AN OUTLINE OF THE GENUS *ANISOPAPPUS* HOOK. & ARN. *(COMPOSITAE)*

by

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Resumen

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Presentamos una sinopsis del género *Anisopappus* Hook. & Arn. *(Asteraceae)*. Hemos prestado atención particular a la delimitación del género y a sus relaciones filogenéticas, así como a lo que se ha dicho sobre agrupaciones posibles de sus especies. Las 40, más cuatro subespecies, que hasta el presente se admitían quedan reducidas a 17, más diez subespecies y cuatro variedades. Proponemos once nuevas combinaciones: seis en el rango subespecífico y cinco en el varietal.

Palabras clave: *Spermatophyta, Compositae, Inuleae, Anisopappus*, taxonomía, sudeste de Asia, África, Madagascar.

Abstract

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We present a synopsis of the genus *Anisopappus* Hook. & Arn. *(Asteraceae)*. Particular attention is paid to the taxonomic delimitation of the genus, to phylogenetic relationships and to possible supraspecific groupings. Until now, more than 40 species and four subspecies of this genus have been recognized. We recognize only 17 species, plus ten subspecies and four varieties, and propose eleven new nomenclatural combinations, six for subspecies and five for varieties.

Key words: *Spermatophyta, Compositae, Inuleae, Anisopappus*, taxonomy, south-eastern Asia, Africa, Madagascar.

INTRODUCTION

There can be little doubt that the genus *Anisopappus* Hook. & Arn. *(Compositae, Inuleae)* is the most confusing of all the asteracean genera of southern and central Africa. Such was the opinion of WILD (1964) as he embarked on his study of the *Compositae* for the *Flora Zambesiaca*, and HUMBERT (1962) expressed similar views in his study of the genus *Epallage* DC. (synonym of *Anisopappus*) for the *Flora of Madagascar and Comoros*. This latter author found it very difficult to clearly delimit boundaries between the different species (particularly those of the *E. dentata* DC. complex) occurring on these islands.

In recent years, we have carried out a detailed morphological study of material of the genus *Anisopappus* in the COI and K herbaria, and of selected specimens from BM,

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LISC, LISJC, LISU, LUA, LUAI, P and PRE. The principal aim of this work has been to clarify the taxonomy of the *Anisopappus* of south and southeast Asia, tropical and south Africa and Madagascar (see fig. 1).

We have paid particular attention to certain characteristics selected *a priori* as likely to be of value for discriminating between the most difficult taxa. These characteristics are life strategy (annual or perennial), flowering shoot length, type of pilosity, leaf morphology and texture, inflorescence peduncle length, capitulum size, involucrum bract morphology, arrangement of the corolla lobes, size and morphology of the anther tails, and size and shape of the pappus, achene and receptacular paleae.

In *Anisopappus* taxonomy, great emphasis has traditionally been placed on pappus morphology, and a number of putative species have been described on the basis of this character alone. We carried out a detailed analysis of relationships between pappus morphology and other vegetative and reproductive characters. This approach proved illuminating. In some cases, a particular pappus type appears to be consistently associated with a particular set of other characters; in many cases, however, no such association is apparent, and specimens which are otherwise very similar may show very considerable variability in pappus morphology.

These findings suggest that the importance of pappus morphology as a discriminant character has been exaggerated. Indeed, the confusion encountered by WILD (1964) and HUMBERT (1962) is perhaps largely attributable to this over-dependence on a single, highly variable character.

