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The Taxonomic Significance of Cyanogenesis in *Lotononis* and Related Genera

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Key Word Index—*Buchenroedera*; *Lotononis*; Leguminosae; cyanogenesis; taxonomy; sectional classification.

Abstract—Reports on cyanogenesis in the genus *Lotononis* are limited to five species. In a survey using the Feigl–Anger spot test, a further 52 species of *Lotononis* and four species of the closely related *Buchenroedera* were found to by cyanogenic. Species of other genera in the tribe Crotalarieae all gave a negative result. Cyanogenesis appears to be a character of considerable chemotaxonomic value in *Lotononis*, with some groups of species cyanogenic and others acyanogenic. These groups usually follow the traditional sectional classification. Lack of morphological uniformity within a section is also reflected in the cyanogenesis data and this may provide useful additional evidence to improve the existing classification. The data support the view that the genera *Lotononis* and *Buchenroedera* are congeneric.

Introduction

Cyanogenesis is particularly common in the Leguminosae and is known to occur in at least 18 of the tribes (Seigler, personal communication). Among the Crotalarieae *sensu* Polhill [1], five species are reported to be cyanogenic [2, 3]: *Lotononis carnosa* (Eckl. & Zeyh.) Benth., *L. crumanina* Burch. ex Benth., *L. involucrata* (Berg.) Benth., *L. laxa* Eckl. & Zeyh. and *L. oxyptera* (E. Mey.) Benth. Some of these have proved to be responsible for hydrocyanic poisoning in stock [2]. Cyanogenesis in *Lotononis* is due to the presence of the glucoside prunasin (derived from L-phenylalanine) [3]. In the Leguminosae, this biochemical pathway to the production of cyanogenic compounds is less common than the more usual valine- and isoleucine pathways, which lead to linamarin and lotaustralin, respectively [4].

In the latest available taxonomic treatment of *Lotononis* [5], the original sectional limits of Bentham [6] were modified to accommodate newly described species. This resulted in what appears to be an unnatural classification. Not only were species of other genera included, but the section *Oxydium* was transferred to the genus *Crotalaria*. In view of new insights into generic limits [1] and numerous undescribed species, the sectional classification of *Lotononis* should be reconsidered as a first step towards a complete revision.

This survey was done to evaluate cyanogenesis as a chemotaxonomic character at generic and infrageneric levels in *Lotononis* and related genera.

Results

The tests showed that at least 57 species of *Lotononis* and four species of *Buchenroedera* are cyanogenic (Table 1). Not a single positive result was obtained for 98 samples from nine other genera of the tribe.

Within the genus *Lotononis*, a distinct pattern emerged amongst the various groups of related species (Table 2). Very few species showed indications of intra- and/or interpopulational variation. Such differences were observed only in a few species of section *Krebsia*, the *L. falcata*- and *L. laxa* groups of section *Leptis* and in *Buchenroedera*. The data for individual species and species groups of *Lotononis* and *Buchenroedera* are presented in Table 3 and discussed below.

Discussion

In Tables 2 and 3, the existing sectional classification of Bentham [6], Harvey [7] and Duemmer [5] is followed, except for some modifications:

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TABLE 1. SUMMARY OF CYANOGENESIS TEST RESULTS FOR VARIOUS GENERA OF THE TRIBE CROTALARIEAE

Genus	Total number of samples	Total number of species		
		In group	Tested	HCN⁺
Lotononis (DC.) Eckl. & Zeyh.	351	*ca* 130	113	57
Buchenroedera Eckl. & Zeyh.	32	*ca* 14	9	4
Argyrolobium Eckl. & Zeyh.	7	*ca* 70	4	0
Aspalathus L.	9	278	8	0
Crotalaria L.	22	*ca* 600	17	0
Dichilus DC.	9	5	5	0
Lebeckia Thunb.	21	*ca* 35	11	0
Melolobium Eckl. & Zeyh.	11	*ca* 20	6	0
Pearsonia Duemmer	6	11	4	0
Polhillia Stirton	9	5	4	0
Wiborgia Thunb.	4	10	3	0

TABLE 2. SUMMARY OF CYANOGENESIS TEST RESULTS FOR THE DIFFERENT SECTIONS OF *LOTONONIS*. Some of the sections are divided into informal groups, as defined in the footnotes

Section/Group	Total number of species			
	In group	Tested	HCN⁺	%HCN⁺
Aulacinthus (E. Mey.) Benth.	*ca* 7	7	7	100
Krebsia (Eckl. & Zeyh.) Benth.				
L. carnosa group*	*ca* 10	10	9	90
L. carinata group†	2	2	0	0
L. digitata group‡	*ca* 2	2	0	0
Telina (E. Mey.) Benth.	*ca* 13	11	5	48
Polylobium (Eckl. & Zeyh.) Benth.				
L. umbellata group§	*ca* 9	8	7	88
L. angolensis group‖	*ca* 5	5	0	0
Oxydium Benth.	*ca* 9	8	6	75
Lipozygis (E. Mey.) Benth.				
L. anthylloides group¶	*ca* 8	7	0	0
L. eriantha group**	*ca* 8	7	0	0
Leobordea (Del.) Benth.	*ca* 6	3	0	0
Leptis (Eckl. & Zeyh.) Benth.				
L. laxa group††	*ca* 9	9	8	90
L. falcata group‡‡	*ca* 22	20	15	75
L. quinata group§§	*ca* 5	5	0	0
L. calycina group‖‖	*ca* 16	9	0	0
Total	*ca* 130	113	57	50

**Krebsia* (Eckl. & Zeyh.) Benth. *sensu stricto*; †species added to *Krebsia* by Duemmer [5]; ‡species added to *Krebsia* by Harvey [7] and Duemmer [5]; §*Polylobium* (Eckl. & Zeyh.) Benth. *sensu stricto*; ‖species later added to *Polylobium* and related species; ¶species with indehiscent fruit; **species with dehiscent fruit; ††perennials with the carina acute and glabrous; ‡‡annuals with the carina acute and glabrous; §§short-lived, prostrate perennials usually with 5-digitate leaves; ‖‖annuals or perennials with the carina obtuse and pubescent.

—Morphologically heterogenous sections are split into smaller groups of related species.

—Species that were obviously misplaced are transferred to more appropriate positions.

—Species of other genera wrongly assigned to *Lotononis* are excluded.

—Newly described or undescribed species are allocated to those groups that seem the most appropriate on morphological considerations.

The groups are used here in an informal sense for comparative purposes and no formal taxonomic hierarchy or rank is implied. Future studies however, may show some of these to be worthy of sectional status, while others (and even some

TABLE 3. RESULTS OF CYANOGENESIS TESTS FOR INDIVIDUAL SAMPLES AND SPECIES OF *LOTONONIS* AND *BUCHENROEDERA*

Groups and species	Number of samples tested			
	Total	HCN^+	HCN?	HCN^-
Lotononis (DC.) Eckl. & Zeyh.				
Section *Aulacinthus* (E. Mey.) Benth.				
L. leucoclada (Schltr.) Duemmer	6	6	—	—
L. gracilis (E. Mey.) Benth.	6	6	—	—
L. rigida (E. Mey.) Benth.	2	2	—	—
L. viborgioides Benth.	3	3	—	—
L. dahlgrenii B-E. van Wyk	1	1	—	—
L. comptonii B-E. van Wyk	7	7	—	—
L. dissitinodis B-E. van Wyk	2	2	—	—
Section *Krebsia* (Eckl. & Zeyh.) Benth.				
Part 1: *L. carnosa* group				
L. carnosa (Eckl. & Zeyh.) Benth.	3	3	—	—
L. biflora (H. Bol.) Duemmer	4	3	1	—
L. cytisoides (E. Mey.) Benth.	7	4	1	2
L. trisegmentata Phillips	5	—	—	5
L. divaricata (Eckl. & Zeyh.) Benth.	12	8	—	4
L. galpinii Duemmer	2	2	—	—
L. pottiae Burtt Davy	1	1	—	—
L. dichiloides Sond. (yellow)	1	1	—	—
L. dichiloides Sond. (pink)	1	—	1	—
L. bachmanniana Duemmer	3	3	—	—
L. caerulescens (E. Mey.) B-E. van Wyk	5	5	—	—
Part 2: *L. carinata* group				
L. carinata (E. Mey.) Benth.	5	—	—	5
L. hirsuta Schinz	3	—	—	3
Part 3: *L. digitata* group				
L. digitata Harv.	2	—	—	2
L. benthamiana Duemmer	3	—	—	3
Section *Telina* (E. Mey.) Benth.				
L. minor Duemmer	1	—	—	1
L. azurea (Eckl. & Zeyh.) Benth.	2	2	—	—
L. prostrata (L.) Benth.	2	2	—	—
L. acuminata Eckl. & Zeyh.	3	3	—	—
L. varia (E. Mey.) Steud.	2	2	—	—
L. argentea Eckl. & Zeyh.	2	—	—	2
L. azureoides B.-E. van Wyk	1	1	—	—
L. gracilifolia B.-E. van Wyk	2	—	—	2
L. elongata (Thunb.) D. Dietr.	2	—	—	2
L. macrocarpa Eckl. & Zeyh.	3	—	—	3
L. solitudinis Duemmer	2	—	—	2
Section *Polylobium* (Eckl. & Zeyh.) Benth.				
Part 1: *L. umbellata* group				
L. umbellata (L.) Benth.	6	6	—	—
L. acocksii B-E. van Wyk	1	1	—	—
L. purpurescens B-E. van Wyk	2	2	—	—
L. peduncularis (E. Mey.) Benth.	2	2	—	—
L. involucrata (Berg.) Benth.	3	3	—	—
L. angustifolia (E. Mey.) Steud.	3	2	—	1
L. exstipulata L. Bol.	3	3	—	—
L. serpens (E. Mey.) Dahlgr.	7	—	1	6
Part 2: *L. angolensis* group				
L. angolensis Welw. ex Bak.	4	—	—	4
L. bainesii Bak.	4	—	—	4
L. listii Polhill	4	—	—	4
L. listioides Dinter & Harms	2	—	—	2
L. marlothii Engl.	2	—	—	2

TABLE 3—*CONTINUED*

Groups and species	Number of samples tested			
	Total	HCN^+	HCN?	HCN^-
Section *Oxydium* Benth.				
L. monophylla Harv.	1	1	—	—
L. trichopoda (E. Mey.) Benth.	4	4	—	—
L. rostrata Benth.	3	3	—	—
L. acutiflora Benth.	3	3	—	—
L. oxyptera (E. Mey.) Benth.	3	3	—	—
L. stenophylla Eckl. & Zeyh.	5	4	1	—
L. carnea B-E. van Wyk *ined.*	9	—	1	8
L. arenicola Schltr.	5	—	1	4
Section *Lipozygis* (E. Mey.) Benth.				
Part 1: *L. anthylloides* group				
L. anthylloides Harv.	2	—	—	2
L. bolusii Duemmer	3	—	1	2
L. rosea Duemmer	2	—	—	2
L. pentaphylla (E. Mey.) Benth.	2	—	—	2
L. polycephala (E. Mey.) Benth.	5	—	—	5
L. longicephala B-E. van Wyk *ined.*	3	—	—	3
L. brevicaulis B-E. van Wyk	4	—	—	4
Part 2: *L. eriantha* group				
L. eriantha Benth.	4	—	—	4
L. sutherlandii Duemmer	1	—	—	1
L. pulchra Duemmer	1	—	—	1
L. corymbosa (E. Mey.) Benth.	1	—	—	1
L. foliosa H. Bol.	1	—	—	1
L. lanceolata (E. Mey.) Benth.	1	—	—	1
L. procumbens H. Bol.	3	—	—	3
Section *Leobordea* (Del.) Benth.				
L. platycarpa (Viv.) Pichi-Serm.	5	—	—	5
L. furcata (Merxm. & A. Schreib.) A. Schreib.	2	—	—	2
L. stipulosa Bak. f.	4	—	—	4
Section *Leptis* (Eckl. & Zeyh.) Benth.				
Part 1: *L. laxa* group				
L. laxa Eckl. & Zeyh.	6	5	—	1
L. woodii H. Bol.	5	4	—	1
L. humilior Duemmer	3	3	—	—
L. macrosepala Conrath	3	3	—	—
L. curtii Harms	3	3	—	—
L. brachyantha Harms	4	4	—	—
L. serpentinicola Wild	3	3	—	—
L. crumanina Burch. ex Benth.	3	3	—	—
L. burchellii Benth.	3	—	—	3
Part 2: *L. falcata* group				
L. falcata (E. Mey.) Benth.	4	4	—	—
L. fruticoides B-E. van Wyk *ined.*	2	2	—	—
L. brachyloba (E. Mey.) Benth.	5	5	—	—
L. aurea B-E. van Wyk *ined.*	5	5	—	—
L. strigillosa (Merxm. & A. Schreib.) A. Schreib.	1	1	—	—
L. schreiberi B-E. van Wyk *ined.*	1	1	—	—
L. sabulosa Salter	2	2	—	—
L. pachycarpa Dinter *in sched.*	1	1	—	—
L. leptoloba H. Bol.	3	2	—	—
L. maximiliani Schltr.	7	4	—	—
L. pumila Eckl. & Zeyh.	1	1	—	—
L. tenuis Bak.	1	1	—	—
L. linearifolia B-E. van Wyk *ined.*	1	1	—	—

TABLE 3—*CONTINUED*

Groups and species	Number of samples tested			
	Total	HCN^+	HCN?	HCN^-
L. sparsiflora (E. Mey.) B-E. van Wyk *ined.*	4	—	1	3
L. rabenaviana Dinter & Harms	3	1	—	2
L. lenticula (E. Mey.) Benth.	1	1	—	—
L. maculata Duemmer	2	—	—	2
L. pallidirosea Dinter & Harms	2	—	—	2
L. delicata (Bak. f.) Polhill	2	—	—	2
L. pungens Eckl. & Zeyh.	3	—	—	3
L. flava Duemmer	3	—	—	3
Part 3: *L. quinata* group				
L. quinata (E. Mey.) Benth.	4	—	—	4
L. delicatula H. Bol.	3	—	—	3
L. longiflora H. Bol.	3	—	—	3
L. mirabilis Dinter	2	—	—	2
L. magnifica B-E. van Wyk *ined.*	3	—	—	3
Part 4: *L. calycina* group				
L. calycina (E. Mey.) Benth.	4	—	—	4
L. adpressa N. E. Br.	3	—	—	3
L. lupinifolia (Boiss. ex Jaub. & Spach) Benth.	2	—	—	2
L. genistoides (Fenzl) Benth.	1	—	—	1
L. maroccana Ball	2	—	—	2
L. stolzii Harms	3	—	—	3
L. arida Duemmer	3	—	—	3
L. humifusa Burch. ex Benth.	1	—	—	1
L. mucronata Conrath	3	—	—	3
Buchenroedera Eckl. & Zeyh.				
B. amajubica Burtt Davy	3	—	—	3
B. glabrescens Duemmer	2	—	—	2
B. lotononoides Scott Elliot	3	2	—	1
B. meyeri Presl	5	3	—	2
B. multiflora Eckl. & Zeyh.	6	4	—	2
B. sparsiflora Wood & Evans	2	—	—	2
B. tenuifolia Eckl. & Zeyh.				
var. *tenuifolia*	3	3	—	—
var. *pulchella* (E. Mey.) Harv.	3	—	—	3
B. trichodes Presl	3	—	—	3
B. viminea (E. Mey.) Presl	2	—	—	2

of the existing sections) may have to be combined. Similarly, some of the species will probably be reduced to subspecific rank.

Lotononis section *Aulacinthus* consists of woody shrubs with a remarkable similarity to species of *Lebeckia*. This similarity is so marked that a mixed collection comprising flowering twigs of *Lotononis gracilis* and fruiting twigs of *Lebeckia sericea* have, in the past, been designated as a type specimen [7]. All the material of this section reacted strongly positive, while none of the *Lebeckia* species tested appear to be cyanogenic. The Feigl–Anger test allows the rapid identification of vegetative material of these two groups that would otherwise be very difficult.

The section *Krebsia* comprises the only other essentially woody group. Species added to it by Harvey [7] and Duemmer [5] are treated here as separate groups. *Lotononis digitata* and *L. benthamiana* are closely related to *L. quinata* and its allies, traditionally placed in the section *Leptis*. *L. carinata* and *L. hirsuta* are very different from the species of *Krebsia sensu stricto* and are more closely related to species of the *L. calycina* group of *Leptis*. Nearly all the species of *Krebsia sensu stricto* are cyanogenic, while the other two groups are not. The test results

supported the transfer of *L. caerulescens* (previously considered to be a species of *Lebeckia*) to *Lotononis* section *Krebsia* [8].

The section *Telina* is poorly presented in the herbarium record so that the data are not conclusive for some species. It is the only group that is not predominantly cyanogenic or acyanogenic. This may be significant in view of some anomalous species that are included here. *L. minor* should perhaps be transferred to *Krebsia* and the last two species listed show a distinct affinity to the *L. angolensis* group of *Polylobium*. *Telina*, as presently circumscribed, may indeed not be a natural group.

The section, *Polylobium*, is readily divisible into two distinct groups. The first of these, consisting of *L. umbellata* and its allies, is restricted to the winter and all year rainfall areas of the south-western and southern Cape. These species all have a woody, usually subterranean, caudex from which flowering shoots develop annually. Newly described species such as *L. acocksii* are intermediate between this group and the section *Aulacinthus* (both predominantly cyanogenic), indicating that the traditional limits are not longer valid. A suggestion [9] that the anomalous *L. serpens* (previously classified in the monotypic genus *Euchlora* Eckl. & Zeyh.) belongs here is not supported by the results. *L. angolensis* and related species form the second group, which has a summer rainfall distribution in the central and eastern parts of southern Africa and also extends into tropical Africa. All these species have a tendency to produce adventitious roots at the nodes, giving it a stoloniferous appearance. It is also the only group in *Lotononis* where small but well-developed bracteoles are consistently present. Epidermal hairs are virtually absent, but those that do occur are devoid of the striations and tubercles found on the hair surfaces of all other species, with the exception of *L. macrocarpa* and *L. solitudinis*. The latter two also have well-developed bracteoles and are much better placed here than in *Telina*. That this second group of *Polylobium* is acyanogenic is perhaps predictable, since it includes *L. bainesii*, a well-known pasture legume cultivated in many parts of the world. *L. bainesii* was indeed previously also found to be acyanogenic [3].

Lotononis section *Oxydium* includes species that are superficially very similar to species of *Crotalaria*. For this reason, most members of the group were excluded from *Lotononis* in the last revision [5] but it has since been shown [10, 11] that the presumed relationship with *Crotalaria* was based on a superficial characterization. With the exception of two species, this group is cyanogenic, while none of the 17 species of *Crotalaria* tested reacted positively.

Lotononis section *Lipozygis* is kept here in its traditional circumscription, except for the inclusion of *L. procumbens*. It is obviously better placed here than in section *Polylobium*, with which it was previously associated on account of the pseudo-umbellate inflorescences [12]. The section falls naturally into two distinct groups with a winter and summer rainfall distribution, respectively. The first has a distinctive appearance due to the dense rounded inflorescences and prostrate habit. *L. brevicaulis* fits uneasily into this group [13] and further evidence may indicate other affinities, perhaps closer to *L. serpens*. The data indicate that both groups are acyanogenic.

The geographically most widespread section *Leobordea* is easily recognized by the opposite leaves and axillary, subsessile flowers. The species seem similar to the *Lotononis calycina* group of section *Leptis* and these two groups may be more closely related than previously thought. All samples reacted negatively.

Leptis, the largest section, is a poorly defined group, traditionally accommodating annuals and herbaceous perennials that do not seem to fit comfortably elsewhere. Even a cursory examination reveals suits of correlated characters and the section is here divided into four basic groups. The first (all perennial herbs from the central and eastern parts of southern Africa, extending thinly into tropical Africa) is similar to section *Oxydium* in the presence of an acute carina. The second group also has the carina acute as in *Oxydium*, but the species are all annuals with a south-western and western distribution in southern Africa. In these species the claw of the standard is markedly dilated at its base, a character also present in most species of *Oxydium*. The *L. quinata* group comprises short-lived perennials with a prostrate habit and usually digitate leaves. These species are closely related to *L. digitata* and *L. benthamiana* that were previously associ-

ated with the section *Krebsia* on account of the somewhat more woody habit.

Finally, all annuals and herbaceous perennials with an obtuse, usually pubescent carina are gathered in a somewhat poorly defined group. Some species are similar to the *L. eriantha* group of *Lipozygis*, others to the *L. angolensis* group of *Polylobium* and some perhaps also to *Leobordea*. The first two groups, as defined here, are predominantly cyanogenic, while the latter two appear to be totally acyanogenic. The data are therefore in close accordance with presumed affinities as stated above.

The genus *Buchenroedera* shows considerable variation, but four of the nine species tested are cyanogenic. This is roughly the same proportion as in *Lotononis* and would seem to indicate a chemical similarity. Polhill [1] found no consistent diagnostic characters other than the short ovate fruit to separate *Buchenroedera* from *Lotononis* and suggested that the two may not be distinct at generic level. This view is also supported by the presence of the same macrocyclic pyrrolizidine alkaloids in both genera [14, 15].

