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The Impact of Copper and Cobalt Orebodies upon the Evolution of Some Plant Species from Upper Shaba, Zaïre

By

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Abstract: The flora of the copper-cobalt ores of Upper Shaba, Zaïre, comprises some 220 taxa including 42 endemics. The origin of this flora is examined and an assessment has been made of its relationship with the flora of the high plateaux steppe-savannah (*dilunguan flora*). A first group consists of undifferentiated species limited to these two floras. A second group comprises cupriphilous taxa derived from closely-related and widely distributed species observed on the high plateaux and elsewhere. A third group consists of closely-related species or ecotypes confined to the areas. In the *Silene burchelli* complex (*Caryophyllaceae*) there is a gradual transition from the widespread *S. burchelli* var. *angustifolia* on the high plateaux to a newly discovered *S. burchelli* ecotype from a cupriferous outcrop at Luita, and to *S. cobalticola* from highly mineralized copper-cobalt deposits at Mindigi. This ecophyletic series provides a gradient of morphological anatomical, and physiological changes whose end members are distinct species. The subject of palaeoendemism and neoendemism in relation to metallophytes of Upper Shaba is also discussed. Colonisation of metalliferous soils by elements of the non-mineralised high plateau is believed to be a neoendemic process.

About 100 copper-cobalt ore deposits totalling some 20 km² are disseminated in a 20 000 km² area of the Shaban metallogenic province in Southeast Zaïre (Morrison & al. 1980). These metalliferous outcrops bear specific vegetation assemblages which are made up of smaller species, principally annual herbs, and caespitose grasses found in carpets, steppes and steppe-savannahs, which contrast sharply with the surrounding woodlands (locally known as *miombo*). This copper-cobalt flora has been the subject of several studies (Robyns 1932, Duvigneaud

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1958, 1959, Duvigneaud & Denaeyer-de Smet 1960, 1963, Malaisse & Grégoire 1978, Malaisse & al. 1979, Shewry & al. 1979).

Several biogeochemical aspects of metal-tolerant taxa of this flora have also been investigated recently and include studies on the genera *Haumaniastrum* (Brooks 1977), *Crotalaria* (Brooks & al. 1977 b) and *Aeolanthus* (Brooks & al. 1978, Malaisse & al. 1978). These studies have revealed the existence of hyperaccumulators which are defined as plants whose foliage contains over 1 000 µg/g (dry mass) of copper, nickel or cobalt (Brooks & al. 1977 a). Brooks & al. (1980) listed 12 copper-hyperaccumulators and 15 cobalt-hyperaccumulators, all found in Shaba, of which five plants hyperaccumulated both copper and cobalt, namely *Bulbostylis mucronata*, *Aeolanthus biformifolius*, *Haumaniastrum robertii*, *Buchnera henriquesii* and *Lindernia perennis*.

The uptake of cobalt and/or copper by hyperaccumulators is not necessarily proportional to the concentrations of these elements in the soil. In general there is a high correlation between cobalt in leaves and soils, whereas for copper the leaves show a low gradient (plant/soil concentration ratio) at lower concentration in the soil followed by a sharp increase of this gradient at higher concentration levels (Morrison & al. 1980). It has also been established (Morrison & al. 1981) that copper and cobalt complexes in the plant material involve a number of different ligands. There is also a pronounced inverse correlation between spatial distributions of cobalt and potassium as well as a direct relationship between cobalt and calcium. Some of the cobalt may be immobilized with calcium in oxalate crystals.

As far as is known at present, the copper-cobalt flora of upper Shaba comprises some 220 taxa including at least 42 endemics. Some of the latter may later be discovered elsewhere and this would affect some of our statements, although the main facts will remain valid. It should be noted that although most of the endemic metallophytes have been identified and described, very little information is available on their systematics or mechanisms of their speciation. The present paper will examine the origin of the copper-cobalt flora and will be especially concerned with the contribution made to it by the flora of the steppe-savannah occurring on the high plateaux. It will also make preliminary observations on the speciation of copper-cobalt endemics in Upper Shaba.

Materials and Methods

Our present knowledge results from floristic investigations carried out on 47 copper-cobalt deposits. The reference collection contains 1 365 voucher specimens which are deposited in the herbarium of the Université Nationale du Zaïre at Lubumbashi (LSHI). Duplicates are at the Jardin Botanique National de

Belgique (BR) at Meise, Brussels. Nevertheless only three sites have been visited all the year round, during the five seasons (early, main and late rainy, cold and warm dry) (MALAISSE 1974) recognized for Upper Shaba. Furthermore as the flowering sequence is virtually continuous, i.e. each week at least some species are in flower, and as the flowering time is frequently very short, the present available knowledge is not complete. It should further be noted that several taxa need additional study in order to specify their systematic status and this could sometimes even necessitate the recognition of new taxa.

Metallophytes were compared with some 22300 voucher specimens collected by one of us (F. M.) in Upper Shaba during the past 15 years and covering a large selection of the various vegetation types existing in the country (woodlands, high termitaria, dambos, savanna-steppe vegetation on Kalahari sands, dense dry evergreen forests, riparian forests, aquatic vegetation, rocky outcrops, etc.).