TAXONOMIC DELIMITATION

Anisopappus Hook. & Arn., Bot. Beechey Voy.: 196 (1837)

= *Astephania* Oliv. in Hook., Icon Pl. 16, tab. 1506 (1886)

= *Eenia* Hiern & S. Moore in J. Bot. 37: 373 (1899)

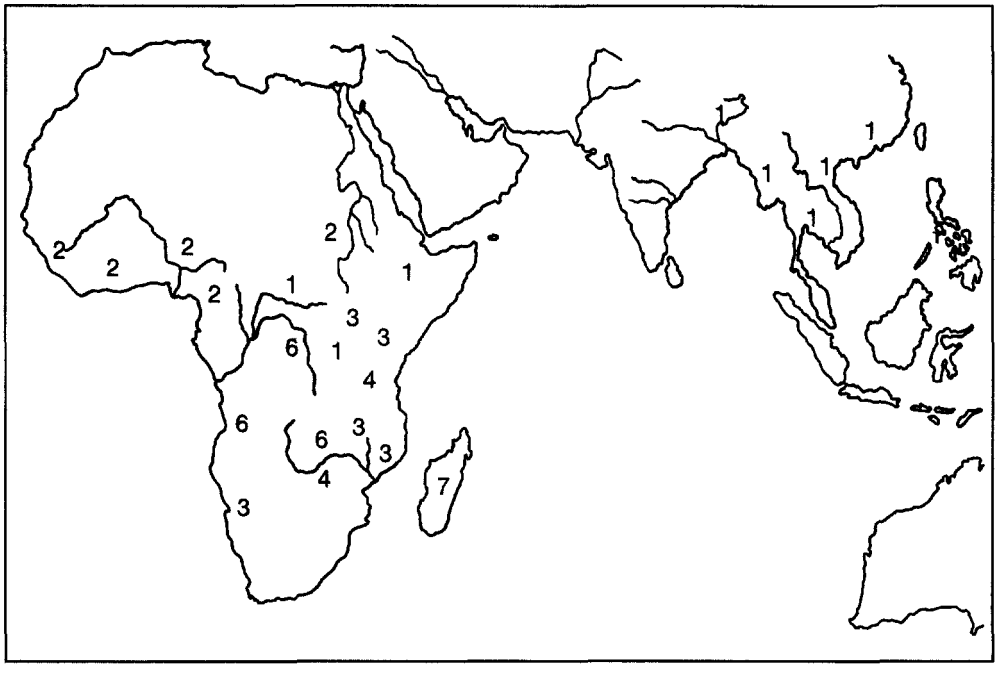

Fig. 1.–Worldwide distribution of *Anisopappus*. Numbers indicate number of species and subspecies present in each area.

= *Epallage* DC., Prodr. 6: 3 (1838)
= *Sphacophyllum* Benth. in Hook., Icon Pl. 12: 32 (1873)
= *Temnolepis* Baker in J. Linn. Soc., Bot. 22: 495 (1887)

Since the genus *Anisopappus* was erected in 1837, it has undergone a series of contractions and expansions, largely as a result of differing opinions as to the taxonomic importance of pappus morphology. For some time, material with unequal pappus scales was assigned to *Anisopappus*, material with more or less equal pappus scales to *Sphacophyllum* or *Epallage*, and material without pappus to *Astephania*. WILD (1964), in the only monographic study to date, merged these four genera into one, on the grounds that there were no clear discontinuities between them.

Equally, species otherwise falling within the definition of *Anisopappus* have in the past been assigned to other genera because they lack ray florets (*Eenia damarensis*, *Temnolepis scrophulariaefolia*) or receptacular paleae (*Anaglypha latifolia*). The assignment of species of *Anisopappus* to other genera (*Telekia* Baumg., *Matricaria* L., *Anthemis* L., *Verbesina* L., *Athanasia* L., *Buphthalmum* L., *Aspilia* Thouars) is basically attributable to the confusion which previously reigned in the systematics of this complex and highly diversified family.

In accordance with the most recent delimitations (ANDERBERG, 1991; BREMER, 1994), *Anisopappus* can distinguished from the remaining genera of the tribe *Inuleae* as follows: Stem not winged, without resin canals; anthers with very short tails, exceptionally long and branched; style with obtuse sweeping-hairs or exceptionally acute; cypselas with-out crystals in the epidermis; pappus of short acute or obtuse scales, sometimes missing; basic chromosome number, $x = 7$.