Conclusions

The data indicate that cyanogenesis in the tribe Crotalarieae is characteristic of *Lotononis* and *Buchenroedera*. Other genera should be tested in more detail, however. The data also support the view that *Buchenroedera* may be no more than a section of *Lotononis*.

Cyanogenesis is a useful taxonomic character in *Lotononis*, since the ability to produce HCN is correlated with patterns of morphological variation. It is clear from the data that the basic groups of *Lotononis* are either cyanogenic or acyanogenic and, furthermore, that the cyanogenic and acyanogenic groups are mutually more closely related. Very few species do not fit this general pattern and some may well turn out to conform if more material from different localities can be tested. The striking pattern that emerged from this survey shows that cyanogenesis may provide supporting evidence for a more natural infrageneric classification of the genus *Lotononis*.

Experimental

Plant materials. Since care was taken to use only very rich collections, some species with poor herbarium records could not be tested and others are inadequately represented. Results obtained for 351 samples of *Lotononis* (129 samples from 41 species tested fresh), 32 samples of *Buchenroedera* and 98 samples of other genera are reported here. Authorities for names are given in Table 3 and are not repeated elsewhere. Species from genera other than *Lotononis* and *Buchenroedera* are not listed individually but have been included in a comprehensive list of voucher specimens. This has been deposited in the Rand Afrikaans University Herbarium.

Procedures. Fresh and dried leaf samples were tested for the presence of HCN using the spot test of Feigl and Anger [16], as modified [17]. This test is highly specific [17] and very sensitive, allowing the detection of only 1 μg HCN [16]. A few leaves (*ca* 0.5 cm^3) were crushed in polytop vials, moistened with deionized water and test strips suspended above the material. A deep blue discolouration, indicating the presence of HCN, usually developed after a few minutes. If no colour change occurred within 12 h, the sample was taken to be acyanogenic. In a few rare cases, only a very slight reaction was observed, usually after several hours. These are indicated by a question mark in Table 3 and interpreted as negative results. The response of fresh samples never differed significantly from dried ones, even after the latter was subjected to freezing at −18°C for 48 h.

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References

1. Polhill, R. M. (1976) *Bot. Syst.* **1**, 143.
2. Watt, J. M. and Breyer-Brandwijk, M. G. (1962) *Medicinal and Poisonous Plants of Southern and Eastern Africa*, 2nd edn, pp. 624 and 1140. E. & S. Livingstone, London.
3. Fikenscher, L. H. and Hegnauer, R. (1981) *Planta Med.* **43**, 323.
4. Conn, E. E. (1981) in *The Biochemistry of Plants* (Conn, E. E., ed.), Vol. 7, p. 479. Academic Press, New York.
5. Duemmer, R. A. (1913) *Trans. Roy. Soc. S. Afr.* **3**, 275.
6. Bentham, G. (1843) *Hook., Lond. Journ. Bot.* **2**, 504.
7. Harvey, W. H. (1862) in *Flora Capensis* (Harvey, W. H. and Sonder, O. W., eds), Vol. 2, p. 47. Hodges, Smith & Co., Dublin.
8. Van Wyk, B-E. (1988) *S. Afr. J. Bot.* **54**, 175.
9. Dahlgren, R. (1964) *Bot. Notiser* **117**, 371.
10. Verdoorn, I. C. (1928) *Bothalia* **2**, 371.
11. Polhill, R. M. (1968) *Kew Bull.* **22**, 169.
12. Bolus, H. (1896) *J. Bot.* **1896**, 18.
13. Van Wyk, B-E. (1987) *S. Afr. J. Bot.* **53**, 161.
14. Van Wyk, B-E. and Verdoorn, G. H. (1988) *Biochem. Syst. Ecol.* **16**, 287.
15. Van Wyk, B-E. and Verdoorn, G. H. (1989) *Biochem. Syst. Ecol.* **17**, 225.
16. Feigl, F. and Anger, V. (1966) *Analyst* **91**, 282.
17. Tantisewie, B., Ruijgrok, H. W. L. and Hegnauer, R. (1969) *Pharm. Weekbl. Ned.* **104**, 1341.