The material was studied from the aspects of biosystematics, phytogeography, foliar anatomy and phytochemistry. Rererence sources were various floras (Flore d'Afrique Centrale, Flora Zambesiaca, Flora of Tropical East Africa, Prodromus einer Flora von Südwestafrika, Flora of Southern Africa, and Adumbratio Florae Aethiopieae) and also collectors' notes accompanying voucher specimens of the very rich African herbarium at Meise, Brussels.

For studies on foliar anatomy, the leaf samples were immersed in a 1 : 1 : 1 water/glycerine/ethanol (95%) preservative. Thin sections were made with a scalpel and a microtome. The principal staining agents were iodine green and ruthenium red (3 min) after washing for 10 min in 40% acetic acid.

General levels of copper and cobalt in various species were established by analysis of 350 voucher specimens. Soils were also analyzed. The procedure used was atomic absorption spectrophotometry on solutions of plant ash and soils. Data for plants were recalculated to a dry mass basis. For further details of analytical procedures see MALAISSE & al. (1979).

Geology of the Shaban Copper Belt

In the Shaban Copper Belt there are three distinct stratigraphic formations which are from top to bottom: the overburden; the Katanga Group; the Kibara Basement Group. The Katanga Group is of Upper Cambrian age (i.e. over 620 m.y. old). It comprises three large series: the Upper Kundelungu Series: the Lower Kundelungu Series; the Roan Series (FRANÇOIS 1973). This latter series comprises four facies among which is the Série des Mines or Middle Roan Series. Copper/cobalt mineralization in Shaba Province is found in these Série des Mines strata. They are mainly calcareous rocks with dark minerals, dolomitic schists, cellular siliceous rocks, flakey siliceous rocks, stratified dolomites and argilliceous talcs.

The Origin of the Cupro-cobalticolous Flora of Upper Shaba

The origin of the 220 species found on the copper-cobalt ore deposits of Upper Shaba Province is one of fundamental importance. There are basically two separate components of this flora: namely, endemic taxa and also species found outside the metalliferous outcrops. Both of these will be discussed in this paper.

Species which have a widespread distribution in south-central Africa have been able to colonize metalliferous occurrences because of their tolerance with regard to heavy metals. According to DUVIGNEAUD (1958), these plants are derived from four main sources: i.e. steppe-like formations on relatively toxic soils from: (i) periodically-inundated steppe-savannahs overlying laterites, (ii) steppe-savannahs from the sandy high plateaux (dilungus), (iii) formations on non-mineralized rocky soils, (iv) marshlands on yellow compact soils (the phyto-sociological unit is known as the Xerobrachystegion alliance). However two other ecological groups have also been noted by us: namely, (v) widely-distributed savannah species whose precise ecology is at present unknown, (vi) ruderal species.

Colonization of ore deposits by metal-resistant species should favour the appearance of tolerant races, the so-called "mine-ecotypes" of ANTONOVICS & al. (1971). It is nevertheless difficult to identify such tolerant ecotypes unless their appearance is accompanied by heavy metal accumulation or changes in chromosome numbers. As shown by ANTONOVICS & al. (1971) determination of chromosome numbers may indicate the way in which "mine ecotypes" may have been selected. Physiological and phytochemical investigations on plants growing in metal-rich soils may also shed light on the tolerance mechanism by indicating whether uptake of metals is internally or externally controlled, i.e. whether such uptake is controlled by edaphic conditions of the soil or by the plant's own regulatory mechanisms.

In direct contrast to the theory of widespread plants being able to colonize ore deposits, there is the converse proposition that certain endemic species originating on such deposits may be able to survive over other substrates to a limited degree and principally an anthropogenic metalliferous sites such as those of ancient (12th century) copper smelting activities where a cuprophilous vegetation is to be found (DE PLAEN & al. 1981). These secondary sites may indeed one day be sources for further expansion of the endemic species into other substrates.

The occurrence of endemic species is a result of either palaeoendemism or neoendemism. The relatively great age of copper-cobalt mineralization gives evidence of an ancient selection of endemic taxa (palaeoendemism). On the other hand the dramatic changes in climate which occurred in the Tertiary could have produced important floral modifications leading to a marked impoverishment of the flora hence creating numerous vacant ecological niches at the beginning of the

Quaternary. This would have favoured a marked differentiation in "plastic" survivor species up to the present. A second argument in favour of neoendemism is that widespread cuprophile plants at present are annuals with wind-borne dispersion of seeds. Endemic perennials have somewhat restricted distributions which in some cases are confined to a single hillock.