PHYLOGENETIC RELATIONSHIPS

Following ANDERBERG's (1991) morphology-based cladistic analysis of the *Inuleae*, the genus *Anisopappus* constitutes a sister group to the rest of the tribe, and is thus the tribe's most primitive component. In view of the marked morphological heterogeneity within the genus, this author considers *Anisopappus* to be para- or even polyphyletic; *A. smutsii* in particular shows many atypical characters. A recent cladistic study of *Anisopappus* and related genera by ELDENÄS (1994), however, concluded that *Anisopappus* is monophyletic, and that the atypical species *A. latifolius* (which lacks receptacular paleae) constitutes a sister group to the rest.

SUPRASPECIFIC GROUPINGS

WILD (1964) divided *Anisopappus* into two sections: *Anisopappus* with a pappus comprised of scales, and *Astephania* (Oliv.) Wild in Kirkia 4: 49 (1964) with pappus absent or reduced to a narrow entire or dentate rim.

In view of the very considerable variability in pappus morphology even within a single species (as discussed above), we consider that Wild's division of *Anisopappus* into two sections is untenable. For example, WILD (1964) places the large *A. chinensis* group in the section *Anisopappus*, despite the fact that the pappus is often absent in specimens of the subspecies *chinensis*, *buchwaldii* and *oliveranus*. The situation is similar with *A. davyi* (for example, the synonymous *A. lawalreanus*) and *A. abercornensis* (for example, *A. anemonifolia* var. *calva*). On the other hand, some of the species which WILD (1964) places in the section *Astephania*, specifically *A. oliveranus*, *A. lastii*, *A. rhombifolius*, *A. boinensis* and *A. alticola*, are, in our opinion, no more than pappus-lacking forms of *A. chinensis*. Furthermore, WILD (1964) himself recognized difficulties in assigning some species –such as *A. pumilus* and *A. longipes*– to one or the other section. ELDENÄS (1994), on the basis of the results of his cladistic analysis, has similarly concluded that there is no justification for dividing *Anisopappus* into these two sections.

ANDERBERG (1991) in his cladistic analysis of the tribe *Inuleae* considered *A. smutsii* to be distinct from the rest of the genus, in view of its acute sweeping style hairs and long (0.8-

1 mm) branched anther tails. Since this author considered *Anisopappus* to be para- or even polyphyletic, one would expect the analysis of ELDENÄS (1994) to have confirmed the relative unrelatedness of *A. smutsii* (and of the related species *A. junodii*). As mentioned above, however, Eldenäs in fact concluded that *Anisopappus* was monophyletic.

In addition to the characters mentioned by Anderberg, *A. smutsii* and *A. junodii* display a number of other atypical features, such as exsert anthers and (generally) spreading corolla lobes. Our own examination of herbarium material confirmed that most species, unlike *A. smutsii* and *A. junodii*, have obtuse sweeping style hairs, short (0.1-0.3 mm) unbranched anther tails, nonexsert anthers and erect corolla lobes. There is thus some justification for considering these two species to constitute a separate section. However, species with intermediate characters exist. For example, the anther tails of *A. kirkii* are 0.4-0.7 mm long and sometimes highly branched (despite Anderberg's statement to the contrary); in addition, this species shows obtuse to subacute sweeping style hairs, exsert or nonexsert anthers, and erect or slightly spreading corolla lobes. *Anisopappus pinnatifidus*, *A. pseudopinnatifidus* and *A. holstii* likewise display intermediate characters: anthers are exsert and corolla lobes more or less spreading, but style hairs are obtuse and anther tails are short (except in *A. holstii*, in where they are 0.3-0.4 mm long).

In what follows we present a key to the species of *Anisopappus* recognized by us. We then present a species-by-species account, with a key of subspecies and information on nomenclatural type, synonymy and geographical distribution, taking as our starting point WILD's (1964) monograph. The proposed nomenclatural charges are fully justified, and we comment in detail on the controversial taxa of this genus.

