

THE TAXONOMY, ECOLOGY AND POSSIBLE METHOD OF EVOLUTION OF A NEW METALLI- FEROUS SPECIES OF DICOMA CASS. (COMPOSITAE)

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ABSTRACT

A new species of Compositae belonging to the Mutisieae *Dicoma niccolifera* WILD is described. Its distribution is compared with that of the most nearly related species of *Dicoma*, i. e. *D. schinzii* O. HOFFM. and *D. macrocephala* DC. *D. niccolifera* is almost entirely confined to nickel bearing soils and most often the mother rock of these nickeliferous soils is serpentine. It occurs in Rhodesia and in one small area near Lusaka in Zambia whilst *D. schinzii* is found in sandy soils, in more arid areas on the whole, in the Transvaal, Orange Free State, Northern Cape Province, Botswana, South West Africa, Southern Angola, Zambia and Rhodesia. *D. macrocephala* also occurs on sandy soils in more arid areas in the Transvaal, Natal, Orange Free State, Northern Cape Province, Botswana, South West Africa and Rhodesia. As *D. niccolifera* has been recorded in two widely separated areas in non-nickeliferous and serpentiniferous soils and shows no visible morphological differences in these two types of locality, it is suggested that this is an "old" relic species produced by biotype depletion and not a species produced by edaphic modification from say *D. schinzii* or *D. macrocephala*, or a common ancestor, through the influence of metalliferous soils. However, it is suggested that there may be other endemic species confined entirely to serpentine soils in Rhodesia, such as *Aloe ortholopha* CHRISTIAN and MILNE-REDHEAD, *Lotononis serpentinicola* WILD, *Pearsonia metallifera* WILD and *Vernonia accommodata* WILD, which could have evolved on these toxic soils from populations isolated by restriction of gene flow through processes analogous to those described by BRADSHAW (1959) and others who have investigated population differentiation in such European species as *Agrostis tenuis* under different edaphic conditions, even when these populations are separated by very short distances. Cytogenetic and cultural investigations are desirable to investigate the possibility that there may be two different types of evolution which have produced the endemic heavy metal or serpentine species in Rhodesia, where suitable research material of this kind is so abundant.

INTRODUCTION

In preparing the treatment of the Composite tribe Mutisieae for the Flora Zambesiaca, it became necessary to describe a new species of *Dicoma* CASS. occurring in Rhodesia and Zambia which in Rhodesia has been found to be confined (with only three records excepted) on nickel bearing soils, in so far as information is available at present. As considerable attention has been

paid to evolutionary divergence in adjacent plant populations in Europe and N. America of recent years (JAIN & BRADSHAW, 1966 and EHRLICH & RAVEN, 1969) and its importance in the evolution of plant as well as animal taxa, it was thought worthwhile to consider the taxonomic relationships of this species and its ecology, particularly in relation to metalliferous soils.

The species is therefore first described, its distribution in relation to the distributions of its nearest relatives discussed and then the problem of how it might have evolved considered.

THE NEW SPECIES, ITS DISTRIBUTION AND THAT OF ITS NEAREST RELATIVES

Dicoma niccolifera WILD, sp. nov.

Type: Rhodesia, Bindura, Kingston Hill, WILD 7770 (K; SRGH, holotype)

Dicoma schinzii sensu F. C. WILSON in Kew Bull. 1923: 384 (1923) pro parte quoad specim. WALTERS 2345; 2347. — WILD in Kirkia, 5, 1:81 (1965).

Dicoma macrocephala, subsp., sensu WILD in Kirkia, 7, Suppl.: 7, 10, 14, 16, 26, 28, 41, 57, fig. 1, 58, photo. 6, 8, t. 1 (1970).

Affinis *D. macrocephalae* DC. sed lobis corollae recurvatis, pappi setis interioribus ad bases nec latis nec undulatis; affinis *D. schinzii* O. HOFFM. sed foliis sessilibus vel pseudopetiolatis, lobis corollae recurvatis, pappi setis interioribus ad bases nec latis nec undulatis.