Affinity Between the Dilunguan Flora and the Cupro-cobalticolous Flora

Several high plateaux may be distinguished in Upper Shaba. These are characterized by altitudes exceeding 1 500 m, reaching 2 400 m at Marungu. They usually have poor soils formed from Kalahari sands or occasionally from granitic or rhyolitic rocks, and support a steppe-savannah type of vegetation. These high plateaux are the Marungu (S.W. of Lake Tanganyika), and four plateaux arranged in the form of a broad horseshoe: Kundelungu, Kibara, Biano and Manika (LISOWSKI & al. 1971). In the extension of the Manika plateau into Zambia, sand deposits bearing a similar steppe-savannah are found in the Mwinilunga area.

Plants whose distribution is limited to several or all of the above six high plateaux form a particular floral subelement named the dilunguan (French "dilunguien" from the swahili term "dilungu" or grassland) by MALAISSE (1969). Besides this endemic subelement exist other types of vegetation assemblage, including some plants occurring both on the high plateaux and on Shaban cupriferous outcrops. Affinities between the dilunguan flora and the flora of cupro-cobalticolous hillocks appear at several levels as discussed below.

Firstly a number of plants are confined solely to the high plateaux and to the metalliferous outcrops. They constitute a floral group which is generally poorly understood. This type of distribution has already been noted for *Haumaniastrum polyneurum* (S. MOORE) DUVIGN. & PLANCKE and *Triumfetta digitata* (OLIV.) SPRAGUE & HUTCH. (DUVIGNEAUD & DENAEYER-DE SMET 1963). Other phytogeographical observations made by ourselves have added other plants to this list. Thus *Triumfetta likasiensis* DE WILD., formerly considered to be a cupricolous endemic (ROBYNS 1932, DUVIGNEAUD & DENAEYER-DE SMET 1963), also exists on the Kibara Plateau. Of the six *Gladiolus* species (*Iridaceae*) known from cupriferous sites, two belong to the above floral group. *G. actinomorphanthus* DUVIGN. & VAN BOCKSTAL and *G. ledoctei* DUVIGN. & VAN BOCKSTAL (GEERINCK 1972) both occur on high plateaux and in the vicinity of Kolwezi and Tenke on copper-rich soils.

A second affinity between the dilunguan flora and plants growing on copper-cobalt deposits is found in plants with a wide distribution outside of these metalliferous sites. A good example is *Crassula vaginata* ECKL. & ZEYH. (= *C. abyssinica* A. RICH.), which is widely distributed in tropical and subtropical Africa above 900 m altitude. In Shaba the plant is commonly found on the sandy high plateaux (Biana, Kibara, Kundelungu and Marungu) and also colonizes the cupriferous steppe at Fungurume MALAISSE & al. 1979) and Kwatebala, becoming there a hyperaccumulator of cobalt (BROOKS & al. 1980). *Crotalaria variegata* WELW. ex BAKER, a plant with a Zambezian distribution has a similar behaviour in Shaba (BROOKS & al. 1977 b). *Gnidia kraussiana* MEISSNER var. *mollissima* (E. A. BRUCE) A. ROBYNS, a plant previously known in Zaïre only on the Kundelungu Plateau (ROBYNS 1975), has recently been found at the Mindigi and Kasonta mines.

A third group consists of closely related species or ecotypes each occurring separately in one of the mentioned areas. In his revision of the genus *Wahlenbergia* in tropical Africa and Madagascar, THULIN (1975) recognized the close affinity between *W. ericoidella* (DUVIGN. & DENAEYER-DE SMET) THULIN, an endemic plant of Kasompi and Menda copper outcrops, and *W. upembensis* THULIN, whose distribution corresponds typically to the dilunguan subelement. Both belong to the *W. abyssinica* group and are perennial herbs with a dimeric gynoecium, trigonous seeds, and very densely spinuliferous pollen grains. The Zambezian genus *Haumaniastrum* comprises a group of shrubby species with a short woody stem which is found only on the Shaban high plateaux with the exception of some shrubby steppe-savannas dominated by *Uapaca robynsii* DE WILD. and which occurs on the periphery of cupriferous outcrops. In this latter region, at Kambove and Swambo mines, there is a subspecies (ssp. *kambovianum* [DUVIGN.] DUVIGN. & PLANCKE) of *H. timpermanii* (DUVIGN. & PLANCKE) DUVIGN. & PLANCKE, while the typical subspecies occurs on the Biano and Kundelungu high plateaux.

An exemplary link between the flora on metalliferous soils and that on the high plateaux is provided by the *Silene burchelli* OTTH. complex. This will be discussed below.

Speciation in the *Silene burchelli* Complex and Its Evolutionary Significance

The genus *Silene* L. comprises some 400 species which are mainly distributed in Europe, the Mediterranean region and temperate Asia. These species include several heavy metal tolerant taxa such as the metallophyte *S. cucubalus* WIB. and the serpentine-invading *S. armeria* L. and *S. otites* (L.) WIB. (ERNST 1974).

One of the best-known of these metal-resistant species of *Silene* is *S. dioica* (= *Melandrium dioicum*) which has been studied by several workers (PRAT 1934, PRAT & KOMAREK 1934, FEJDIOVA 1970). It is a major component of copper resistant assemblages and of serpentine communities in Fennoscandia (TANNER 1931, BJÖRLYKKE 1938, VOGT 1942, VOGT & BRAADLIE 1942, KOTILAINEN 1944, RUNE 1953). Indeed BROOKS & al. (1979) analysed about 300 herbarium specimens of *S. dioica* and from anomalously high levels of copper, lead, and nickel were able to identify a number of copper occurrences and ultrabasic areas in Fennoscandia. Pot trials on some species (BROOKS & CROOKS 1980) showed an extremely high tolerance to elevated concentrations of copper, lead, nickel and zinc. From the European experience alone, there appears to be some evidence that metal-tolerance has evolved repeatedly in this genus and that it has an inherent tendency in this direction.

The European tendency for heavy metal resistance by *Silene* is repeated in Central and Southern Africa where several perennial species are recorded and include *S. biafrae* HOOK. f. from West Africa, *S. macrosolen* (STEUD. ex A. RICH.) from East Africa, *S. undulata* Ait. from Zimbabwe and South Africa, *S. crassifolia* L. from south Africa, and *S. burchelli* OTTH. This latter species is widely distributed from Ethiopia to the Cape of Good Hope and is also recorded in Arabia and Syria. This appears to be a very polymorphic complex and has been subdivided into various varieties. There is however much disagreement on its infraspecific taxonomy. TURRILL (1956) after having described several varieties, considered finally that it was not possible to subdivide the material into clearcut subspecies or varieties. WILD (1961) on the other hand, considered var. *burchelli* to be a most distinct and relatively uniform coastal variety confined to the southwestern and eastern Cape Province, the plants in the remainder of the range being var. *angustifolia* SOND.

S. burchelli is locally present on nickeliferous serpentine soils of the Great Dyke, Zimbabwe (WILD 1965, ERNST 1974). Its var. *angustifolia* (a) occurs in Upper Shaba and is relatively common in the steppe-savannah covering the sandy high plateaux. DUVIGNEAUD (1959) reported the discovery of a new taxon from the copper-cobalt ores of Mindigi which was described as *S. cobalticola* Duvign. et Plancke (c) and is related to *S. burchelli*. The recent discovery of a *S. burchellii* copper ecotype (b) on the Luita cupriferous outcrop, some 42 km N.N.E. of Mindigi, provides a link and further evidence on speciation in the *S. burchelli* complex.

We have compared material of *S. burchelli* [reference material has been deposited at the Jardin Botanique National de Belgique (BR) and at the Université Nationale du Zaïre, Lubumbashi (LSHI) from three sources: (a) sandy high plateau (MALAISSE 4665, Kundelungu Plateau near Katshupa, 17. 10. 1966); (b) cupriferous outcrop (MALAISSE 10073, Luita hillock, 27. 10. 1979); (c) copper-cobalt outcrop (MALAISSE 10799, Mindigi hillock, 16. 5. 1980)]. Our comparison has involved a study of flower morphology, leaf anatomy, and phytogeography.

The floral morphology shows minor differences: the mean length of the tubular-clavate calyx for the sampled material is 15, 14 and 11 mm respectively for *S. burchelli* var. *angustifolia*, the *S. burchelli* copper ecotype, and *S. cobalticola*. The greatest width of the calyx was 6, 3.5 and 3 mm respectively. Limb length decreases in the same sequence but with a concomitant increase of width and insertion angle (Fig. 1).

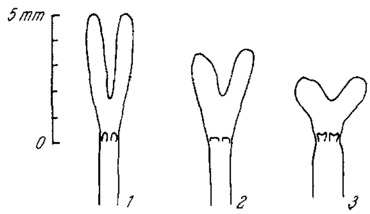

Fig. 1. Flower morphology of the *Silene burchelli* complex. The diagram shows the upper part of the petal with the limb flattened. *a S. burchelli* var. *angustifolia*; *b S. burchelli* copper ecotype; *c S. cobalticola*

A study of leaf anatomy has shown conspicuous differences in the palisade parenchyms, epidermis and vascular bundles (Fig. 2). These differences are reinforced by leaf morphological differences in size and pilosity.

As dried leaves of *Silene cobalticola* (a) contain a similar amount of cobalt and copper as those of *S. burchelli* from Luita hillock (b) (Table 1), this is probably a tolerant species as is confirmed by the behaviour of this taxon in Zimbabwe. Thus, the succession to progressively more rigorous ecological conditions as in the sequence: Kalahari sandy soils (a), copper orebodies, (b) copper-cobalt outcrops (c) [Mindigi soils contain 2550 μg/g (0.26%) cobalt and 13100 μg/g (1.31%) copper] has induced an ecophyletic series. This series provides a gradient of morphological and anatomical modifications which still allows for the distinguishing of two separate species, namely *S. burchelli* and *S. cobalticola*. A similar conclusion was reached during a biosystematic survey of the genus *Dianthus* L. (*Caryophyllaceae*) of South-central Africa (LISOWSKI & MALAISSE 1972).

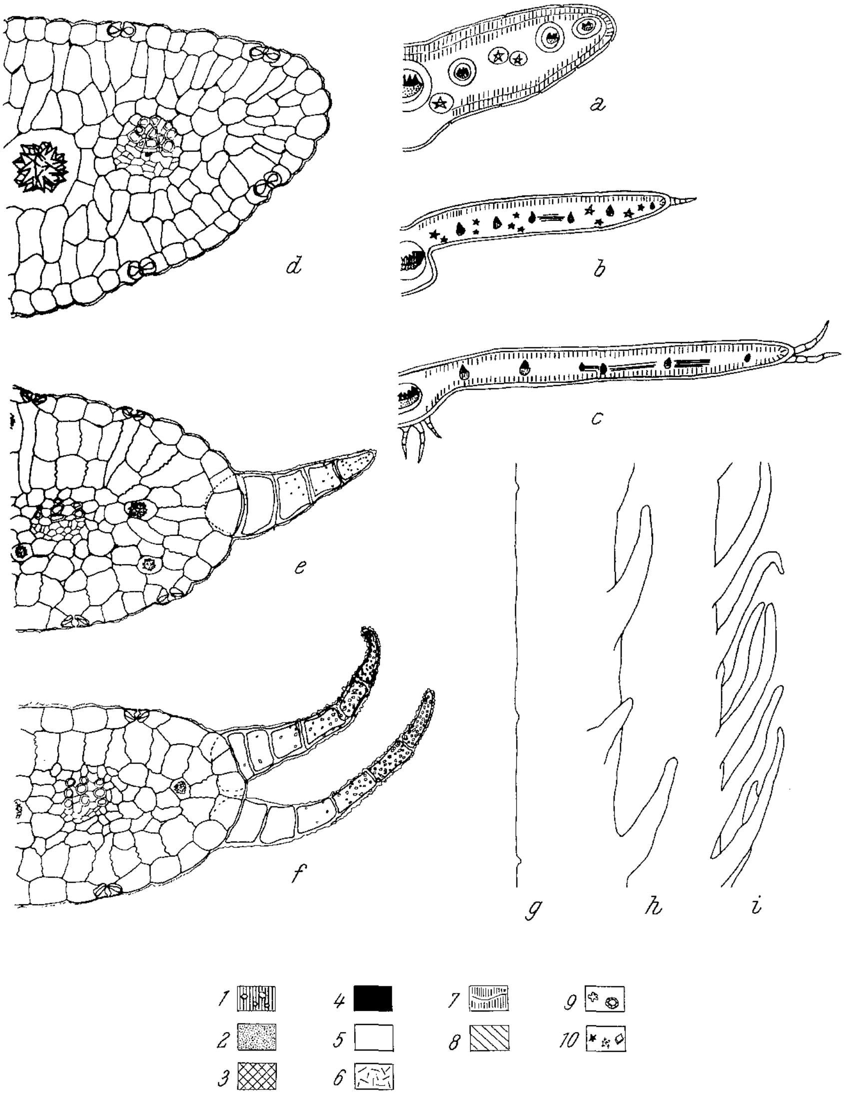

Fig. 2. Leaf anatomy in the *Silene burchelli* complex. *a*, *b* and *c* = diagrammatic transverse section; *d*, *e* and *f* = detail of leaf extremity of transverse section; *g*, *h* and *i* = leaf lamina margin; *a*, *d* and *g* = *S. cobalticola*; *b*, *e* and *h* = *S. burchelli*, copper ecotype; *c*,*f* and *i* = *S. burchelli* var. *angustifolia*.—Key to symbols used in the figure: *1* xylem; *2* phloem; *3* collemchyma; *4* phloem cells and tissues; *5* colourless parenchyma; *6* green-leaved lacunose parenchyma; *7* green-leaved palisade parenchyma; *8* other green-leaved parenchyma; *9* lactiferous and resin channels; *10* spinulose calcium oxalate grains and crystals

Table 1. Differences of anatomy and cobalt and copper concentrations in the *Silene burchelli* complex

	S. burchelli (a)	*S. burchelli* (b) copper ecotype	*S. cobalticola* (c)
Voucher reference number	4655	10073	10799
Copper concentration (μg/g)	9	27	24
Cobalt concentration (μg/g)	1	35	38
Leaf width (mm)	4.2	3.0	1.18
Thickness of principal vein (μm)	270	400	540
Thickness of leaf lamina (μm)	220	260	450
Hair length on lamina side (μm)	200–280	140	—
Hair length on principal vein (μm)	175	—	—

Other studies reinforce the above hypotheses. Populations of *Indigofera dyeri* BRITT. from Copper King in Zimbabwe are much more tolerant to zinc and cobalt than populations tested from other soils (ERNST 1972). WILD & HEYTING (1966) proposed differences in leaf shapes and dimensions in populations of *Becium homblei* (DE WILD) DUVIGN. & PLANCKE from different origins. HOWARD-WILLIAMS (1971) has found similar differences in seed size and corolla shape in the same species, the "copper flower" of Zambian prospectors. SHEWRY & al. (1979) when comparing mean heights, numbers of basal branches, and numbers of growing parts of *Xerophyta* on different sites (exposed rocks, cupriferous dambos) distinguished two basic morphological forms which corresponded probably to *X. equisetoides* BAK. The same authors considered populations of *Cryptosepalum maraviense* OLIV. growing on cupriferous soils to be basically different from those growing on non-cupriferous soils in Shaba. These differences concern the size of the leaves and the number of leaflets. It should be noted that this genus is very variable and difficult to divide into separate species (DUVIGNEAUD & BRENAN 1966). *Justicia elegantula* S. MOORE is also a variable species for which an ecotype with very glabrescent and unusually narrow leaves has been described. In addition, a hairy broad-leaved ecotype has been observed in Zimbabwe (WILD 1968). According to JACOBSEN (1970), the first ecotype is definitely confined to soils with high copper contents and ranks as a true indicator plant. In Shaba, speciation of *J. elegantula* leads to *J. metallorum* DUVIGN., a neo-endemic plant found in the Shinkolobwe-Swambo-Kasompi area (DUVIGNEAUD & DENAEYER-DE SMET 1963). Similar evolution has been observed in the *Buchnera henriquesii* complex (*Scrophulariaceae*) on heavy-metal outcrops in the vicinity of Lubumbashi (MALAISSE & al. 1981).

Neo- and Palaeoendemism in the Shaban Copper Belt Flora

The metalliferous soils of Upper Shaba provide abnormal ecological niches that influence the evolution of plant species. For South-central Africa these niches have been present for a very long time and this has increased the probability of evolution (WILD 1978). Taxa endemic o specific mines exist at least in the case of copper and cobalt. Several workers consider the so-called "mine taxa" as a palaeo-endemic as defined by TURRILL (1951). This is supported by WILD (1971) in the case of *Dicoma niccolifera*, a plant which is not however entirely restricted to the serpentine soils of the Great Dyke of Zimbabwe. WILD & BRADSHAW (1977) consider that most of the Zimbabwean species endemic to metalliferous soils appear to be palaeo-endemics. Another paleo-endemic taxon could be *Ascolepis metallorum* DUVIGN. & G. LÉONARD, a well established and sharply limited species of the *A. protea* complex (GEOTGHEBEUR 1980). This sedge is present on all of the Shaban copper hillocks and also on the calamine-rich soils of Kengere. Other workers strongly suggest that most of the characteristics of plants from these areas are typical to neo-endemics. This is particularly applicable to the Zambezian region (ANTONOVICS & al. 1971).

As far as speciation of endemic taxa on heavy-metal anomalies is concerned, it is generally supposed that evolution could be linked to the existence of tolerant populations or to the acquisition of physiological adaptations. Thus the first step generally consists of a development of high tolerance to mineralization. This adaptation may be accompanied by, or linked to, minor morphological modifications. This process leads to neo-endemism, which will be restricted, at least initially, to a single mineralized outcrop. A study of the distributions on some 40 Shaban copper-cobalt endemic taxa supports this last assumption even though endemism on heavy-metal hillocks is of various types. This is illustrated for the Lubumbashi area in Fig. 3. These endemics may subsequently colonize neighbouring hillocks or even man-made environments (DE PLAEN & al. 1981) though specialised taxa seem to remain generally restricted to their narrowly defined habitats because of the costs of their specialisation (WERGER & al. 1978).

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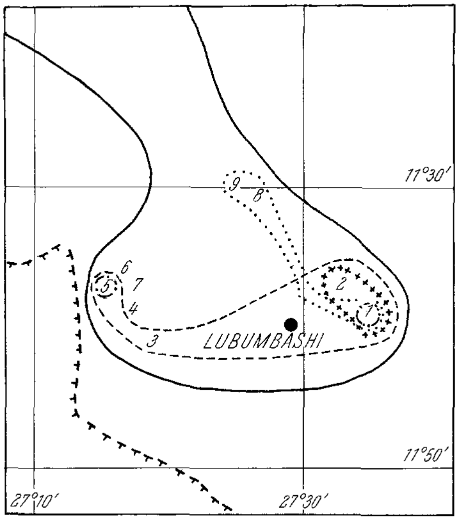

Fig. 3. Types of endemism for the copper-cobalt flora of Upper Shaba in the vicinity of Lubumbashi (see also Fig. 4). Numbers are mine sites and mineralized hillocks: 1 = Étoile, 2 = Ruashi, 3 = Kasombo, 4 = Karavia, 5 = Lupoto, 6 = Kasonta, 7 = Nianumenda, 8 = Luiswishi, 9 = Lukuni. The distribution range of the various taxa is indicated by the following symbols: —·—· *Thesium pawlowskianum* Lawalrée, —··—·· *Lindernia perennis* Duvign. and *Vigna dolomitica* Wilczek, + + + + + *Faroa chalcophila* P. Taylor, ····· *Aeolanthus biformifolius* De Wild., — — — — — — *Lindernia damblonii* Duvign., ———————— *Ascolepis metallorum* Duvign. et G. Léonard. The first three plants are restricted to one mineralized outcrop, *Faroa* is found on two sites, *Aeolanthus* on three sites and *Ascolepis* on all sites

References

Antonovics, J., Bradshaw, A. D., Turner, R. G., **1971**: Heavy metal tolerance in plants. — Adv. Ecol. Res. **7**, 1—85.

Björlykke, B., **1938**: Vegetasjonen på olivensten på Sunmöre. — Nyt. Mag. Naturvid. **79**, 64.

Brooks, R. R., **1977**: Copper and cobalt uptake by *Haumaniastrum* species. — Pl. Soil **48**, 541—544.

— Crooks, H. M., **1980**: Studies on uptake of heavy metals by the Scandinavian Kisplanten *Lychnis alpina* and *Silene dioica*. — Pl. Soil **54**, 491—495.

— Lee, J., Reeves, R. D., Jaffré, T., **1977** a: Detection of nickeliferous rocks by analysis of herbarium specimens of indicator plants. — J. Geochem. Explor. **7**, 49—57.

— McCleave, J. A., Malaisse, F., **1977** b: Copper and cobalt in African species of *Crotalaria* L. — Proc. Roy. Soc. Lond. Sec. **B 197**, 231—236.

— Morrison, R. S., Reeves, R. D., Malaisse, 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., MALAISSE, F., 1980: Hyperaccumulation of copper and cobalt—a review. — Bull. Soc. Roy. Bot. Belg. **113**, 166—172.

— TROW, J. M., BØLVIKEN, B., 1979: Biogeochemical anomalies in Fennoscandia: a study of copper, lead and nickel in *Melandrium dioicum* and *Viscaria alpina*. — J. Geochem. Explor. **11**, 73—87.

DE PLAEN, G., MALAISSE, F., BROOKS, R. R., 1982: The upper flowers of Central Africa and their significance for archaeological and mineral prospecting. — Endeavour **6**, 72—77.

DUVIGNEAUD, P., 1958: La végétation du Katanga et ses sols metallifères. — Bull. Soc. Roy. Bot. Belg. **90**, 127—286.

— 1959: Plantes cobaltophytes dans le Haut Katanga. — Bull. Soc. Roy. Bot. Belg. **91**, 111—134.

— BRENAN, J. P. M., 1966: The genus *Cryptosepalum* BENTH. (*Leguminosae*) in the areas of the "Flora of Tropical East Africa" and the "Flora Zambesiaca". — Kew Bull. **20**, 1—23.

— DENAEYER-DE SMET, S., 1960: Actions de certains métaux lourds du sol (cuivre, cobalt, manganèse, uranium) sur la végétation dans le Haut-Katanga. — In VIENNOT-BOURGIN, G. (Ed.): Rapports du Sol et de la Végétation, 121—139. — Paris: Masson.

— — 1963: Cuivre et végétation au Katanga. — Bull. Soc. Roy. Bot. Belg. **96**, 93—231.

ERNST, W., 1972: Ecophysiological studies on heavy metal plants in South Central Africa. — Kirkia **8**, 125—145.

— 1974: Schwermetallvegetation der Erde. — Stuttgart: G. Fischer.

FEJDIOVA, V., 1970: K problematike botanického výskumu háld. — Biologia (Bratislava) **25**, 255—256.

FRANÇOIS, A. P., 1973: L'extrémité occidentale de l'arc cuprifère Shabien. Étude géologique. — Publ. Gécamines, Likasi, p. 1—120.

GEERINCK, D., 1972: Révision du genre *Gladiolus* L. (*Iridaceae*) au Zaïre, au Rwanda et au Burundi. — Bull. Jard. Bot. Nat. Belg. **42**, 269—287.

GOETGHEBEUR, P., 1980: Studies in *Cyperaceae*—2. Contribution towards a revision of the mainly African genus *Ascolepis* NEES ex STEUDEL. — Adansonia Sér. **2**, **19**, 269—305.

HOWARD-WILLIAMS, C., 1971: Environmental factors controlling the growth of plants on heavy metal soils. — Kirkia **8**, 91—102.

JACOBSEN, W. B. G., 1970: Further note on the vegetation of copper-bearing soils at Silverside. — Kirkia **7**, 285—290.

KOTILAINEN, M. J., 1944: Kasvit erikoislaatuisen substraatin indikattoreina. — Soc. Sci. Fenn. Arsbok **22**, 1—18.

LISOWSKI, S., MALAISSE, F., 1972: Le genre *Dianthus* L. (*Caryophyllaceae*) au Zaïre. — Bull. Soc. Roy. Bot. Belg. **105**, 239—244.

— — SYMOENS, J. J., 1971: Une flore des hauts plateaux du Katanga. — Mitt. Bot. Staatssamml. München **10**, 51—56.

MALAISSE, F., 1969: Note à propos de la flore du Plateau des Kundelungu (Haut Katanga, Rep. Dem. Congo). — Trav. Serv. Sylv. Pisc. Univ. Off. Congo Lubumbashi **2**, 1—10.

