by arrow).

The third case of a male cone with six orthostichies was found among the seven male cones of a specimen of *Schweickerdt* of *W. mirabilis* subsp. *namibiana* in the Fruit and Seed Collection at B (Fig. 12c).

Postscript. – The explosive increase of *Welwitschia* images on the World Wide Web made it impossible to include an updated analysis of images found after submission of the paper. Shortly before this paper went to press, a search with http://www.google.com (retrieved on 31 October 2001) produced over 4270 entries under the name *Welwitschia* and 386 references to images. Only few show sufficient details of male cones. Examples are: an untitled image compatible with subsp. *mirabilis* at the botanical garden Karlsruhe (http://wwwdt.rz.uni-karlsruhe.de/~db26/_Fotos/Sukkulente/Welwitschia_mirabilis-3-301000.jpg), and one representative of subsp. *namibiana* in "botany images" (http://www.wisc.edu/botit/img/) at the University of Wisconsin (http://www.wisc.edu/botit/ img/bot/401/Gnetophyta/Welwitschiaceae/Welwitschia%20mirabilis/Male%20cone%20KS%20.jpg). No origin of the specimens is given.

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