

Studies in the Ericoideae (Ericaceae). VI. The generic relationship between *Erica* and *Philippia* in southern Africa

E. G. H. OLIVER*

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ABSTRACT

Problems in placing certain species satisfactorily in *Philippia* or *Erica* have led to an investigation of characters delimiting the genera mainly in southern African species. The only character used in placing problem species was partial versus total recaulescence of the bract. This separation breaks down completely in a few species in which ericoid and philippioid flowers occur within the same inflorescence. Not all species of *Philippia* are closely related, some being more closely related to various sections within *Erica*. It is evident that *Philippia* is an unnatural polyphyletic group. It is concluded that *Philippia* should be placed in synonymy under *Erica*.

UITTREKSEL

Probleme met die bevredigende plasing van sekere spesies in *Philippia* of *Erica* het gelei tot 'n ondersoek na die kenmerke wat die genusse hoofsaaklik by spesies in suidelike Afrika omgrens. Die enigste kenmerk wat gebruik is om probleemspesies te plaas, is gedeeltelike teenoor totale rekaulesens van die skutblaar. By 'n paar spesies met erikoïede en philippioidede blomme in dieselfde bloeiwyse, verval hierdie onderskeid eger heeltemal. Nie alle spesies van *Philippia* is naverwant nie; sommiges is nader verwant aan verskeie seksies van *Erica*. *Philippia* word beskou as 'n onnatuurlike polifiletiese groep. Daar word voorgestel dat *Philippia* onder *Erica* in sinonimie geplaas word.

CONTENTS

Introduction.....	1
Morphology.....	2
Analysis.....	6
<i>Philippia</i>	6
<i>Erica</i>	6
Species outside southern Africa.....	8
Phylogeny of the genus <i>Philippia</i>	8
Conclusions.....	9
Acknowledgements.....	9
References.....	9

INTRODUCTION

Philippia is a widespread genus of ± 65 species native to Africa and the Madagascan region. *Erica* occurs from the Cape to northern Europe and consists of ± 660 species, 98 % of which occur in the Cape. Work in progress on the genera of the subfamily Ericoideae for the *Flora of southern Africa* has revealed problems of generic delimitation within this highly diversified group of approximately 800 species. One such problem area lies between the extremely large genus *Erica* and the small genus *Philippia*, with 636 and 15 species respectively within the southern African region.

The genus *Philippia* was described by Klotzsch (1834) who distinguished it from *Erica* on the possession of an unequal calyx. Ever since then the genus has been universally upheld. *Philippia* is a pan-African genus of

some 65 species with the majority (± 40 species) occurring on Madagascar (Figure 1).

Erica is distinguished from *Philippia* by having a single bract, two bracteoles and a calyx consisting of four more or less equal segments or lobes. This applies to the vast majority of the ± 660 species in the genus. *Philippia*, on the other hand, is generally described as having 'no bract nor bracteoles and a zygomorphic 4-partite or 4-lobed calyx', a condition found in most of the species in the genus.

The first indication of any problems regarding the distinction between *Philippia* and *Erica* was given by Alm & Fries (1927a: 8) in the only complete revision of the genus *Philippia*. They noted 'In der Tat finden wir bei der Gattung *Erica* noch derartige Übergangsformen', and further on (p. 36) 'Diese beiden Arten [i.e. *P. keniensis* S. Moore and *P. jaegeri* Engl.] stellen darum fast Übergangstypen zwischen den Gattungen *Philippia* und *Erica* dar.'. Nevertheless, in this revision and the revision of the genus *Erica* in tropical Africa (Alm & Fries 1927b) they retained both genera. No problems were recorded in distinguishing *Philippia* from *Erica* in southern Africa until the present revisionary work during which species were carefully examined and evolutionary relationships were sought within *Erica*. Investigations have revealed a complete series of intermediates within a few species.

In the African Ericoideae only *Erica*, *Philippia*, *Blaeria* L. and *Ericinella* Klotzsch possess a multiseeded dehiscent capsule. The genus *Philippia* seems likely to have evolved from ancestral stock related to *Erica* section *Arsace* (Alm & Fries 1927a; Pichi-Sermolli & Heiniger 1953), and the majority of species in southern Africa are related to this section. However, two species, *P. stokoei* and *P. pallida*, are clearly allied to *Erica* species in other sections.

* Botanical Research Unit, P.O. Box 471, Stellenbosch 7600.

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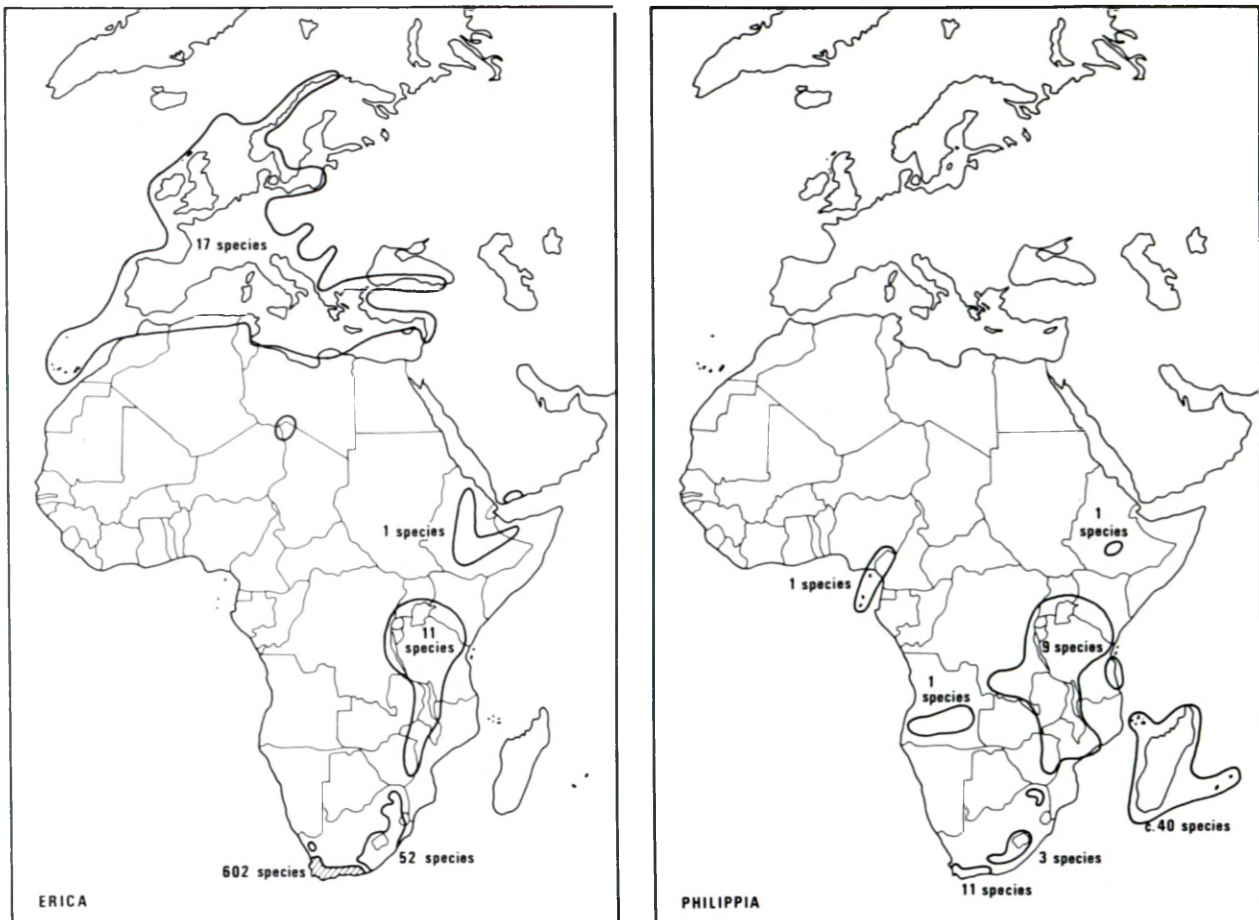


FIGURE 1.—Maps showing the approximate distribution of the genera *Erica*, left, and *Philippia*, right.

MORPHOLOGY

Alm & Fries (1927a) pointed out that in *Erica* and *Philippia* the bract is recaulescent on the pedicel (Figure 2). This is a well known occurrence in the Angiospermae (Weberling 1981: 228). However, Alm & Fries postulated that the bract fused with the abaxial sepal—'Wir halten es für sehr wahrscheinlich . . . [dass] die unpaarige untere Bractee . . . mit dem vorderen Kelchblatte verschmolzen [ist]' (their floral diagram, 3.c, clearly shows this feature). They continued 'Denkbar, aber sehr unwahrscheinlich ist, dass das vordere Kelchblatt vollständig reduziert worden ist.'. Pichi-Sermolli & Heiniger (1953: 35), on the other hand, referred to the recaulescent bract as the fourth calyx segment, which in *Philippia* is replaced by the bract which has undergone a 'phyletic slide' upwards and has become part of the calyx. Ross (1957: 735) found clear evidence that in *Philippia* at least, the zygomorphic calyx has arisen by the migration of bracts up the pedicel, followed by their fusion with the calyx, but he did not give any evidence to

support his view of fusion. Friedmann (1981: 6) held the same opinion as Pichi-Sermolli & Heiniger in his revision of the Ericaceae in the Flore des Mascareignes having found that some abnormal flowers in *P. abietina* Klotzsch show transitions indicating that the major sepal is in fact the modified floral bract and later on (p. 8) 'le sépale destiné à être remplacé par la bractée a déjà regresse totalement'.

I would support the opinion of Pichi-Sermolli & Heiniger and of Friedmann that the totally recaulescent bract does suppress the abaxial sepal and takes over its position and 'function'. No anatomical investigations have been carried out to support this view but I have observed morphological variation which suggests it, particularly in *E. peltata* Andr. in which there may sometimes be a thin, hair-like abaxial sepal on the inside of the recaulescent bract (Figure 5.4). A similar situation was noted by Pichi-Sermolli & Heiniger in their *P. abyssinica*. In another genus, *Coilostigma* (*C. glabrum* Benth.), various stages in reduction of the abaxial sepal are often

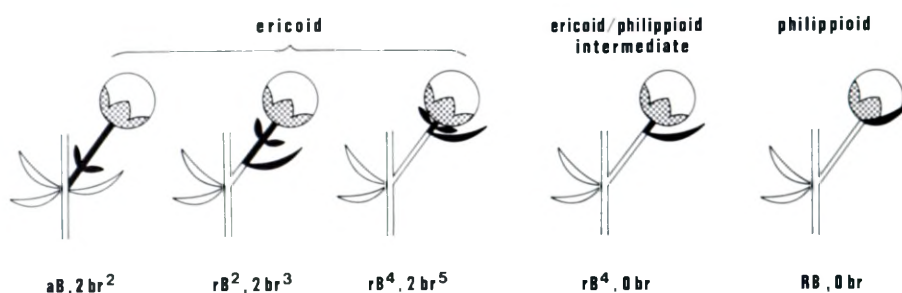
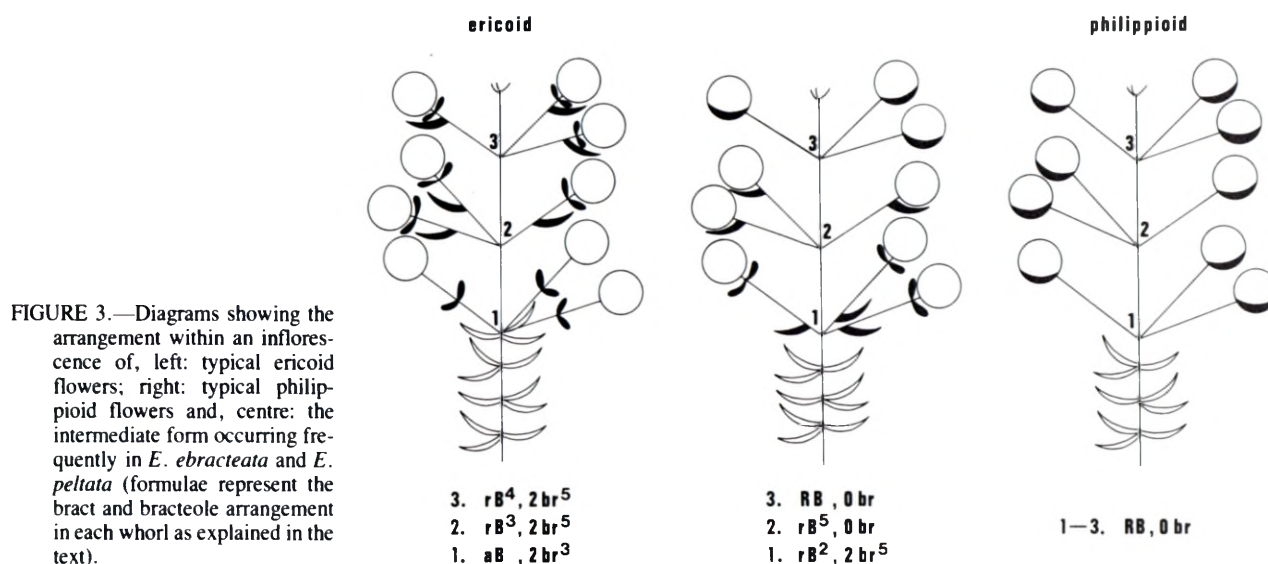


FIGURE 2.—Series of diagrams showing stages in the recaulescence of the bract up the pedicel in the Ericoideae from axial on the left to totally recaulescent on the right (formulae represent each stage and are explained in the text).



clearly visible. In its calyx, this is the most variable species in the subfamily as it often has the adaxial sepal reduced as well (Oliver 1987a).

Additional evidence to support this opinion was noted by Pichi-Sermolli & Heiniger (1953: 35) in their *P. abyssinica*, which they stated exhibits a very characteristic dimorphism of the calyx. The peripheral flowers of an inflorescence have a regular calyx and a single foliar bract lower down on the pedicel whereas the central or upper flowers have a zygomorphic calyx with a totally recaulescent bract. There is thus a complete gradation series in the recaulescence of the bract within a single inflorescence. I have found this gradation occurring in a number of inflorescences of *E. ebracteata* H. Bol. from the Natal Drakensberg, of *E. peltata* from the southern Cape Province (Figure 3) and frequently in *Coilostigma glabrum* (Oliver 1987a).

It has always been stated that, when the bract is totally recaulescent, the two bracteoles (prophylls) are missing or absent. Nobody has queried this statement or discussed the fate of these two organs. In my investigations of *E. peltata* I have come to the conclusion that the bracteoles do not disappear but also become part of the calyx. A paper on the fate of the bracteoles is in preparation (Oliver in prep. b).

In the typical philippoid condition the bract is fully recaulescent up the pedicel, totally suppressing the abaxial sepal and fusing with the calyx, in some cases to such an extent that it is difficult to distinguish it as not being a sepal, as in *P. simii* H. Bol., *P. irrorata* E. G. H. Oliver and *P. procaviana* E. G. H. Oliver (Figure 4.1–4.3). Ross (1957: 738), however, stated that in the east African species with flowers of the philippoid type, the bract-like calyx lobe is always free to the base and never fused with the others. He added that it is never inserted at the same level as the other segments but is always at least slightly lower. This occurs in the southern African *P. stokoei* L. Guthrie, *P. drakensbergensis* E. G. H. Oliver, *P. pallida* L. Guthrie and *P. alticola* E. G. H. Oliver (Figure 4.4–4.7). On the other hand, the bract is often slightly to considerably larger than the other lobes of the calyx resulting in an unequal or zygomorphic calyx (Figure 5.1–5.3, *P. evansii* N.E. Br.).

This condition is found in a number of genera in the Ericoideae other than *Philippia*: *Ericinella*, the *Salaxis* Salisb.—*Coccosperma* Klotzsch—*Scyphogyne* Brongn. complex, *Coilostigma* Klotzsch and the unique monotypic *Nagelocarpus* Bullock. Except for the single species *Ericinella microdonta* (C.H. Wr.) Alm & Fries, these genera are all Cape endemics.

It is therefore clear that the abaxial 'sepal', which is often enlarged and separate from the rest of the calyx in the species of *Philippia* and also of *Ericinella*, *Coilostigma*, *Salaxis*, *Coccosperma*, *Scyphogyne* and *Nagelocarpus*, is homologous with the bract in *Erica*. The bract thus exhibits three character states: nonrecaulescent (axial), partially recaulescent and totally recaulescent.

In the distinction between *Philippia* and *Erica*, Alm & Fries (1927a: 36) made use only of the actinomorphic versus zygomorphic calyx and glossed over those species that have some flowers with the intermediate condition.

Phillips (1944) re-examined the Ericaceae for the revision of his *The genera of South African flowering plants* (1951) and came to the conclusion that not more than eight genera could be justified. He sank numerous genera into what I regard as heterogeneous assemblages. *Philippia* was combined with *Blaeria* and *Ericinella*, a very valid step, but was kept separate from *Erica*, whereas *Thamnus* and *Coccosperma* were included solely on the basis of ovary and stamen complement. The last two are, however, very distinct unrelated genera with indehiscent fruits. Phillips did not consider there to be any close relationship between *Erica* and *Philippia*. His work was never seriously considered by subsequent workers and was not taken up in herbaria.

Ross (1957), in preparing the account for the *Flora of tropical east Africa*, published some detailed notes on the genus *Philippia* in which he not only dealt with the taxonomic problems of species restricted to that area, but he also considered generic limits within the whole tribe. He pointed out several problems, but under the section dealing with the concept of the genus he did not discuss the relationship of *Philippia* and *Erica*. He retained them as distinct genera and in his key gave the following differentiating characters:

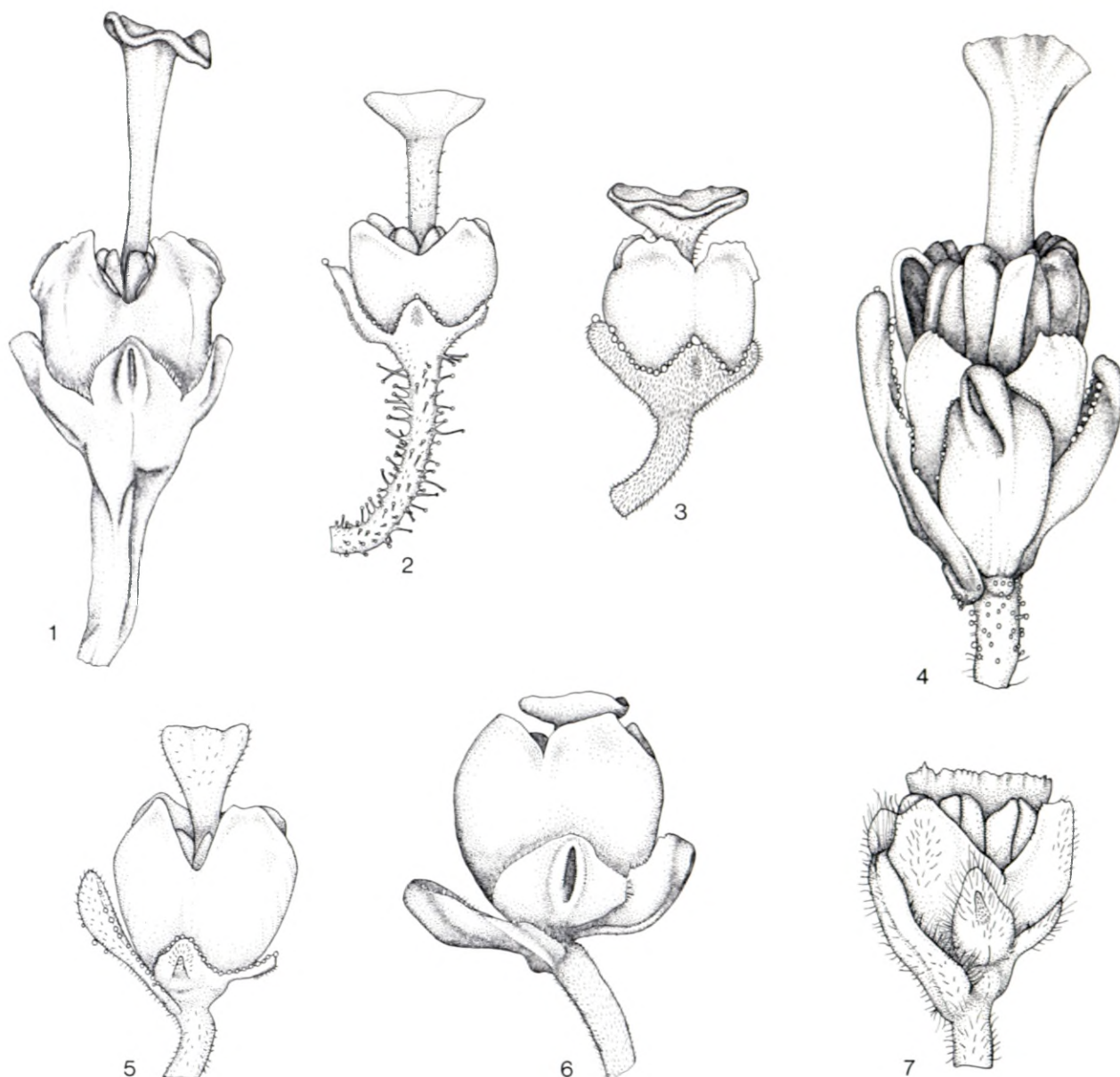


FIGURE 4.—Flowers of *Philippia* showing the bract (on left hand side of each flower) totally recaulescent and fused to lateral sepals in 1, *P. simii*; 2, *P. irrorata*; 3, *P. procaviana*; showing the bract (on left hand side of each flower) almost totally recaulescent and free from lateral sepals in 4, *P. stokoei*; 5, *P. drakensbergensis*; 6, *P. pallida*; 7, *P. alticola*; all drawn $\times 20$ from type material (BOL, STE).

*Pedicels with one or more bracts and calyx actinomorphic in all flowers *Erica*
 Pedicel without bracts and calyx with one sepal larger than the others in many or all flowers *Philippia**

However, he did mention the problem of the placing of certain specimens of *P. trimera* Engl. and *P. keniensis* S. Moore which exhibit variation in the bract/calyx relationship (see later in this article).

For the species occurring in the area covered by the *Flora Zambesiaca* there appear to be no problems with generic distinctions, as Ross (1983: 157) mentioned none under the generic or specific treatments. However, in the key he noted for *Erica*, 'bract, and often bracteoles, present on pedicel', which indicates that he regarded material with only the partially recaulescent bract present as belonging to *Erica*, but in his earlier work (1957: 38) he regarded material having equal proportions of one bract and no bract as belonging to *Philippia*. He noted that all the populations having these proportions

also agree with all other species of *Philippia* in having a disciform stigma and anthers without appendages, and furthermore, the anthers are united before dehiscence and united anthers occur in a number of species of *Philippia*. He thus implied that these were characters he used to define the genus.

Pichi-Sermolli & Heiniger, in upholding *Philippia* for their highly variable species *P. abyssinica*, stated (1953: 35) that, even if typical actinomorphic flowers are found in the Abyssinian plant, the presence of zygomorphic flowers and, at the same time, the shape of the terminal part of the style head 'lead us confidently to refer this species to the genus *Philippia*'.

The use of the above additional characters to distinguish *Philippia* from *Erica* is rejected on the grounds that they also occur within the genus *Erica*. The enlarged terminal portion of the style is an adaptation to wind pollination (Rebello *et al.* 1985) and occurs in 5% of the

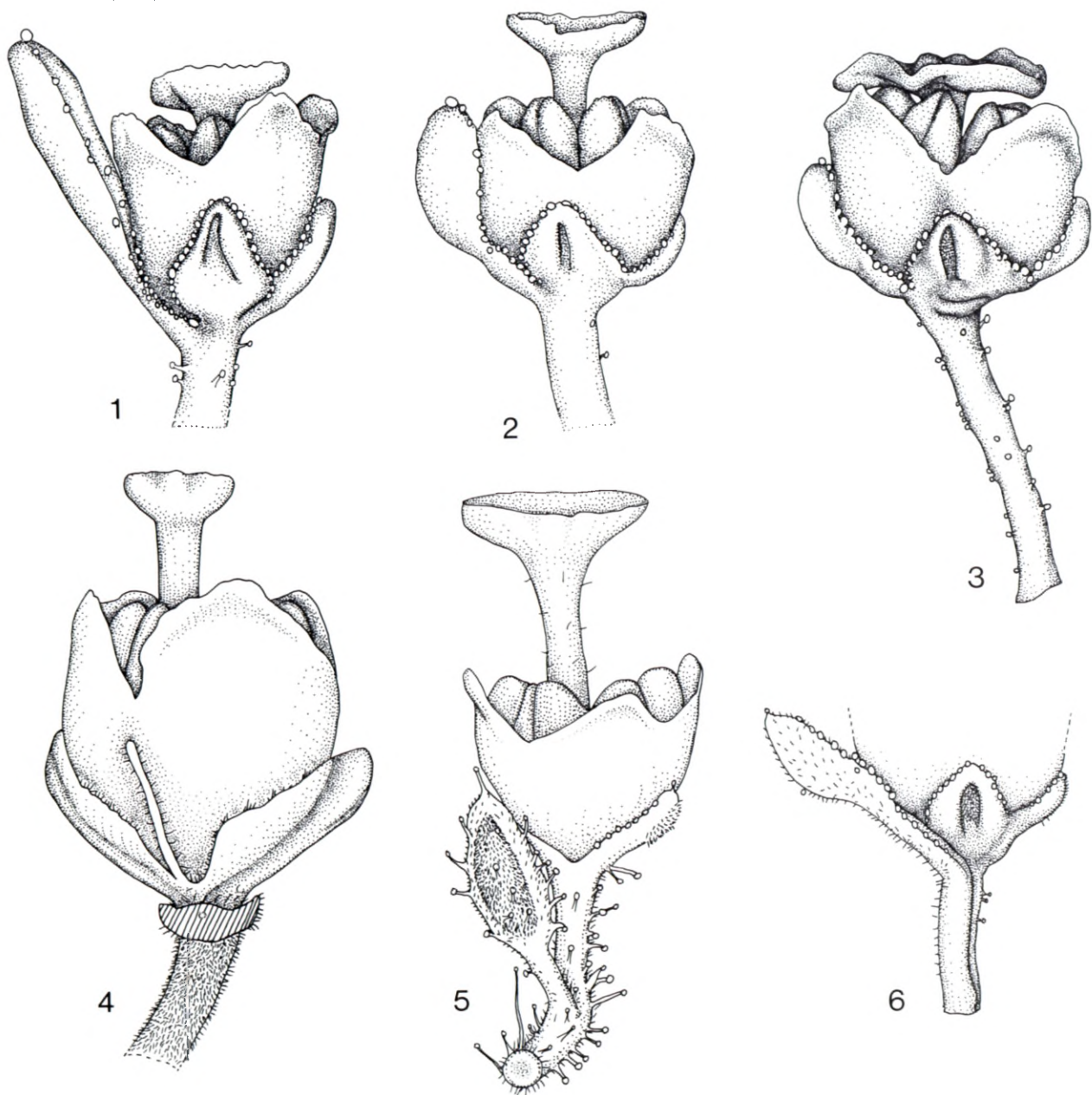


FIGURE 5.—Flowers of *Philippia* (with bract on left hand side of each flower): 1, 2 & 3 showing variation in size of the totally recaulescent bract in *P. evansii* from (1) Killick 1527, (2) Edwards 2163, (3) an isotype, Evans 62 (all PRE); 4, showing a partially recaulescent bract in position rB^5 (hatched) removed to reveal the reduced and hair-like abaxial sepal in *E. peltata* from Oliver 8815 (STE), (compare with Figure 4.6); 5, showing a partially recaulescent bract in the position rB^2 , and with the abaxial sepal suppressed, in *P. irrorata* from the type (STE); 6, showing recaulescence of the bract up the pedicel in an unusual flower of *P. drakensbergensis* from Oliver 8394 (STE); all drawn $\times 20$.

426 species of *Erica* occurring in the south-western Cape Province. This pollination syndrome of small flowers, a large cyathiform to peltate stigma and the absence of conspicuous nectaries, although not restricted to the section *Arsace*, is typical of that section. It is also found in all species of the genera *Salaxis*, *Coccosperma*, *Scyphogyne* and *Nagelocarpus*.

In all species of Ericoideae the anthers are united before anthesis and in the ornithophilous and entomophilous species often remain adhering until disturbed by the pollinator when an explosive separation causes the pollen to be dispersed (Rebello *et al.* 1985). There are a few species of *Erica*, notably *E. embothriifolia* Salisb. (with long tubular flowers), *E. coronanthera* Compton and *E. syngenesia* Compton, in which the anthers remain fused together. Within the genus *Philippia*, Alm & Fries

(1927) list 17 of the 40 species as having free anthers. In southern Africa 12 of the 15 species have free anthers although some have filaments slightly joined at their bases.

The above additional characters, used to justify the separation of variable intermediate specimens, are therefore of no value in generic delimitation between *Erica* and *Philippia*.

A detailed examination of bract recaulescence in the southern African species was undertaken to ascertain the situation prevailing in the genus there and to assess the validity of the generic boundaries.

A formula has been developed to express in short simple terms the number and arrangement of the bract, bracteoles and calyx within the genera and species of Ericoideae: **B** represents the bract; **br** the bracteoles; **a**

indicates that the bract is axial (situated on the main axis); *r*, that the organs are partially recaulescent with the indices¹⁻⁵ indicating the position up the pedicel (1 at the base, 5 at the top); and *R*, fully recaulescent; *K* represents the calyx. Thus the structure of a typical *Erica* (ericoid) flower can be indicated by the formula $aB-rB^{1-5}, 2br^{2-5}, 4K$ and that of a typical *Philippia* (philippioid) flower by the formula $RB, 0br, 3K$ or just $RB, 3K$ (Figures 2 & 3). This is an elaboration of the 'formula' briefly mentioned by Ross (1957: 738).

The question arises whether any deviations from these basic formulae exist. Indeed, within *Philippia* some flowers occur in which the bract may suppress the abaxial sepal but is free from the calyx (Figure 4.6, *P. pallida*) and even as low down the pedicel as $rB^3, 3K$ (Figure 5.4, *P. irrorata*); some flowers may even be $rB^{3-5}, 4K$ which also occurs in some species of *Erica* (see later). This is clearly an intermediate *Erica/Philippia* condition. A detailed analysis of these bract/bracteole-/calyx conditions in *Erica* and *Philippia* was made and the results are discussed below.

ANALYSIS

Philippia

The majority of species occurring within southern Africa are typical of the genus in having a fully recaulescent bract forming a zygomorphic calyx represented by $RB, 3K$; these are *P. leeana* Klotzsch, *P. absinthoides* (Thunb.) E. G. H. Oliver, *P. evansii*, *P. notholeana* E. G. H. Oliver, *P. elsieana* E. G. H. Oliver, *P. irrorata*, *P. procaviana*, *P. alticola*, *P. petrophila* E. G. H. Oliver, *P. esterhuyseniae* E. G. H. Oliver and *P. drakensbergensis* E. G. H. Oliver. This formula does hold in all except a few flowers. The remaining three species, *P. pallida*, *P. stokoei* and *P. tristis*, showed highly significant variations (Table 1).