— 1974: Phenology of the Zambezian woodland area, with emphasis on the miombo ecosystem. — In LIETH, H., (Ed.): Phenology and Seasonal Modeling, p. 269—286. — Berlin: Springer.

MALAISSE, F., BROOKS, R. R., MORRISON, R. S., 1981: Les espèces de *Buchnera* L. (*Scrophulariaceae*) des gisements cupro-cobaltifères du Shaba méridional (Zaïre) (in prep.).

— GRÉGOIRE, J., 1978: Contribution à la phytogéochimie de la Mine de l'Étoile (Shaba, Zaïre). — Bull. Soc. Roy. Bot. Belg. **111**, 252—260.

— — BROOKS, R. R., MORRISON, R. S., REEVES, R. D., 1978: *Aeolanthus biformifolius:* a hyperaccumulator of copper from Zaïre. — Science **199**, 887—888.

— — 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., MALAISSE, F., 1979: Copper and cobalt uptake by metallophytes from Zaïre. — Pl. Soil **53**, 535—539.

— — — MALAISSE, F., HOROWITZ, P., ARONSON, M., MERRIAM, G. R., 1981: The diverse chemical forms of heavy metals in tissue extracts of some metallophytes from Shaba Privince, Zaïre. — Phytochemistry **20**, 455, 458.

PRAT, S., 1934: Die Erblichkeit der Resistenz gegen Kupfer. — Ber. Deutsch. Bot. Ges. **52**, 65—67.

— KOMAREK, K., 1934: Vegetace u medenych dolu. Zolastni Otisk Ze Sborniku Map. **VII**, **8**, 1—16.

ROBYNS, A., 1975: *Thymelaeaceae.* — In: Flore d'Afrique Centrale, Zaïre, Rwanda, Burundi: *Spermatophyta.* — Bruxelles: Jardin Botanique National du Belgique.

ROBYNS, W., 1932: Over plantengroei en flora der kopervelden van Opper-Katanga. — Natuurwet. Tijdschr. **14**, 101—107.

RUNE, O., 1955: Plant life on serpentinites and related rocks in the north of Sweden. — Acta Phytogeogr. Suec. **31**, 1—139.

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. Lond. **79**, 1—35.

TANNER, V., 1931: Eine Assoziation von *Viscaria alpina — Anthelia nivalis — Oligotrichum incurvum.* — Mem. Soc. Fauna Flora Fenn. **6**, 145—148.

THULIN, M., 1975: The genus *Wahlenbergia* s. lat. (*Campanulaceae*) in tropical Africa and Madagascar. — Acta Univ. Upsaliensis Symbolae Bot. Upsaliensis **21**, 1—223.

TURRILL, W. B., 1951: Some problems of plant range and distribution. — J. Ecol. **39**, 205—227.

— 1956: *Caryophyllaceae.* — In TURRILL, W. B., MILNE-REDHEAD, E., (Eds.): Flora of Tropical East Africa, 1—38. — London: Crown Agents.

VOGT, T., 1942: Geokjemisk og geobotanisk malmleting. II. *Viscaria alpina* (L.) G. Don. som "Kisplante". III. Litt. om planteveksten ved Røsrosmalmene. — Kgl. Norske Vidensk. Selsk. Forh. **15**, 5—8, 21—24.

— BRAADLIE, O., 1942: Geokjemisk og geobotanisk malmleting. IV. Plantevekst og jordbunn ved Rørosmalmene. — Kgl. Norske Vidensk. Selsk. Forh. **15**, 25—28.

WERGER, M. J. A., WILD, H., DRUMMOND, B. R., 1978: Vegetation structure and substrate of the northern part of the Great Dyke, Rhodesia: gradient analysis and dominance-diversity relationships. — Vegetatio **37**, 151—161.

WILD, H., 1961: *Caryophyllaceae.* — In: EXELL, A. W., WILD, H., (Eds.): Flora Zambesiaca **1**, 337—358. — London: Crown Agents.

— 1965: The flora of the Great Dyke of Southern Rhodesia with special reference to the serpentine soils. — Kirkia **5**, 49—86.

WILD, H., 1968: Geobotanical anomalies in Rhodesia. 1—The vegetation of copper bearing soils. — Kirkia **7**, 1—71.
— 1971: The taxonomy, ecology and possible method of evolution of a new metalliferous species of *Dicoma* CASS. (*Compositae*). — Mitt. Bot. Staatssamml. München **10**, 266—274.
— 1978: The vegetation of heavy metal and other toxic soils. — In WERGER, M. J. A., (Ed.): Biology and Ecology of Southern Africa, p. 1301—1332. — The Hague: Junk.
— BRADSHAW, A. D., 1976: The evolutionary effect of metalliferous and other anomalous soils in South Central Africa. — Evolution **31**, 282—293.
— HEYTING, A., 1966: An analysis of variation of leaf dimensions in *Becium homblei* DE WILD. DUVIGN. & PLANCKE and *Becium obovatum* (E. MEY.) N. E. BR. — Bot. Notiser. Lund **119**, 349—357.

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