Herba perennis, prostrata vel subprostrata; caules ad 25 cm longi, cylindrici, albido-lanati. Folia alterna, sessilia vel pseudopetiolata, ad 4 (6) x 1,3 (1,7) cm, elliptica, apice acuta mucronata, basi cuneata vel angustissime auriculata vel in pseudopetiolum longe et anguste attenuata, margine integra, supra griseo-viridia lanata demum glabrescentia, subtus dense albido-lanata, costis supra immersis subtus prominentibus, nervis lateralibus utrinsecus 1—2 supra immersis vel inconspicuis subtus \pm prominentibus. Capitula ad apices ramorum inter folia sessilia. Involucrum c. 2 cm longum, c. 1,7 cm latum, campanulatum; foliola c. 4-seriata, ad 2 cm longa, coriacea, rigida, versus interiora sensim majora; foliola extima c. 4 mm longa, angusta, lanceolata, apice rigide setosa demum valde reflexa; foliola interiora 2 cm. longa attingentia, c. 1,7 mm lata, linearia, scariosa, extus pubescentia purpurea vel purpurea suffusa, apice cuspidata. Flores radii asexuales, corollae desunt; ovarium rudimentale c. 0.5 mm. longum, turbinatum, compressum, glabrum sed ad bases pilis longis ornatum, ad apicem pappi setis albidis ciliatis c. 1,8 cm longis coronatum. Flores disci numerosi, pallide purpurei, c. 11 mm longi, parte inferiore c. 4 mm longa cylindrica glabra, parte superiore c. 7 mm longa anguste campanulata 5-lobata, lobis maturis c. 4 mm longis versus apices valde recurvatis, extus minute sparse puberulis, apice minute pilosis; stylus 1 cm longus, ad apicem minute bifidus; ovarium c.

2,2 mm longum, c. 1,1 mm latum, turbinatum, 4-sulcatum, pilis longis albidis ornatum, ad apicem pappi seti albidis 1 cm longis coronatum; setae 2-seriatae, extimae angustissime setosae ciliatae, interiores crassiores parte inferiore angustissime alatae ciliatae. *Achenea* brunnea, 2,2 cm longa, dense longe albido-hirsuta; pappus in siccitate quasi rotatae.

ZAMBIA: Central Province. Lusaka, 8 km. E. Munali. sandy laterite soil, short grass, 5.VIII.1955, KING 86 (K), flowers purple; Woodlands Extension, gravel pit, bare ground, 1400 m., 7.VIII.1960 BEST 221 (SRGH), florets purple; *ibid.*, savanna woodland, trampled soil, 1400 m., 7.VIII.1960, BEST 222 (SRGH).

RHODESIA. Northern Division. Darwin Distr., Great Dyke, Mpingi pass, serpentine 16.III.1960, DRUMMOND 6853 (SRGH); Lomagundi Distr., Great Dyke, Caledonia Ranch, 12.IV.1969, DRUMMOND 6050 (SRGH). Darwendale, on serpentine, 20.IV.1948, RODIN 4345 (K; PRE); Mtoroshanga, chrome hills, VI.1959, LEACH 8928 (SRGH), prostrate, silvery leaves; Bindura, Kingston Hill, near Trojan Nickel Mine, on nickel anomaly, 7.V.1969, WILD 7770 (K; SRGH), prostrate, pale mauve flowers; Urungwe Distr., Sengwe Gorge, *Brachystegia* woodland, sandy soil, 12.V.1969, N. JACOBSEN 655 (SRGH), flowers pale mauve; Gokwe Distr., Chimakaze Hill, nickeliferous greenstones, 1.VII.1969, WILD 7783 (K; SRGH). Western Division. Bubi District, Ndumba Hill, bare stony ground, 1500 m. 15.VI.1947 KEAY in FH, I/21320 (K; SRGH), straggling, flowers pale mauve. Central Division. Selukwe, IX.1917, WALTERS in GHS 2345 (SRGH); *ibid.* IX.1917, WALTERS in GHS 2347 (SRGH). Eastern Division. Umtali; Forbes Border Post, open grassy area on hill, 4.V.1947, CHASE 364 (COI; SRGH).

For a good many years herbarium workers have assumed that this species was merely a form of the widespread species *Dicoma schinzii* O. HOFFM. It was even considered as such by F. C. WILSON (1923) in his revision of the genus in Kew Bulletin, as is shown by his inclusion here of the two specimens WALTERS 2345 and 2347. Our plant differs from this species, however, in a number of characters; the leaves are not petiolate but sessile, or the lamina tapers gradually into a pseudopetiole; the corolla lobes are minutely pubescent outside not glabrous and there is a tuft of small hairs on the outside of the lobes at the apex; the corolla lobes are strongly recurved except when the corolla is immature and finally the broader pappus setae do not have undulate wings near their bases. Separation of the two species is also easy because the sessile or tapering pseudopetiolate leaves of *D. niccolifera* as compared with the distinctly petiolate leaves of *D. schinzii* change the general appearance or facies of the two plants. In fact from the general appearance point of view our plant is more easily confused with *D. macrocephala* DC. Here, the leaves are very similar in both cases. Nevertheless, since the florets of *D. macrocephala* do not develop recurved lobes and the broader pappus setae are also strongly alate and undulate towards the base, as in *D. schinzii*, *D. niccolifera* must be considered specifically distinct from this latter species also. It was at first thought that *D. niccolifera* was only separable from *D. macrocephala* at the subspecific level only but no true intermediates were

found and the difference between them was not confined to one character. These differences may be set out in a diagnostic key as follows:

Leaves distinctly petiolate *D. schinzii*
 Leaves sessile or pseudopetiolate with the lamina tapering gradually at the base:
 Broader pappus setae dilated or winged, and undulate in the lower part;
 corolla lobes not recurved at maturity *D. macrocephala*
 Broader pappus setae lacking undulate wings in the lower part;
 corolla lobes strongly recurved at least when mature . . . *D. niccolifera*

Apart from the morphological differences, the differences and similarities in ecological behaviour and distribution (Fig. 1) of these closely related species are interesting. *D. macrocephala* is recorded from the Transvaal, Natal, Orange Free State, Northern Cape (the old British Bechuanaland), Botswana, South West Africa and Rhodesia. In so far as the collectors'



Fig. 1. The distribution of *Dicoma niccolifera* in relation to serpentine areas in Rhodesia.

records go it is only recorded from sandy soils or sandy loams (one record from calcareous gravels) and seems to prefer open grassy places in low or very low rainfall areas. *Dicoma schinzii* is recorded from the Transvaal, Orange Free State, Northern Cape, Botswana, South West Africa (many records), Rhodesia (Western and Central Divisions), southern Angola, and Zambia (Barotseland and the neighbouring parts of the Southern Province). All available records show it as occurring on sandy soils (both red and white sands), sand dunes, sandy flats, sandy river banks, calcareous sand and often in open grassy areas. Once again it is a plant of from very dry to dry areas, except that it does extend into Rhodesia and Barotseland and so into some areas of higher rainfall up to about 1000 mm per annum. These plants of somewhat higher rainfall areas, e. g. EYLES 771 from Beatrice in Rhodesia and CODD 7499 from Barotseland are different from the remainder in being more robust and with a fulvous instead of a grey indumentum. The possibility of their being subspecifically distinct was considered but plenty of intermediate specimens exist and no evidence was found of any reliable differences.

When we come to *D. niccolifera* the distribution (Fig. 2) and ecology are noticeably different. The species is common on the serpentine soils of the Great Dyke of Rhodesia from its northern end at the edge of the Zambezi escarpment as far south as Selukwe in the region of the northern escarpment of the Limpopo River. In addition, it also occurs near Umtali (CHASE 364),

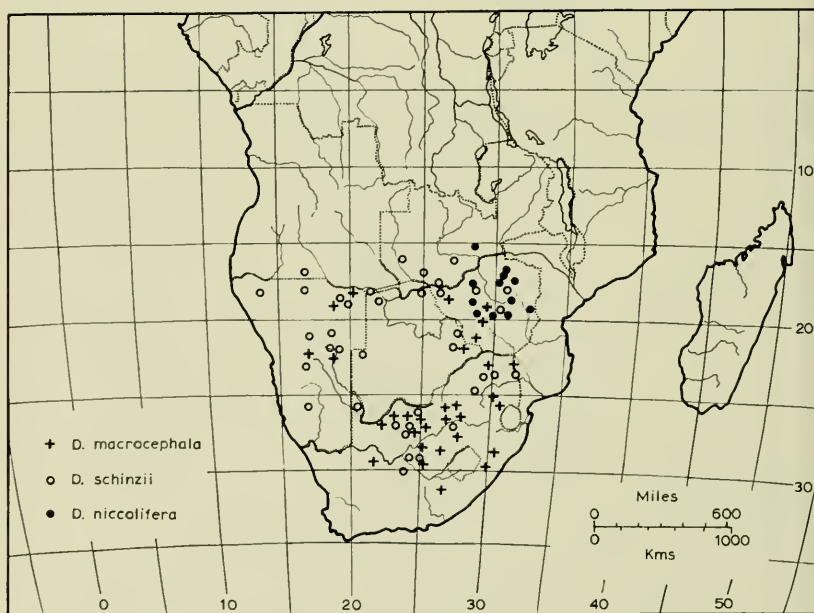


Fig. 1. The distribution of *Dicoma macrocephala*, *D. schinzii* and *D. niccolifera*.

Bindura (WILD 7770) and Ndumba Hill near Lonely Mine (KEAY in FHI 21 320) but very strikingly all these latter records, together with others from Wedza and the Tipperary claims near Salisbury where no specimens were collected, are from serpentine soils. Furthermore, wherever soil samples have been taken from near the base of the plants high values of soil nickel have been recorded, i. e. up to about 9000 p. p. m. So marked is this correlation that in Rhodesia the plant serves as a reliable nickel indicator (WILD 1970). Not only does the species tolerate very high soil nickel values but it carries in its tissues (whole plant) as much as 2120 p. p. m. nickel (WILD, 1970, fig. 1). When it is recalled that some plants like oats (*Avena sativa*) cannot survive more than a few parts per million of available nickel (HUNTER & VERGNANO, 1952) this is a remarkable phenomenon. It must also be remembered that other plants such as the grasses *Loudetia simplex* and *Themeda triandra* which can similarly tolerate up to 9000 p. p. m. nickel (WILD, loc. cit) are nevertheless resistant to take up of the metal in their above ground parts (but not into their roots) and in fact do not contain under these circumstances more than 100 p. p. m. of nickel (WILD, loc. cit.). If we now turn to the three Zambian records of this species it will be seen that they were all found near Lusaka and were growing in sandy or gravelly soil. It is also as good as certain that one Rhodesian specimen, JACOBSEN 665 was growing in non-nickeliferous soil since the collector says it was growing in *Brachystegia* woodland with sandy soil. These few occurrences in sandy soils with an absence of heavy metals are not so surprising in that a precisely similar situation occurs with the well known copper indicator *Becium homblei* which frequently indicates copper in Rhodesia, Zambia and the Congo but is not completely confined to these soils, and for example, grows in granite sand in the Chinamora Reserve near Salisbury (WILD, 1968a: 68).

The question now arises as to how such a species evolves and perpetuates itself under these rather peculiar edaphic circumstances. We now know that gene flow in populations considered to be conspecific is much more restricted in nature than was commonly thought until recently (EHRlich and RAVEN, 1969, p. 1228) and that tolerant and non-tolerant populations growing on and off heavy metal occurrences often occur when separated by distances of only about 100 m (JAIN & BRADSHAW, 1966, p. 408). Furthermore, these characters of tolerance and non-tolerance are hereditary as shown by culture experiments and their consequent isolation could be expected through subsequent mutation to lead to the evolution of distinct taxa, either as subspecies or species. Much of the European work in this field by BRADSHAW (1959 and subsequently) and latterly a number of other workers was on grass species such as *Agrostis tenuis* SIBTH. This is a grass species with wind-borne pollen and such populations are quoted as being exposed to pollen contamination over distances as little as 20—50 m and with only very minute proportions beyond. *Dicoma niccolifera* is an insect pollinated species like so many Compositae but, even with these, pollen contamination is also very rare beyond about 15 m (EHRlich and RAVEN, 1969, p. 1229). This

means that a metalliferous or otherwise isolated species could evolve relatively rapidly and easily from more closely related species. Subsequently both species, i. e. the parental species and that evolved from it, might remain growing successfully in the same area but on different soil types. Alternatively both could have evolved from a common ancestor now extinct or perhaps surviving elsewhere. This sequence of events could perhaps apply in the case of *Becium homblei* (DE WILD.) DUVIGN. & PLANCKE since this well known copper tolerant species always occurs in Rhodesia contiguously with the only marginally tolerant *B. obovatum* (E. MEY.) N. E. BR. which is in addition very closely related taxonomically to *B. homblei*.

This method might also be thought applicable to the evolution of *Dicoma niccolifera* but the nearest relatives of this species *D. schinzii* and *D. macrocephala*, although they both occur in Rhodesia, have never been found growing in contiguous areas so far, although the number of occurrences of *D. niccolifera* is greater than for *Becium homblei* in Rhodesia. Another species of *Dicoma*, *D. kirkii* HARV. does grow adjacent to *D. niccolifera* on lower nickel values quite frequently but this species is widely separated taxonomically from *D. niccolifera*, as it is in a different section (Plumosae F. C. WILSON). Furthermore, in the case of *D. niccolifera* sufficient passage of time must have elapsed since the evolution of the species to have allowed changed conditions, probably of climate, to have induced an isolation of the related species or the extinction of intermediate or more ancestral species.

However, it cannot be assumed that the metalliferous soils have been a factor in the evolution of *D. niccolifera* since it has been found on non-metalliferous soils in Zambia some three hundred miles north of the next most northerly record of *D. niccolifera*, and it has proved impossible to detect any morphological differences between the metalliferous and non-metalliferous plants.

One should perhaps instead consider EHRlich & RAVEN's statement that "populations that have been completely isolated for long periods often show little differentiation (1969)". These authors quote as examples animals such as a sand crab (*Emerita analoga*) with strongly disjunct Northern-Southern Hemisphere distributions with no possibility of significant gene flow. In this part of the world we may quote the tree *Bivinia jalbertii* TUL. which occurs in very restricted localities in Rhodesia, Tanganyika, Kenya and Madagascar with no significant taxonomic differences between the Madagascan and African material (WILD, 1960). There are many other similar cases. It seems that the material of *Dicoma niccolifera* on non-metalliferous soils near Lusaka and the same species in Rhodesia on metalliferous soils falls into the same category. This is not to say that we should not consider the various populations as distinct ecospecies with no recognisable morphological differences but perhaps with well developed physiological differences. This possibility needs to be tested by cultural experiments with seeds from both types of locality. It does seem in such cases as *Dicoma niccolifera*, and probably also *Becium homblei*, that we must be dealing with examples of biotype

depletion in the sense used by STEBBINS (1942) as suggested by WILD (1968a) with reference to endemic species on serpentines (WILD, 1965, p. 85) and on copper soils (WILD, 1968a), i. e. that these species were once widespread and perhaps through the change of a climate most suited to the species have become extinct in all but a few localities; particularly in those, such as areas bearing heavy metals, which are favourable to selected populations of the species which are tolerant of heavy metals but not to many other intolerant species which would otherwise enter into competition with them.

Although such species may not therefore have arisen through significant evolution induced by heavy metals, nevertheless these edaphic pressures on species exist and, as with *Agrostis tenuis* in Europe, Dr. G. H. WILTSHIRE, of this department, has recently found that hereditary differences in populations of species such as *Eragrostis viscosa* and a *Borreria* species can be found between populations from heavy metal soils and nearby populations on non-metalliferous soils. This work will be published in the near future. Species other than *Dicoma niccolifera* and *Becium bomblei* may have or maybe evolving by this method. *Dicoma niccolifera* and *Becium bomblei* are not the only local species with this type of distribution, the following also occur on the serpentines of Rhodesia, and in Rhodesia are confined to them although they also occur on other soils in S. Africa, e. g. *Indigofera williamsonii* (HARV.) N. E. BR., *Euclea linearis* ZEYH. ex HIERN and *Sutera brunnea* HIERN (WILD, 1965). Other species entirely confined to serpentines in Rhodesia such as *Aloe ortholopha* CHRISTIAN and MILNE-REDHEAD, *Lotononis serpentinicola* WILD, *Pearsonia metallifera* WILD, *Vernonia accommodata* WILD, etc. may also have evolved in the same way and become completely extinct elsewhere. On the other hand they could equally well have evolved *a b i n i t i o* on these toxic soils from populations isolated by the same processes as the populations of *Agrostis tenuis* on metalliferous soils in Britain, or those of *Eragrostis viscosa* etc. now being investigated in Rhodesia.

As it is well known that some species are made up of stable populations and some much more active from an evolutionary point of view, we should perhaps look among the species of our heavy metal floras for more than one kind of evolutionary type. In one case we may have "young" species evolving rapidly in response to edaphic isolation and on the other hand, 'ancient' relic species, of which *Dicoma niccolifera* is one, that have remained unchanged over very long periods. It has already been stated (WILD, 1968a, p. 210) that the Cape Flora and its Subcentres (from a phytogeographical point of view) on Rhodesia's Eastern Border (Inyangani Subcentre) have probably been isolated from each other since the beginning of the Tertiary (70 million years ago) or earlier. This was perhaps the most significant period of climatic change that produced the radical fragmentation of our now disjunct phytogeographical elements as well as of single species distributions. Our metalliferous species like *Dicoma niccolifera* and *Becium bomblei* are more likely to be very ancient stable species whose disjunct distributions have been produced by important climatic changes rather than by

edaphic conditions, although each species is of course very tolerant of heavy metal soils. A recent, as yet unpublished, paper (WILLIAMS MS.) comes to a similar conclusion regarding *Becium homblei* and is based on more statistical taxonomic evidence than is available at present in the case of *Dicoma niccolifera*.

In other cases we must look for taxa, probably among those entirely isolated on metalliferous soils, whose evolution may have occurred in the distant past but could also have occurred mainly in more recent times because of edaphic influences. We have yet to identify species falling into this second category although we know the necessary evolutionary process can occur here as it does in Europe. In Britain of course, due to isolation from the rest of Europe caused by the Ice Ages in the Pleistocene, the evolution of metal-tolerant species can only have been a relatively recent process.

There is clearly a great need for cultural and cytogenetical investigations into these plants in Africa and especially in Rhodesia where the occurrence of metal tolerant species is common. Furthermore, this type of research might be more suited to our area than it is to Europe where metalliferous soils are very rarely natural but are mostly formed from the artificial spoil of old mines.

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