P. pallida L. Guthrie

Until recently this species was known only from the type collection from near Riversdale (Muir 2542 in BOL*) and this is unfortunately in the bud stage. The taxon is not closely related to any species within *Philippia*. During an examination of the type it was recognized as being identical to *Erica peltata* Andr. which occurs along the foothills of the mountain ranges from Riviersonderend to George. An analysis of 269 flowers from a selection of 15 collections of this species in STE provided a ratio of 22% ericoid: 38% ericoid/philippioid: 40% philippioid flowers. An analysis was then made of 900 flowers from three well separated populations (Oliver 8736, 8737 & 8815 in STE). These showed considerable variation with the above ratios being 16:40:40, 3:30:67 and 0:38:68 respectively. In the last population one would probably not hesitate to label the plants as belonging to *P. pallida*. The various flower types were found to be randomly scattered in inflorescences, occasionally with all three represented in one inflorescence.

P. stokoei L. Guthrie

This species is very localized on the low mountains and hills of the western part of the Bredasdorp District. It

has no close relatives within *Philippia* but was found to have been described as *E. accommodata* Klotzsch var. *ebracteata* H. Bol. (Guthrie & Bolus 1905). Material of the species was thus filed under two separate genera in herbaria. The taxon bears some resemblance to *E. accommodata* Klotzsch, which inhabits the high mountains of the Riviersonderend Range. It is, however, remarkably similar to *E. lasciva* Salisb. of the Cape Town and Bredasdorp Districts, which species shows no signs of any bract/bracteole irregularities. An analysis of several collections of *P. stokoei* (250 flowers) in STE provided a ratio of 0:50:50 with not a single flower having the ericoid condition. The only difference between *P. stokoei* and *E. lasciva* is in the absence of bracteoles versus two bracteoles, otherwise the two taxa are identical in shape, size, indumentum and texture of the flowers and vegetative parts.

P. tristis H. Bol.

This species was known only from the type collection made by Bolus in 1877 in the mountains near Graaff-Reinet in the central Karoo (Bolus 2594 in BOL, K). The specimen in BOL has flowers that are in fruit, but it can be seen that they are mostly of the $RB, 3K$ type with a few $rB, 0br, 4K$. A capsule included on the type sheet in BOL containing a very small specimen collected farther east by Weale, appeared to be identical but had flowers of the $rB, 0br, 4K$ type which would indicate its being an *Erica/Philippia* intermediate following the definition as given above.

I was sent for comment, several new taxa of *Erica* from the north-eastern Cape and Natal by Dr O. M. Hilliard and Mr B. L. Burt who intended describing them for their work on the flora of the southern Drakensberg. The material of *P. tristis* was recognized as being very similar to one of their species, *E. caespitosa* Hilliard & Burt. This problem will be discussed later under *Erica*.

Erica

E. hispidula L./*E. inops* H. Bol.

E. hispidula is probably the commonest species of *Erica* in the Cape Floral Region occurring from the Cape Peninsula eastwards to the George District and forming dense stands on mountain slopes. A survey of 1000 flowers from numerous collections (BOL, NBG, STE) covering the distribution range east of the Cape Peninsula provided convincing evidence that it belonged to *Erica*: it has a ratio of 100:0:0, i.e. all flowers examined were of the $rB^{1-3}, 2br^{2-4}, 4K$ type.

There is, however, a problem on the Cape Peninsula where the species *E. inops* occurs. This species was separated from *E. hispidula* (Guthrie & Bolus 1905; Salter 1950) solely because of its possession of a bract but no bracteoles, i.e. it had the formula $rB, 0br, 4K$, the ericoid/philippioid condition. The problem populations exist on Constantiaberg. Here an examination of *E. hispidula* (Baker 992 in BOL) showed that the flowers had a formula rB^{1-3} and $2br^{3-5}$ or $1br^{4-5}$ or even $0br$, all with $4K$; 110 flowers from all the other specimens had a ratio of 55:45:0. A collection of *E. inops* (Baker 791 in BOL) had the ratio 0:23:77 and 291 flowers from other collections 87:13:0, suggesting that some of them were *E.*

* Abbreviations follow those listed in Holmgren, Keuken & Schofield, *Index Herbariorum*, Regnum Vegetabile 106 (1981).

hispidula. An examination of 1370 flowers of my own collection on Constantiaberg (Oliver 8741 in STE) produced the ratio 3:96:1. It has been concluded from these findings that the two species should be merged.

E. ebracteata H. Bol.

The very name of this species points to the generic problem. It is a species confined to the Natal Drakensberg. A survey of 238 flowers from 15 specimens (PRE) gave a ratio of 11:46:43 similar to that found in *E. peltata* and indicates that 43% of the flowers on the collections were in fact philippioid flowers and 46% intermediate and only 11% ericoid. In this species the variation from partially to totally recaulescent bracts often occurs within a single inflorescence (Figure 3).

Erica taxa described by Hilliard & Burt (1985)

In personal communications with the authors, prior to the publication of their paper, I pointed out the problem existing between *Erica* and *Philippia*, which was highlighted by several of their new taxa (see also Hilliard & Burt 1985). I have been able to examine their cited material and some additional collections.

E. caespitosa Hilliard & Burt

This species is widespread in the eastern parts of the country from Somerset East in the Karoo region to the Drakensberg of the north-eastern Orange Free State. A survey of 256 flowers from 10 collections (BOL, NU, STE) gave a ratio of 3:83:14. The philippioid condition was confined to a few scattered collections, one of which, *Ruddock* 55 in NU, had only RB,3K flowers. This latter collection possessed flowers identical to those of *P. tristis* mentioned earlier.

E. anomala Hilliard & Burt

The specific epithet was chosen to indicate that the flowers were not typical of *Erica*. A survey of 100 flowers from 5 collections in NU gave a ratio of 0:40:60 indicating that the majority were of the philippioid type. The species is in fact no more anomalous than the others referred to in the present paper. It is also peculiar in having coherent anthers which are exerted in a ring around the style in the fruiting stage.

E. dissimulans Hilliard & Burt

Like *E. anomala* this species is confined to the Natal Drakensberg. A survey of 160 flowers from 7 collections in BOL and NU gave a ratio of 2:98:0.

Flora capensis

A survey of the descriptions of the species of *Erica* listed in *Flora capensis* (Guthrie & Bolus 1905) was made to see if there were any other species with similar irregularities. (Note that in that work no distinction is made between the bract and the bracteoles, all being referred to as bracts).

E. alticola Guth. & Bol.

This very rare species, probably confined to the eastern Transvaal near Barberton, is described as having 'bracts variable, mostly entirely absent, occasionally 2, sometimes one only'. An examination of the type collection (Bolus 7678 in BOL) showed that the flowers are

very variable, most of the visible ones having the formula aB,0br,3K. Two flowers have aB,2br³,4K and a few have rB²⁻³,0br,4K or rB⁵,0br,4K-RB,3K. Too few flowers were available for this species to be included in Table 1.

TABLE 1.—Distribution of bract/bracteole/calyx characters in nine species of *Erica* (Ericoideae) in southern Africa*

Species	<i>Erica</i> rB,2br,4K	<i>Erica/Philippia</i> rB,0br,4-3K	<i>Philippia</i> RB,3K
<i>E. anomala</i>	0	40	60
<i>E. dissimulans</i>	2	98	0
<i>E. caespitosa</i> (= <i>P. tristis</i>)	3	83	14
<i>E. hispidula</i> **			
<i>sensu stricto</i>	100	0	0
Constantiaberg	55	45	0
<i>E. inops</i> †			
Oliver	3	96	1
Baker	0	23	77
Others	0	87	13
<i>E. ebracteata</i>	11	46	43
<i>E. lasciva</i> (= <i>P. stokoei</i>)	100 (0)	0 50	0 50
<i>E. peltata</i> ‡ (= <i>P. pallida</i>)			
Ashton	16	40	44
Swellendam	0	38	62
Niekerkshek	3	30	67
Others	22	38	40
<i>E. sparsa</i>			
Fourcade	3	89	8
Keet	0	100	0

* Figures express the percentage of flowers in the samples referred to in the text and Table.

** *E. hispidula*, *sensu stricto*, refers to the non-varying populations outside of the Cape Peninsula; Constantiaberg refers to the collections from that mountain.

† *E. inops*: collections Oliver 8741, Baker 791 and all other collections.

‡ *E. peltata* (= *P. pallida*): collections from Ashton (Oliver 8815), Swellendam (Oliver 8737) and Niekerkshek (Oliver 8736) and 15 other collections from the complete range of the species.

E. woodii H. Bol.

This widespread species in the eastern parts of the country is described as having 'flowers mostly axillary, solitary, bracts remote, small, occasionally one wanting'. There is in fact always one bract and two bracteoles, but the bract is large and axial in position appearing like a normal leaf, thus the formula is aB,2br²⁻⁴,4K.

E. leucopelta Tausch

This similarly widespread species is described with 'bracts remote, mostly 3, one rather large and 2 usually small or very minute, or perhaps sometimes wanting'. The bracteoles are always present and the bract is either aB or rB¹.

E. subverticillaris Diels ex Guth. & Bol.

This species is very rare and known from only two collections in the Drakensberg of the eastern Transvaal. It is described as having 'bracts, one foliaceous, two minute or often wanting'. Davidson (1985) in separating off var. *revoluta* as a distinct species, *E. revoluta* (H. Bol.) Davidson, noted that *E. subverticillaris* has 'brac-

teoles 2, or absent, basal to median, hairlike'. It therefore possesses flowers with the intermediate ericoid/philippoid condition in addition to the normal ericoid ones.

E. sparsa Dulfer (= *E. floribunda* Lodd.).

This species is common on the coastal flats of the southern Cape. No indication of any irregularities is given, but during routine examination of herbarium material it was found that variation does occur. Most specimens appear to have $rB^{2-5}, 2br^{3-5}$. An examination of 63 flowers of *Fourcade 5010* (STE) revealed that the collection possessed 56 flowers with the $rB^{2-5}, 0br, 4K$ condition, 2 with $rB^1, 2br^1$ and 5 with RB , whereas the 63 flowers of *Keet 703* (STE) all had the $rB^{3-5}, 0br$ condition. This is very similar to the situation found in *E. peltata* which is placed in the same section.

SPECIES OUTSIDE SOUTHERN AFRICA

A brief reference to material of *Philippia* (BOL. MO & PRE) and to literature on the Ericoideae in tropical Africa (Alm & Fries 1927; Ross 1957; Pichi-Sermolli & Heiniger 1953), in Madagascar (Perrier de la Bathie 1927) and on the Mascarene Islands (Friedmann 1981) revealed a similar variation in the bract/bracteole/calyx arrangement as outlined above for southern Africa, but perhaps only to the same degree in the east African *P. keniensis* S. Moore and *E. kingaënsis* Engl.

Ross (1957: 739) gave a table analysing some 49 collections of the former species and from this table the ratio 0:34:66, of different flower types can be deduced, the 34% having the formula $rB?, 0br, 3K$ (position of bract not given by Ross). The problem is also reflected in the history of one species, first described as *P. elgonensis* Mildbraed (Mildbraed 1922), transferred to *Erica* by Alm & Fries (1927a) and back to *Philippia* (Ross 1957) as *P. keniensis*, subsp. *elgonensis* (Mildbraed) R. Ross.

Ross also mentioned (1957: 738) an intriguing variant of *P. trimera*. He examined 39 gatherings of that species from Ruwenzori and found no ericoid flowers. However, he noted that in some collections, notably *Frédéricq 9325*, the 'bract-like segment of the calyx' was inserted on the pedicel as much as 1.0 mm below the calyx which was always of the 3K type. Sometimes he found 'as well as the normal ones (sepals) two narrower ones flanking the gap on either side'. These in my opinion are the two bracteoles giving the formula $rB?, 2br^5, 3K$ (position of bract not given by Ross) which is virtually the formula for many species of *Erica*. In my investigations of *E. peltata* I have found a similar situation. A paper setting out my views on the fate of the bracteoles in flowers with a totally recaulescent bract, derived from investigations of this species, is in preparation (Oliver in prep.b).

In writing about the very widespread *E. arborea* and its allies in Africa, Ross (1956) found that many of the collections in east Africa, which had previously been allocated to separate species, belonged to one highly variable species, *E. kingaënsis*. One of the variable characters was the presence or absence of the two bracteoles. He did not mention the problem of the relationship with *Philippia* and retained the following under this species:

subsp. *kingaënsis*—upper bracts often absent ($rB, 0-2br$);

subsp. *rugegensis*—upper bracts always present ($rB, 2br$);

subsp. *bequaertii*—upper bracts present or absent ($rB, 0-2br$).

In the collections by Osmaston from Ruwenzori, Ross noted that all the flowers examined lacked upper bracts. Therefore some of the material of this species has flowers with the same formula as those in *P. keniensis*, mentioned above.

PHYLOGENY OF THE GENUS PHILIPPIA

In the subfamily Ericoideae only *Erica*, *Philippia*, *Blaeria*, *Ericinella* and *Bruckenthalia* Salisb. possess a multiseeded dehiscent capsule. *Erica* is widespread in Europe and Africa whereas *Bruckenthalia* is a monotypic genus confined to the south-eastern highlands of Europe. The other three genera are endemic to the African continent (including Madagascar for *Philippia*) where they are widespread, more so than is *Erica*. The remaining 20 genera of the subfamily are confined to the southern tip of Africa and are characterized by a variety of types of indehiscent fruit coupled with a reduction in the complement of floral parts.

The relationships within this group of capsular genera are very close, with generic distinctions being based on the flimsiest of morphological characters. They indicate that these genera have arisen from some ancestral ericoid stock: *Philippia* by the total recaulescence of the bract; *Blaeria* by the reduction in the number of stamens and *Ericinella* by a combination of both processes.

In the southern African representatives of *Philippia*, relationships for the majority of species occur within the section *Arsace* of *Erica*. This section is found throughout Africa and Europe and includes the most widespread species of *Erica*, *E. arborea* L., which is regarded (Hansen 1950) as the most primitive of the European species based on architecture and inflorescence structure. The section is characterized by the small corolline urceolate to cyathiform flowers, mostly dull white or greenish in colour, and a relatively large expanded and exerted stigma which is developed for wind pollination. The flowers being corolline means that the calyx is small, relative to the corolla and is composed of foliar sepals. These characters place the section in the subgenus *Eurica*.

Two species of *Philippia*, *P. stokoei* and *P. pallida*, have been found to be conspecific with two species of *Erica*: *P. stokoei* with *E. lasciva* and *P. pallida* with *E. peltata*. In these two taxa the calyces are different from those in sect. *Arsace*: they are not small and foliar in character. The two species are placed in different subgenera because of the shape of the corolla and form of the calyx. *E. lasciva* is placed in the subgenus *Chlamydanthe* section *Elytrostegia* because of its calycine flowers with the bracts and sepals relatively large and cartilaginous and the stamens exerted. *E. peltata*, on the other hand, is placed in the subgenus *Platystoma* section *Polycodon* which is characterized by broadly cyathiform corollas and broader, more prominent concolorous sepals. Both sections contain species adapted to wind pollination, i.e. with an expanded stigma (Rebello *et al.* 1985). I

consider the expanded stigma in these two species as the result of convergent evolution in the pollination syndromes.

Alm & Fries (1927b: 8) regarded section *Arsace* in *Erica* as containing some species that can be described as 'Ur-Philippien' (proto-philippias). They stated that there can be no doubt about the origin of *Philippia*. However, later on (1927: 11), in discussing the relationships within the section *Euphilippia*, on the grounds that one cannot see close relations between the species in the southern and eastern regions of Africa and those of Madagascar and the Mascarenes, they stated 'kann es nicht ohne weiteres angenommen werden, dass die Section einen einheitlichen Ursprung habe'. They believed that the Madagascar/Mauritian species and the African species had a polyphyletic origin whilst the African species were monophyletic, but earlier on the same page they stated clearly that they could not find any close relationship between the Madagascar/Mauritian species and the continental species nor between the tropical African and the Cape species.

Pichi-Sermolli & Heiniger (1953: 36) supported the hypothesis of Alm & Fries that *Philippia* 'branched off' from the section *Arsace*. They regarded their aberrant ericoid *P. abyssinica* as the species most closely related to *Erica* and, being at the northern limit of the genus *Philippia*, 'the differentiation of *Philippia* took place in the north rather than in the South African ones'.

CONCLUSIONS

It is evident from the above investigation of southern African species that the sole character for distinguishing between the genera *Erica* and *Philippia*, the degree of recaulescence of the bract, breaks down in a number of species, more frequently, relatively speaking, in *Philippia* than in the very large genus *Erica* (Table 1).

A ratio of 100:0:0 representing the aB-rB¹⁻⁵,2br¹⁻⁵,4K condition is characteristic of about 99% of the species of *Erica* whereas a ratio of 0:0:100 or RB,3K (except for the occasional aberrant flower) characterizes 12 of the 15 species of *Philippia* occurring in southern Africa. The possession of flowers falling within the middle portion (X) of the ratio 0:X:0 would place a specimen intermediate between the two genera with the formula rB²⁻⁵,0br,3-4K. From Table 1 it can be seen that only two of the species discussed, *E. dissimulans* and *E. hispidula* sens. strict., tend to the ericoid side and one species, *E. anomala*, tends towards to the philippioid side. Six species, *E. caespitosa* (*P. tristis*), *E. hispidula/inops*, *E. ebracteata*, *E. lasciva* (*P. stokoei*), *E. peltata* (*P. pallida*) and *E. sparsa*, have ratios that make it impossible to place them satisfactorily in either genus.

It could be argued that a species should be placed in *Erica* if it had more flowers that were typically ericoid than typically philippioid, and vice versa. Thus from Table 1 and previous discussion *E. dissimulans* and *E. subverticillaris* could be retained in *Erica* whereas *E. caespitosa*, *E. anomala* and *E. ebracteata* should be transferred to *Philippia*. This would require a thorough analysis of all the flowers on any specimen before it could be correctly identified. What then would be the

fate of *E. alticola*, *E. hispidula/inops*, *E. lasciva* (*P. stokoei*), *E. peltata* (*P. pallida*) and *E. sparsa*? These are five totally unrelated species each exhibiting a complete range of variation from the typical ericoid flower to the typical philippioid flower. They are all natural species whose remarkable variability cannot be ascribed to hybridization between species of *Erica* and *Philippia*.

The problem is compounded by geographical considerations because it is not confined to one small area. This problem as discussed above occurs on the Cape Peninsula, the southern Cape Province and on the Natal Drakensberg in southern Africa as well as on the Mascarene Islands, the East African highlands and the island of Sao Tomé off West Africa. A polyphyletic origin for the genus as presently construed is strongly indicated by this evidence. The genus *Philippia* can therefore not be upheld as a natural grouping of species.

I therefore propose to reduce the genus *Philippia* to synonymy under *Erica*. This action will have far-reaching nomenclatural repercussions in the rest of Africa and Madagascar as pointed out by Hilliard & Burt (1985: 240). The above decision is therefore not made without careful consideration of and due regard for these repercussions. A paper formalizing the above proposal and providing the new combinations for the southern African material is being published separately (Oliver 1987b).

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