KEY TO THE SPECIES

1. Capitula without receptacular paleae ..... **17. A. latifolius**
1'. Capitula with receptacular paleae 2
2. Capitula discoid or with rudimentary inconspicuous ray florets 3
2'. Capitula radiate, with conspicuous ray florets ... 4
3. Capitula racemose; leaves linear ..... **14. A. athanasioides**
3'. Capitula solitary or arranged in a corymb; leaves pinnatipartite or ovate-cordate 5
4. Plant covered with greyish white tomentum; capitula subcampanulate to campanulate with 3-5 rows of involucral bracts; anther tails longer than 0.8 mm, branched 7
4'. Plant glabrescent or with patent or erect-patent hairs; capitula hemispherical with 2-3 rows of involucral bracts; anther tails shorter than 0.8 mm, unbranched (only branched in some specimens of *A. kirki*) 8
5. Leaves ovate-cordate ..... **1. A. chinensis**
5'. Leaves pinnatipartite 6
6. Capitula hemispherical, 8-13 mm wide ..... **12. A. pinnatifidus**
6'. Capitula obconic, 4-7 mm wide ..... **13. A. pseudopinnatifidus**
7. Leaves deltoid, leaf base truncate-sagittate or cordate ..... **15. A. junodii**
7'. Leaves elliptical, leaf base cuneate ..... **16. A. smutsii**
8. Capitula arranged in more or less dense composite corymbs, with peduncles generally shorter than 4 cm 9
8'. Capitula solitary or arranged in lax simple corymbs, with peduncles generally longer than 4 cm 10
9. Involucra more than 5 mm wide; receptacular paleae deeply trifid at the apex; involucral bracts obovate, about 3 mm wide ... **9. A. kirkii**
9'. Involucra less than 5 mm wide; receptacular paleae entire or more or less dentate at the apex; involucral bracts elliptical or oblanceolate, less than 3 mm wide 11
10. Plant with prostrate radicant stems ..... **6. A. longipes**
10'. Plant with erect or suberect nonradicant stems ... 13
11. Leaf base cuneate ..... **11. A. salvifolius**
11'. Leaf base cordate or truncate 12
12. Leaves sessile or with petiole shorter than 1 cm, laminae smaller than 2.5 × 1.5 cm, leaf border markedly dentate ... **5. A. corymbosus**
12'. Leaf petioles longer than 1 cm, laminae larger than 3 × 2 cm, leaf border finely denticulate ..... **10. A. sylvaticus**
13. Involucral bracts acuminate; anthers exsert; achene always lacking pappus ... **7. A. holstii**
13'. Involucral bracts not acuminate; anthers not exsert; achene with or without pappus 14
14. Involucral bracts obtuse; pappus about 4 mm long, extending for more than half of corolla length. ..... **8. A. marianus**

14' Involucral bracts acute; pappus less than 1 mm long or absent 15
15. Receptacular paleae flat, less than 0.3 mm wide; achene without pappus 16
15'. Receptacular paleae conduplicate, more than 0.3 mm wide; achene with or without pappus ... 17
16. Leaves lanceolate or elliptical, border irregularly sinuate, base cuneate ... **3. A. grangeoides**
16'. Leaves entire, deltoid or ovate, with base truncate to hastate-cordate ..... **1. A. chinensis**
17. Leaves pinnatipartite, overall leaf shape ovate-deltoid ..... **4. A. abercornensis**
17'. Leaves entire or, if partite, overall leaf shape suborbicular not pinnate 18
18. Leaves linear, less than 6 mm wide, sometimes revolute ..... **2. A. davyi**
18'. Leaves ovate, deltoid, lanceolate, elliptic or obovate, more than 6 mm wide, not revolute ..... **1. A. chinensis**

TAXONOMY

1. **Anisopappus chinensis** Hook. & Arn., Bot. Beechey Voy.: 196 (1837)

This is a highly polymorphic species, within which we recognize six subspecies. Most of these subspecies were considered by WILD (1964) to be separate species. *A. davyi* and *A. grangeoides* are, in our opinion, clearly direct offshoots of *A. chinensis*; other species such as *A. longipes*, *A. abercornensis* and *A. corymbosus* are likewise very probably descended from *A. chinensis*.

1. Capitula discoid or with greatly reduced, inconspicuous ray florets ..... **1.6.** subsp. **scrophulariifolius**
1'. Capitula radiate, with the ray florets always clearly visible 2
2. Leaf lobate to the medial nerve, overall leaf shape suborbicular ..... **1.4.** subsp. **lobatus**
2'. Leaf entire, crenate or crenate-dentate, overall leaf shape not suborbicular 3
3. Leaf deltoid or ovate, with base truncate or hastate-cordate 4
3'. Leaf lanceolate, elliptical or obovate, base cuneate 5
4. Petiole frequently more than 3 cm long, lamina often more than 4 cm wide; receptacular paleae less than 0.3 mm wide, not conduplicate, pappus absent ..... **1.3.** subsp. **oliveranus**
4'. Petiole generally less than 3 cm long, lamina generally less than 4 cm wide; receptacular paleae more than 0.3 mm wide, conduplicate, with or without pappus ..... **1.2.** subsp. **buchwaldii**
5. Leaf generally obovate, crenate-dentate only in the distal half .... **1.5.** subsp. **paucidentatus**
5'. Leaf lanceolate or elliptical, from near-entire to crenate or crenate-dentate in regular fashion along the full length of the leaf margin ..... **1.1.** subsp. **chinensis**

1.1. **Anisopappus chinensis** Hook. & Arn. subsp. **chinensis**

1. Perennial (including certain robust annual plants); leaves not membranaceous; capitula more than 1 cm wide; peduncles generally more than 1 mm wide ..... var. **chinensis**
1'. Annual; leaves membranaceous; capitula less than 1 cm wide; peduncles generally less than 1 mm wide ..... var. **rupestris**

1.1.1. **Anisopappus chinensis** subsp. **chinensis** var. **chinensis**

= *Verbesina chinensis* L., Sp. Pl.: 901 (1753)
= *Sphacophyllum candelabrum* O. Hoffm. in Bol. Soc. Brot. 13: 27 (1896); *A. hoffmannianus* Hutch., Bot. S. Afr.: 498 (1946)
= *A. gracilis* O. Hoffm. in Warb., Kunene-Sambesi. Exped.: 416 (1903)
= *A. subdiscoideus* O. Hoffm. in Warb., Kunene-Sambesi. Exped.: 416 (1903)
= *Sphacophyllum sparsum* S. Moore in J. Linn. Soc., Bot. 40: 114 (1911)
= *Epallage orbicularis* Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 106, 300 (1923); *A. orbicularis* (Humbert) Wild in Kirkia 4: 65 (1964)
= *Sphacophyllum pratense* S. Moore in J. Linn. Soc., Bot. 47: 273 (1925)
= *A. dalzielii* Hutch. in Hutch. & Dalziel, Fl. W. Trop. Afr. 2(1): 156 (1931)
= *A. aureus* Hutch. & Burtt in Rev. Zool. Bot. Africaines 23: 40 (1932)
= *A. canescens* Hutch., Bot. S. Afr.: 498 (1946)
= *Epallage dentata* var. *alticola* Humbert, Fl. Madagascar, Composées 2: 606 (1962); *A. alticola* (Humbert) Wild in Kirkia 4: 72 (1964)

Occurring in southern China (Guangdong and Jiangxi provinces), the Philippines, Indo-

china (Burma, Thailand and Vietnam), India (Assam State), French Guinea, Ghana, Togo, Nigeria, Cameroon, the Central African Republic, Sudan, Uganda, Zaire, