

# Phytogeography of the copper and cobalt flora of Upper Shaba (Zaire), with emphasis on its endemism, origin and evolution mechanisms

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## ABSTRACT

Copper and cobalt ore deposits occur on at least a hundred outcrops scattered in the Shaban Copperbow, an area of 2 000 square kilometres, in the metallogenic Province of Southern Central Africa. With more than 200 species, this flora includes a large number (42) of endemic species of various degrees. Some species are known from only one site, many are located on neighbouring outcrops, others occur on all the ore deposits. Present migratory pathways have been traced for some species and are reported. The relative importance of palaeoendemism and neoendemism is discussed. The origin of these endemics, as well as that of other plants is to be found in several adjacent floras such as that of steppe-savannas developed on more or less poorly aerated soils (Kalahari sands or dambos overlaying laterite), dwarf vegetation on siliceous cellular rocks and miombo woodlands on poor hydromorphic soils. Examples are given for each vegetation type. Systematic details, leaf anatomy and phytochemistry data support these hypotheses, which are illustrated for several closely related taxa.

## RÉSUMÉ

Au moins cent gisements de cuivre et de cobalt existent dans l'Arc cuprifère shabien, un territoire de quelques 2 000 km<sup>2</sup> situé dans la Province métallogénique d'Afrique centrale méridionale. Avec une diversité spécifique qui excède 200 plantes, cette flore comprend un nombre important de taxa endémiques (42) de niveau varié. Certaines espèces sont connues d'une seule localité, un certain nombre de plantes sont situées sur des gisements voisins, d'autres encore s'observent sur toutes les anomalies métallifères. Les voies de migration actuelle ont été suivies pour certaines espèces et sont signalées. L'importance relative du paléoendémisme et du néoendémisme est discutée. L'origine de ces endémiques, aussi bien que l'origine des autres plantes observées est à rechercher parmi certaines flores voisines telles que celle des savanes steppiques développées sur des sols plus ou moins asphyxiants (sables du Kalahari ou dambos établis sur latérite), la végétation naine des roches siliceuses cellulaires et les forêts claires situées sur des sols à mauvaises conditions hydromorphiques. Des exemples sont donnés de l'apport de chacun de ces types de végétation. Des données systématiques, d'anatomie foliaire et phytochimiques renforcent ces hypothèses, qui sont illustrées pour plusieurs taxa voisins.

## INTRODUCTION

Southern Central Africa is an important metallogenic Province, where many ore deposits occur, namely of copper, a metal with which cobalt is frequently associated (Fig. 1). The flora and the vegetation of these ore deposits have been the subject of many studies, not only in Shaba (Robyns, 1932; Duvigneaud, 1958, 1959; Duvigneaud & Timperman, 1959; Duvigneaud & Denaeyer-De Smet, 1960, 1963; Schmitz, 1963; Brooks, 1977; Brooks *et al.*, 1977, 1978; Malaisse & Grégoire, 1978; Malaisse *et al.*, 1978, 1979, 1982; Morrison *et al.*, 1979, 1981; Shewry *et al.*, 1979; De Plaen *et al.*, 1982; Malaisse & Brooks, 1982), but also in Zimbabwe (Jacobsen, 1967, 1968, 1970; Wild, 1968; Howard-Williams, 1970, 1971, 1972; Ernst, 1972) and in Zambia (Horscroft, 1961; Reilly, 1967, 1969, 1971; Drew & Reilly, 1972). Ernst (1974), Wild (1978) and Brooks *et al.* (1980) reviewed the present state of knowledge.

In Shaba, about 100 copper-cobalt deposits totalling some 20 km<sup>2</sup> are scattered in a 20 000 km<sup>2</sup> area of the Shaban Copperbow in south-east Zaire (Morrison *et al.* 1981). These deposits support a distinct vegetation. Both endemic taxa and a great number of more widely distributed species can be

distinguished within this flora, origin of which is mainly to be found in the surrounding vegetation types, of which the main types were noted by Duvigneaud (1958). However, preliminary lists permitting an appreciation of respective origins, are not yet available. Moreover, as far as endemism is concerned, both palaeoendemism (Wild, 1971; Wild & Bradshaw, 1977) as defined by Stebbins (1942) and neoendemism (Antonovics *et al.*, 1971) have been proposed, although the speciation mechanisms have never been precisely examined. The present study attempts to assemble data relating to this lack of knowledge.

## ENDEMISM OF THE COPPER-COBALT FLORA OF UPPER SHABA

The number of endemic species of the copper-cobalt flora of Upper Shaba may be estimated at present at some 42 taxa. This number will undoubtedly change as a result of new systematic studies and further collecting. Revisions may reveal some taxa, until now considered as endemics, to be synonymous. For instance, Geerinck (1971), whose wider concept of the idea of species differs from the narrower view of Duvigneaud and Van Bockstal (Duvigneaud, 1959; Duvigneaud & Denaeyer-De Smet, 1963), reduces the number of *Gladiolus* occurring on copper soils to six, with only one endemic species, *Gladiolus robiliartianus* Duvign.

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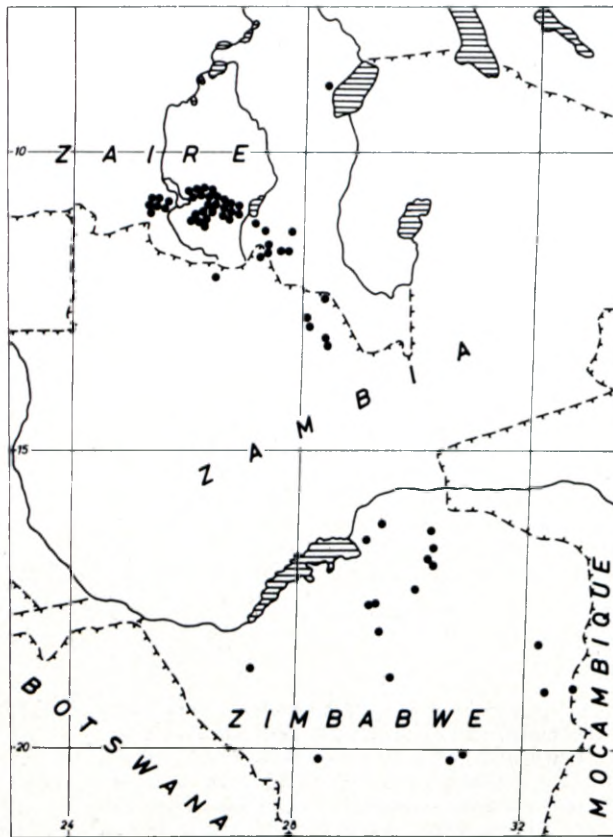


FIG. 1.— Copper (and cobalt) ore deposits in the south central African metallogenic Province.

According to him, several copper endemic taxa, namely *G. tshombeanus* Duvign. & Van Bockst., *G. peschianus* Duvign. & Van Bockst., *G. fungurumeensis* Duvign. & Van Bockst. and *G. duvigneaudii* Van Bockst. appear to be synonyms of species found outside copper soils. On the other hand, some species may be described in error, as was recently the case of *Batopedina pulvinellata* Robbrecht, or are still waiting to be described, such as the new *Monadenium* species (Malaisse 11515) that we have observed recently at Tilwezembe and Fungurume. The examination of recent gatherings may also modify some distributions. For instance, the presence of *Haumaniastrum katangense* (S. Moore) Duvign. & Plancke, outside copper outcrops in N.E. Zambia has recently been noted (Malaisse & Brooks, 1982); moreover, it has been established that this plant occurs on various man-made metalliferous locations, such as the sites of old precolonial furnaces for copper smelting (De Plaen *et al.*, 1982). This plant, considered for a long time as a 'copper flower', is no longer endemic to copper outcrops, even if it remains a very useful indicator of copper anomalies in Shaba. Nevertheless, these preliminary remarks permit certain deductions. Copper-cobalt flora endemism shows several aspects (Fig. 2). Besides plants occurring on all copper-cobalt ore deposits (*Ascolepis metallorum* Duvign. & G. Léonard, *Acalypha cupricola* Robyns) or those with an irregular distribution but widely present in the ensemble of about hundred deposits (*Pandiaka metallorum* Duvign. & Van Bockst., *Rendlia cupricola* Duvign.), endemic plants whose distribu-

tion is restricted to some neighbouring sites exist. There are even plants that are known from only one site, such as *Lindernia perennis* Duvign. and *Vigna dolomitica* Wilczek observed at Etoile Mine, *Sporobolus deschampsoides* Duvign. observed on Kamwali Hill, *Karina tayloriana* Boutique of Kasompi Mine, *Silene cobalticola* Duvign. & Plancke of Mindigi Mine, *Crotalaria françoisiana* Duvign. & Timp. on Mupine hillock and *Acalypha dikuluwensis* Duvign. & Dewit, *Eragrostis dikuluwensis* Duvign. & Jacobs, *Dissotis derriksiana* Duvign. and *Streptocarpus rhodesianus* S. Moore var. *perlanatus* Duvign., all endemics to the Dikuluwe and Mupine. The totally distinct vegetation of Dikuluwe and Mupine is now completely destroyed as a result of mining (annual copper production of Shaba has passed from 10 (1914) to 426 (1980) 10<sup>3</sup> metric tons). Examples of plants restricted to some neighbouring sites or to a part of the Shaban Copperbow are given in Fig. 2. For example, *Buchnera duvigneaudii* Malaisse\* presents a distribution limited to the Kalongwe-Kasompi axis, *Becium peschianum* Duvign. & Plancke is found only on outcrops in the S.E. and *Haumaniastrum robertii* (Robyns) Duvign. & Plancke exists in the central and western part of the Copperbow, etc.

Endemic species, clearly separated from neighbouring taxa not present in Shaba, and which are moreover widely distributed on copper deposits, probably belong to paleoendemism, as is the case of *Ascolepis metallorum*, *Acalypha cupricola* and *Rendlia cupricola*. The first of these three species can still be found on the Kengere deposits, where it resists high zinc-lead concentrations (Duvigneaud & Denaeyer-De Smet, 1963) whereas *Rendlia cupricola*, has been observed outside the Shaban Copperbow at Dikulushi, on copper deposits in the vicinity of Lake Moero. We also noted its presence on anthropic metalliferous sites such as the alluvial soils polluted by waste water of the factory at Likasi, along the Panda River, an ecological niche occupied by *Pteris vittata* L. in the area surrounding Lubumbashi. Neoendemism, on the other hand, should be considered for plastic species, where intermediate forms may still be observed, notably mine ecotypes corresponding to the differentiation of 'small' species, generally having a limited distribution. *Silene cobalticola*, several species of *Becium*, *Haumaniastrum timpermanii* (Duvign. & Plancke) Duvign. & Plancke subsp. *kambovianum* (Duvign. & Plancke) Duvign. & Plancke, etc belong to this last category. In conclusion, the copper-cobalt endemics of Upper Shaba contain a large number of neoendemic species to which may be added a small number of palaeoendemics. This dual origin can be explained (1) by the age of copper-cobalt mineralization in Upper Shaba, which dates from late precambrian era and has therefore been in existence for more than 620 million years and (2) by the extreme climatic changes which

\* *Buchnera duvigneaudii* Malaisse, nomen novum : *Buchnera candida* Duvign. & Van Bockst. syn. nov., non *B. candida* S. Moore (holotype: Duvigneaud 3106 B2, other gathering: Malaisse 10794).

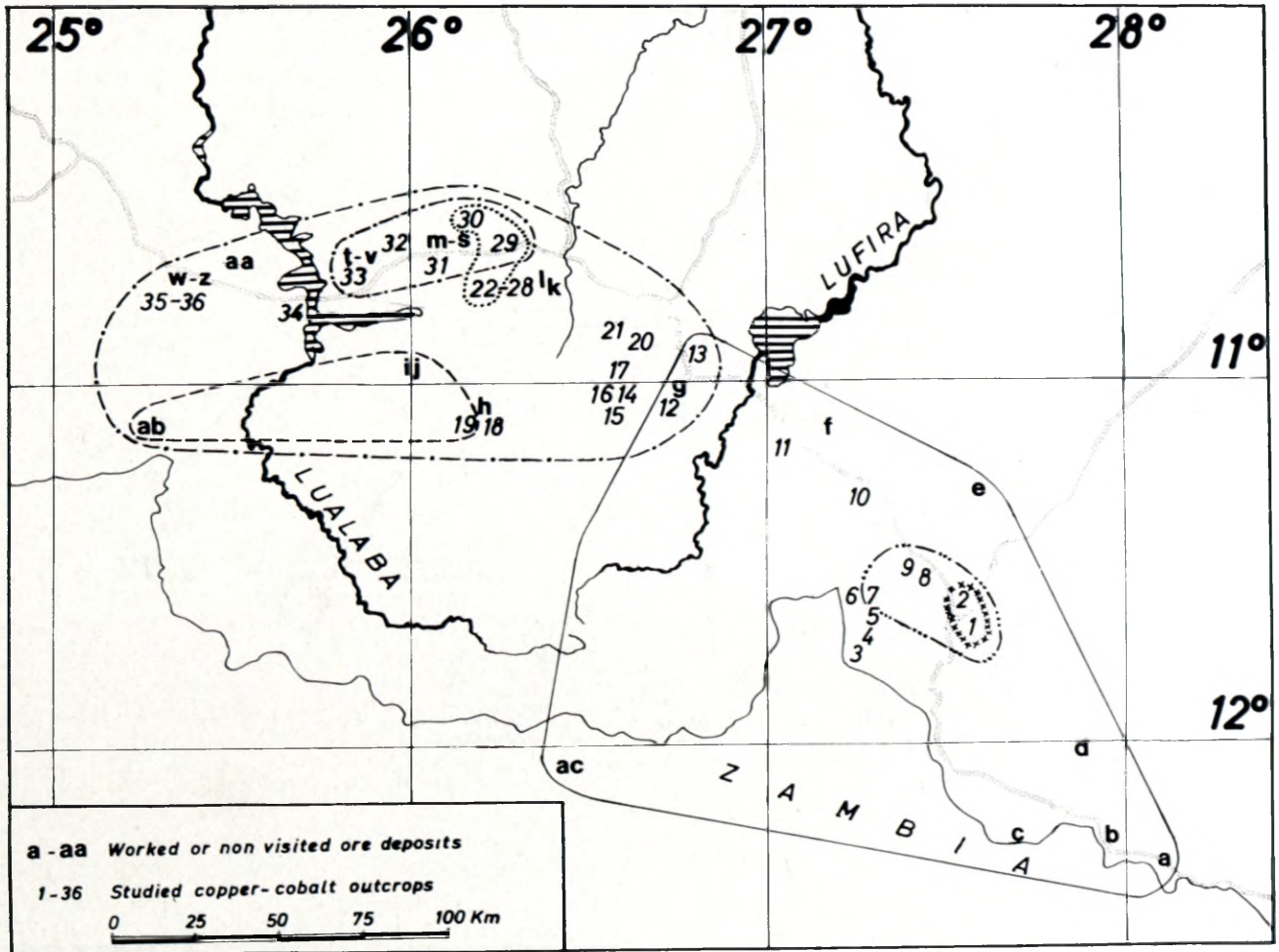


FIG. 2.— Endemism in the Upper-Shaban copper-cobalt flora. Ore deposits are: a, Kamikuba; b, Kinsenda; c, Musoshi; d, Kipapila; e, L. severe; f, Kamwali; g, Likasi; h, Mirungwe; i, Kasompi; j, Menda; k, Kakanda; l, Kiwana; m, Kakavilondo; n, Tenke; o, Goma; p, Shimbidi, q, Kavifwafwaulu; r, Lumbele; s, Mwinansefu; t, Kasunki; u, Chitamba; v, Kakontolwa; w, Mupine; x, Kamoto; y, Musonoi; z, Kolwezi; aa, Ruwe; ab, Kalongwe; ac, Kansanshi; and 1, Etoile; 2, Ruashi; 3, Kipushi; 4, Kasombo; 5, Karavia; 6, Lupoto; 7, Kasonta; 8, Luiswishi; 9, Lukuni; 10, Sokoroshe; 11, Luishia; 12, Shituru; 13, Kamatanda; 14–16, Shinkolowe (principal, signal, borne 13); 17, Tantara; 18, Swambo; 19, Mindigi; 20, Kambove; 21, Sesa; 22, Kela; 23, Mupapala; 24, Lufomboshi; 25, Kankeru; 26, Disele; 27, Kahumbwe; 28, Luita; 29, Fungurume; 30, Kwatebala; 31, Kabwelunono; 32, Kalukundi; 33, Chabara; 34, Tilwezembe; 35, Dikuluwe; 36, Mashamba. Several endemic distributions are represented: ——— *Haumaniastrum katangense*; —●— *Haumaniastrum robertii*; ××××× *Faroa chalcophila*; —●●●— *Becium peschianum*; ●●●●● *Buchnera rubriflora*; ●—●—● *Buchnera foliosa*; — — — — *Buchnera duvigneaudii*. *Ascolepis metallorum* is found on all the ore deposits, whereas some plants are restricted to one mine.

characterized the tertiary era and which therefore created numerous vacant ecological niches at the beginning of the quaternary. These may have favoured the differentiation of species little able to compete in normal conditions, such as *Haumaniastrum katangense*, which reveals a clear weakness to fungal attacks when copper is absent (Morrison *et al.*, 1979).

ORIGIN OF THE COPPER-COBALT FLORA OF UPPER SHABA

As far as is known at present, the copper-cobalt flora of Upper Shaba comprises some 220 taxa including 42 endemics. The origin of this flora is to be found in several vegetation types (Fig. 3). According to Duvigneaud (1958), these plants are derived from four main sources: steppe-savannas on sandy high plateaux (dilungus) (A), seasonally inundated steppe-savannas overlying laterite (dam-bos) (E), woodlands on yellow compact soils (F) and formations on non-mineralized rocky outcrops (I).

However we have also noted other ecological groups, namely grassland plants not subjected to seasonal flooding (B), grassland plants with a wide ecological amplitude (C), plants occurring on derived savannas (D), ruderal species (G) and basi or (and) xerophilous plants (H). Malaisse & Grégoire (1978) listed some ruderal plants occurring on copper mines and Malaisse *et al.* (1983) listed the contribution of the flora of high plateaux steppe-savannas. Table 1 gives a preliminary list of plants belonging to each group.

Regarding endemics, their probable origin confirms the contribution of these vegetation types, as well as revealing the possible rôle of plastic mine ecotypes in the speciation of new endemic taxa (Table 2).

The preliminary analysis of the copper-cobalt flora shows that some 81% of the observed species occur in other vegetation types of Upper Shaba. The three main types are steppe-savannas on high plateaux, woodlands of the Xerobrachystegion

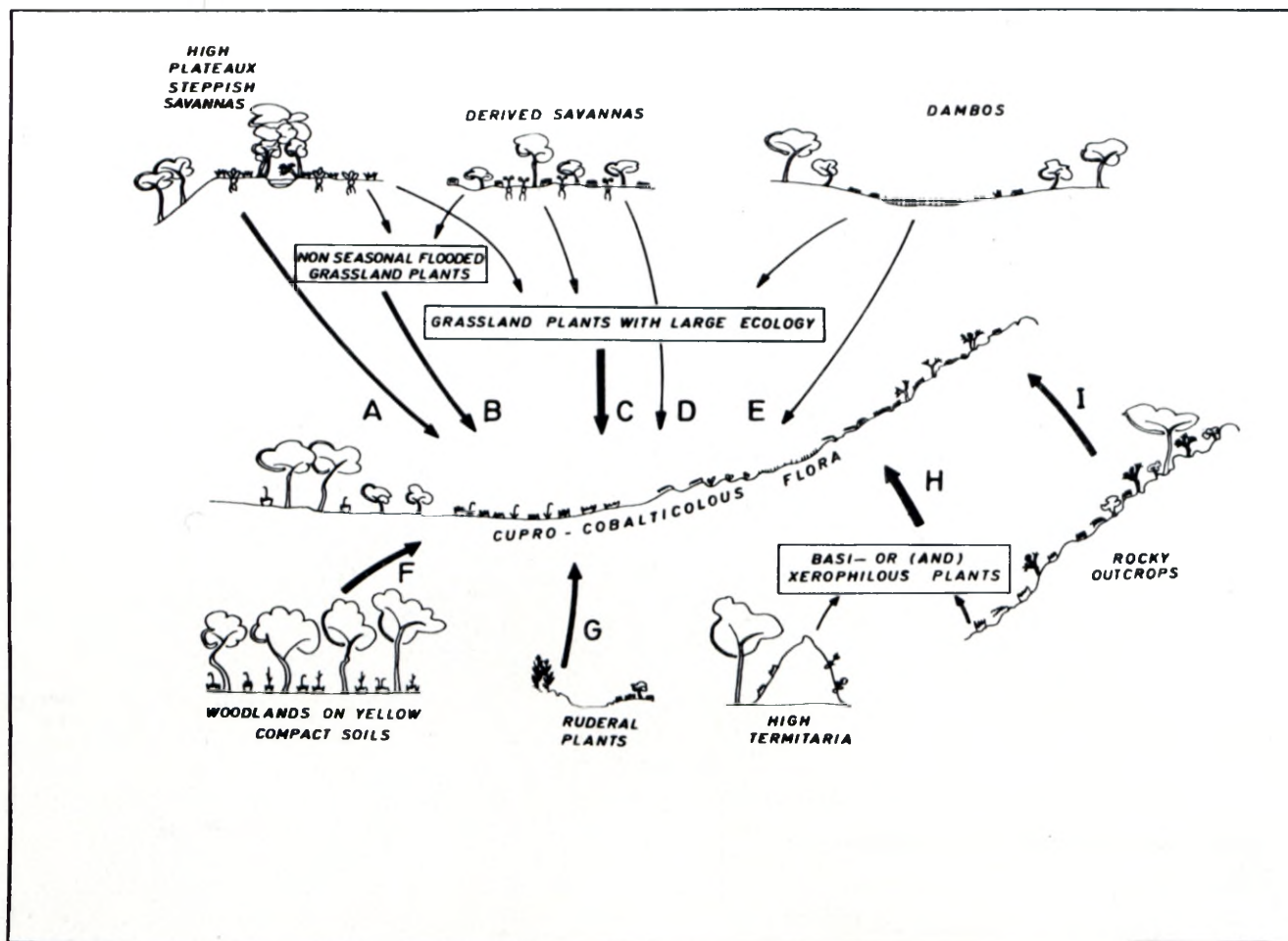


FIG. 3.— Origin of the copper-cobalt flora of Upper Shaba. Species dealing with the nine groups A to I are listed in the text. N.B. For 'grassland plants with large ecology' read 'grassland plants with wide ecological amplitude'.

Alliance and steppes and bushes on rocky outcrops with three other vegetation types (wooded savannas, dambos, high termitaria) playing a secondary rôle. In total, also taking into account the ruderal plants that are frequent on old mine workings, these nine ecological groups represent about 80% of the flora. The remaining 19% is made up of endemic taxa of varying importance, many of which are derived from characteristic species of neighbouring steppe-savannas, woodlands and rocky outcrops with a second fairly important group derived from mine ecotypes.

#### EVOLUTION AND SPECIATION IN THE COPPER-COBALT FLORA OF UPPER SHABA

It is generally accepted that most of the copper-cobalt flora is made up of tolerant taxa able to grow on heavy metallic toxic soils. The establishment of metal-resistant plants on copper-cobalt deposits could have favoured the appearance of tolerant taxa, the 'mine ecotypes' of Antonovics *et al.* (1971). These deposits may also have functioned, at some time, as relay stations or secondary centres of origin in the course of migration or distribution of

some species. Examples illustrating the hypothesis can be found, for instance, in the genera *Ipomoea* and *Becium*. Plastic species complexes could have evolved and given rise to several ecotypes or slightly different species. Malaisse *et al.* (1983) pinpoint the mechanism of speciation for *Silene cobalticola* originating from the widely distributed *S. burchelli* var. *angustifolia*. Evolution here, results in a reduction of leaf width, an increase in leaf thickness and a reduction or even a disparity in trichome linked to floral differences. Similar evolution has been observed for other species. *Justicia elegantula* S. Moore, for example, another variable species, presents an ecotype with very glabrescent and unusually narrow leaves, which is confined to soils with a high copper content in Zimbabwe (Jacobsen, 1970). In Shaba, speciation of the same plant leads to *Justicia metallorum* (Duvigneaud & Denaeyer-De Smet, 1963). In similar way, *Dicoma anomala* Sond. presents abnormally narrow leaves on rocky copper steppes occurring at Luita, Fungurume and Mashamba. It should be noted that this genus has given rise to an endemic on the serpentine soils of the Great Dyke of Zimbabwe (Wild, 1971). The *Pandiaka carsoni-metallorum* complex gives a further example of evolution and copper ecotype

TABLE 1.— Contribution of different vegetation types to the copper-cobalt flora of Upper Shaba

Major vegetation types
<b>Group A.—High plateaux steppe-savannas</b>
<i>Haumaniastrum polyneurum</i> (S. Moore) Duvign. & Plancke
<i>Triumfetta likasiensis</i> De Wild.
<i>Gladiolus actinomorphanthus</i> Duvign. & Van Bockst.
<i>Gladiolus ledoctei</i> Duvign. & Van Bockst.
<i>Crotalaria diloloensis</i> Bak. f.
<i>Gnidia hockii</i> De Wild.
<i>Thesium pawlowskianum</i> Lawalrée
<i>Crassula vaginata</i> Eckl. & Zeyh.
<i>Crotalaria variegata</i> Welw. ex Bak.
<i>Gnidia kraussiana</i> Meissner var. <i>molissima</i> (E.A. Bruce) A. Robyns
<i>Sopubia densiflora</i> Skan
<i>Eriospermum abyssinicum</i> Bak.
<b>Group B.—Non-seasonal flooded grassland plants (including wooded savannas)</b>
<i>Buchnera henriquesii</i> Engl.
<i>Hibiscus rhodanthus</i> Gürke
<i>Uapaca robynssii</i> De Wild.
<i>Crotalaria cornetii</i> Taub. & Dewèvre
<b>Group C.—Grassland plants with wide ecological amplitude</b>
<i>Loudetia simplex</i> C. E. Hubbard
<i>Monocymbium cerasiforme</i> (Nees) Stapf
<i>Pentanisia schweinfurthii</i> Hiern
<i>Sebaea microphylla</i> (Edgew.) Knobl.
<i>Diheteropogon emarginatus</i> (De Wild.) Robyns
<i>Loudetia superba</i> D. N.
<i>Tristachya thollonii</i> Franch.
<i>Tristachya helenae</i> Buscalioni & Muschler
<i>Ctenium concinuum</i> Pilger
<i>Wahlenbergia capitata</i> (Bak.) Thulin
<i>Gnidia kraussiana</i> Meissner var. <i>kraussiana</i>
<b>Group D.—Derived savannas</b>
<i>Monadenium discoideum</i> Bally
<i>Euphorbia zambesiana</i> Benth.
<i>Cryptosepalum maraviense</i> Oliv.
<b>Group E.—Dambos</b>
<i>Thesium quarrei</i> Robyns & Lawalrée
<i>Alectra sessiliflora</i> (Vahl) O. Ktze var. <i>senegalensis</i> (Benth.) Hepper
<b>Group F.—Woodlands on yellow compact soils</b>
<i>Triumfetta dekintiana</i> Engl.
<i>Triumfetta digitata</i> (Oliv.) Sprague & Hutch.
<i>Nephrolepis undulata</i> (Afz. ex Sw.) J. Sm.
<i>Buchnera quadrifaria</i> Bak.
<i>Adenodolichos rhomboideus</i> (O. Hoffm.) Harms
<i>Alloteropsis semialata</i> (R. Br.) Hitchc. var. <i>ecklonii</i> (Eyles) Stapf
<i>Olax obtusifolia</i> De Wild.
<i>Tinneo coerulea</i> Gürke
<i>Oxalis obliquifolia</i> Steud. ex A. Rich.
<i>Aeschynomene pygmaea</i> Welw. ex Bak. var. <i>hebecarpa</i> J. Léonard
<i>Eriosema englerianum</i> Harms
<b>Group G.—Ruderal plants</b>
<i>Tithonia diversifolia</i> Gray

*Arthraxon quartinianus* (A. Rich.) Nash  
*Physalis peruviana* L.  
*Coreopsis oligoflora* Klatt  
*Schizachyrium exile* Hochst.  
*Celosia trigyna* L.  
*Setaria pallide-fusca* (Schum.) Stapf & Hubbard  
*Trema orientalis* (L.) Blume  
*Wahlenbergia collomioides* (A. DC.) Thulin

**Group H.—Basiphilous or (and) xerophilous plants**

*Begonia princeae* Gilg var. *princeae*  
*Anemia angolensis* Alston  
*Selaginella abyssinica* Spring

**Group I.—Rocky outcrops**

*Euphorbia fanshawei* Leach  
*Batopedina pulvinellata* Robbrecht  
*Mohria lepigera* (Bak.) Bak.  
*Actinopteris pauciloba* Pic. Serm.  
*Pellaea pectiniformis* Bak.  
*Cheilanthes inaequalis* (Kuntze) Mett. var. *inaequalis*  
*Dichaetanthera shulinguiana* Duvign.  
*Xerophyta equisetoides* Bak. var. *trichophylla* (Bak.) L. B. Smith & Ayensu  
*Pellaea longipilosa* Bonap.  
*Aeolanthus saxatilis* Duvign. & Denaeyer

## Minor vegetation types

**Forest galleries (banks of rivers)**

*Pteris vittata* L.

**High plateaux narrow fringing forest**

*Delphinium dasycaulon* Fresen

speciation (Fig. 4). On copper outcrops, in Shaba, we have observed a range of forms originating from a broad leaf bearing two types of hair, which was observed at Chabara and Dikulushi among other sites, and giving rise to an ecotype with narrow, glabrous leaves occurring at Luiswishi.

Such evolution may or may not be linked to particular, different accumulation level of copper by each taxon. Among the endemics, numerous hyperaccumulator species are found (Brooks *et al.* 1980): nine of the twelve copper hyperaccumulators and five of the fifteen cobalt hyperaccumulators are actually listed i.e. more than a quarter of the endemics. The acquisition of such an adaptation may constitute the first step in new ecotype speciation. Thus the *Buchnera henriquesii* plants occurring at the Etoile Mine possesses a very high copper content, whereas those found at Mindigi or Chabara have low copper values. In a similar way, the *Pandiaka metallorum* plants of Fungurume accumulate ten times more copper than those of Luiswishi, both growing on soils of the same toxic level. Further research, comparing plants grown from seeds of different origin, is the next step in finding solutions to these speciation problems.

TABLE 2.—Origin of copper-cobalt endemics of Upper Shaba

Copper-cobalt endemics		Nearest taxa	
Taxa	Number of ore deposits where observed	Taxa	Vegetation type
<i>Wahlenbergia ericoidella</i> (Duvign. & Denaeyer) Thulin	2	<i>W. upembensis</i> Thulin	High plateau steppe-savanna
<i>Haumaniastrum timpermanii</i> (Duvign. & Plancke) Duvign. & Plancke ssp. <i>kambovianum</i> (Duvign. & Plancke) Duvign. & Plancke	2	<i>H. timpermanii</i> (Duvign. & Plancke) Duvign. & Plancke) subsp. <i>timpermanii</i>	High plateau steppe-savanna
<i>Justicia metallorum</i> Duvign.	5	<i>J. elegantula</i> S. Moore	High plateau steppe-savanna
<i>Gutenbergia cuprophila</i> Duvign.	2	<i>G. gossweileri</i> S. Moore	High plateau steppe-savanna
<i>Sopubia neptunii</i> Duvign. & Van Bockst.	4	<i>S. conferta</i> S. Moore	High plateau steppe-savanna
<i>Silene cobalticola</i> Duvign. & Plancke	1	<i>S. burchelli</i> Otth. var. <i>angustifolia</i> Sond.	High plateau steppe-savanna + derived savanna
<i>Cyperus kibweanus</i> Duvign.	4	<i>C. margaritaceus</i> Vahl.	Derived savanna
<i>Faroa chalcophila</i> P. Taylor	2	<i>F. affinis</i> De Wild.	Grassland + rocky outcrop
<i>Pandiaka metallorum</i> Duvign. & Van Bockst.	±30	<i>P. carsoni</i> (Bak.) Clarke	Dambo
<i>Lapeirousia erythranta</i> (Klotzsch ex Klatt) Bak. var. <i>welwitschii</i> (Bak.) Marais ex Geerinck et al.	6	<i>L. erythranta</i> (Klotzsch ex Klatt) Bak. var. <i>briartii</i> (De Wild. & Th. Dur.) Geerinck et al.	Woodland
<i>Lopholaena deltombei</i> Duvign.	8	<i>L. alata</i> Duvign.	Woodland
<i>Sopubia metallorum</i> Duvign.	±15	<i>S. myomboensis</i> Duvign. & Van Bockst.	Woodland
<i>Xerophyta demeesmaekeriana</i> Duvign. & Dewit	3	<i>X. equisetoides</i> Bak. var. <i>trichophylla</i> Bak.	Rocky outcrop
<i>Streptocarpus rhodesianus</i> S. Moore var. <i>perlanatus</i> Duvign.	1	<i>S. rhodesianus</i> S. Moore var. <i>rhodesianus</i>	Rocky outcrop
<i>Icomum biformifolium</i> De Wild.	2	<i>I. lineare</i> Burkill	Rocky outcrop.
<i>Icomum tuberculatum</i> De Wild.	7	<i>I. lineare</i> Burkill	Rocky outcrop
<i>Crotalaria françoisiana</i> Duvign. & Timp.	1	<i>C. peschiana</i> Duvign. & Timp.	Copper outcrop.
<i>Haumaniastrum robertii</i> (Robyns) Duvign. & Plancke	±20	<i>H. katangense</i> (S. Moore) Duvign. & Plancke	Copper outcrop
<i>Acalypha dikuluwensis</i> Duvign. & Dewit	1	<i>Acalypha cupricola</i> Robyns	Copper outcrop
<i>Buchnera rubriflora</i> Duvign. & Van Bockst.	4	<i>B. duvigneaudii</i> Malaisse	Copper outcrop
<i>Becium peschianum</i> Duvign. & Plancke	5	<i>B. aureoviride</i> Duvign.	Copper outcrop
<i>Becium empetroides</i> Duvign.	±5	<i>B. ericoides</i> Duvign. & Plancke	Copper outcrop
<i>Lindernia perennis</i> Duvign.	1	<i>Lindernia damblonii</i> Duvign.	Copper outcrop

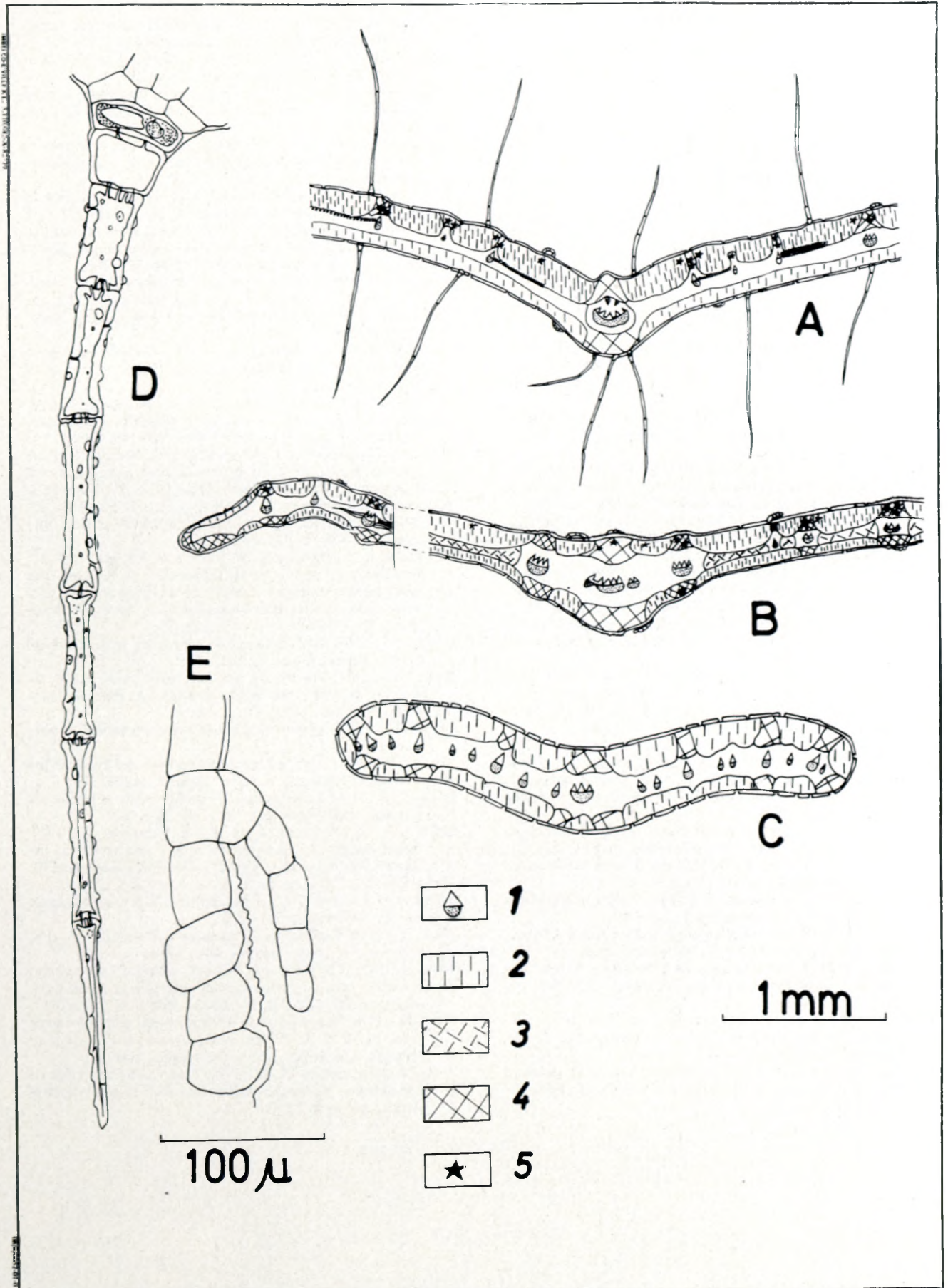


FIG. 4.— Evolution and speciation in the *Pandiaka carsoni-metallorum* complex. Transversal section of leaf and detail of hair for *Pandiaka* from various origins: Chabara (A,D); Kahungwe (B,E); Luiswishi (C). Conventional signs are: 1, vascular bundle; 2, green-leaved palisade parenchyma; 3, green-leaved lacunose parenchyma; 4, collenchyma; 5, calcium oxalate grains and crystals.

ACKNOWLEDGEMENTS

The author is indebted to Mrs E. Colonval of the University of Lubumbashi for assistance with preparation of leaf sections. Thanks are also due to T. Bulaimu, K. Kisimba and Y. Muzinga for assistance with field work. We also thank L. Ngoy and N. Tshibombo for drawings which accompany this paper. Field photographic documentation was provided by the Gécamines Mining Company; we would like to acknowledge the kind assistance of Kalambay, Loshi and Lukoji.

REFERENCES

- ANTONOVICS, J., BRADSHAW, A. D. & TURNER, R. G. 1971. Heavy metal tolerance in plants. *Adv. Ecol. Res.* 7: 1–85.
- BROOKS, R. R., 1977. Copper and cobalt uptake by *Haumaniastrum* species. *Pl. Soil* 48,2: 541–544.
- BROOKS, R. R., MC CLEAVE, J. A. & MALAÏSSE, F., 1977. Copper and cobalt in African species of *Crotalaria* L. *Proc. R. Soc. Lond. B* 197: 231–236.
- BROOKS, R. R., MORRISON, R. E., REEVES, R. D. & MALAÏSSE, F., 1978. Copper and cobalt in African species of *Aeolanthus* Mart. (Plectranthinae, Labiatae). *Pl. Soil* 50: 503–507.
- BROOKS, R. R., REEVES, R. D., MORRISON, R. S. & MALAÏSSE, F., 1980. Hyperaccumulation of copper and cobalt — A review. *Bull. Soc. r. Bot. Belg.* 113,2: 166–172.
- DE PLAEN, G., MALAÏSSE, F. & BROOKS, R. R., 1982. The copper flowers of Central Africa and their significance for prospecting and archeology. *Endeavour* N.S. 6: 72–77.
- DREW, A. & REILLY, C., 1972. Observations on copper tolerance in the vegetation of a Zambian copper clearing. *J. Ecol.* 60: 439–444.
- DUVIGNEAUD, P., 1958. La végétation du Katanga et de ses sols métallifères. *Bull. Soc. r. Bot. Belg.* 90: 127–286.
- DUVIGNEAUD, P., 1959. Plantes 'cobaltophytes' dans le Haut-Katanga. *Bull. Soc. r. Bot. Belg.* 91: 111–134.
- DUVIGNEAUD, P. & DENAEYER-DE SMET, S., 1960. Action de certains métaux lourds du sol (cuivre, cobalt, manganèse, uranium) sur la végétation dans le Haut-Katanga. In Viennot-Bourgin *Rapports du sol et de la végétation* 121–139. Paris: Masson.
- DUVIGNEAUD, P. & DENAEYER-DE SMET, S., 1963. Cuivre et végétation au Katanga. *Bull. Soc. r. Bot. Belg.* 96: 93–231.
- DUVIGNEAUD, P. & TIMPERMAN, J., 1959. Etudes sur le genre *Crotalaria*. *Bull. Soc. r. Bot. Belg.* 91: 135–176.
- ERNST, W., 1972. Ecophysiological studies on heavy metal plants in south central Africa. *Kirkia* 8: 125–145.
- ERNST, W., 1974. Schwermetallvegetation der Erde. In Tüxen, *Geobotanica selecta* 5: 194 p. Stuttgart: Fischer.
- GEERINCK, D., 1972. Révision du genre *Gladiolus* L. (Iridaceae) au Zaïre, au Rwanda et au Burundi. *Bull. Jard. bot. nat. Belg.* 42: 269–287.
- HORSCROFT, F. D. M., 1961. Vegetation. In Mendelsohn, *The geology of the Northern Rhodesian copper belt* 73–80. London: Macdonald.
- HOWARD-WILLIAMS, C., 1970. The ecology of *Becium homblei* in Central Africa with special reference to metalliferous soils. *J. Ecol.* 58: 745–763.
- HOWARD-WILLIAMS, C., 1971. Environmental factors controlling the growth of plants on heavy metal soils. *Kirkia* 8: 91–102.
- HOWARD-WILLIAMS, C., 1972. Factors influencing copper tolerance in *Becium homblei*. *Nature, Lond.* 237: 171.
- JACOBSEN, W. B. G., 1967. The influence of the copper content on trees and shrubs of Molly South Hill, Mangula. *Kirkia* 6: 63–84.
- JACOBSEN, W. B. G., 1968. The influence of the copper content of the soil on the vegetation at Silverside North, Mangula area. *Kirkia* 6: 259–277.
- JACOBSEN, W. B. G., 1970. Further note on the vegetation of copper-bearing soils at Silverside. *Kirkia* 7: 285–290.
- MALAÏSSE, F. & BROOKS, R. R., 1982. Colonisation of modified metalliferous environments in Zaïre by the copper flower *Haumaniastrum katangense*, *Pl. Soil* 64: 289–293.
- MALAÏSSE, F., COLONVAL-ELENKOV, E. & BROOKS, R. R., 1983. The impact of copper and cobalt orebodies upon the evolution of some plant species from Upper Shaba, Zaïre. *Pl. Syst. Evol.* In press.
- MALAÏSSE, F. & GRÉGOIRE, J., 1978. Contribution à la phytogéochimie de la mine de l'Etoile (Shaba, Zaïre). *Bull. Soc. r. Bot. Belg.* 111: 252–260.
- MALAÏSSE, F., GRÉGOIRE, J., BROOKS, R. R., MORRISON, R. S. & REEVES, R. D. 1978. *Aeolanthus bififormifolius*: a hyperaccumulator of copper from Zaïre. *Science* 99:887–888.
- MALAÏSSE, F., GRÉGOIRE, J., MORRISON, R. S., BROOKS, R. R. & REEVES, R. D., 1979. Copper and cobalt in vegetation of Fungurume, Shaba Province, Zaïre. *Oikos* 33: 472–478.
- MORRISON, R. S., BROOKS, R. R., REEVES, R. S. & MALAÏSSE, F., 1979. Copper and cobalt uptake by metallophytes from Zaïre. *Pl. Soil* 53: 535–539.
- MORRISON, R. S., BROOKS, R. R., REEVES, R. D., MALAÏSSE, F., HOROWITZ, P., ARONSON, M. & MERRIAM, G. R., 1981. The diverse chemical forms of heavy metals in tissue extracts of some metallophytes from Shaba Province, Zaïre. *Phytochemistry* 20: 455–458.
- REILLY, C., 1967. Accumulation of copper by some Zambian plants. *Nature, Lond.* 215: 667–668.
- REILLY, C., 1969. The uptake and accumulation of copper by *Becium homblei* (De Wild.) Duvign. & Plancke. *New Phytol.* 68: 1081–1087.
- REILLY, C., 1971. Copper tolerance in *Becium homblei*. *Nature, Lond.* 230: 403.
- ROBYNS, W., 1932. Over plantengroei en flora der kopervelden van Opper-Katanga. *Natuurw. Tijdschr.* 14: 101–107.
- SCHMITZ, A., 1963. Aperçu sur les groupements végétaux du Katanga. *Bull. Soc. r. Bot. Belg.* 96: 233–447.
- SHEWRY, P. R., WOOLHOUSE, H. W. & THOMPSON, K., 1979. Relationships of vegetation to copper and cobalt in the copper clearings of Haut Shaba, Zaïre. *Bot. J. Linn. Soc.* 79: 1–35.
- STEBBINS, G. L., 1942. The genetic approach to rare and endemic species. *Madroño* 6: 241–272.
- WILD, H., 1968. Geobotanical anomalies in Rhodesia. 1— The vegetation of copper bearing soils. *Kirkia* 7: 1–71.
- WILD, H., 1971. The taxonomy, ecology and possible method of evolution of a new metalliferous species of *Dicoma* Cass. (Compositae). *Mitt. bot. St. Samml. Münch.* 10: 266–274.
- WILD, H., 1978. The vegetation of heavy metal and other toxic soils. In M. J. A. Werger, *Biogeography and ecology of southern Africa* 1301–1332, The Hague: Junk.
- WILD, H. & BRADSHAW, A. D., 1976. The evolutionary effect of metalliferous and other anomalous soils in south central Africa. *Evolution* 31: 282–293.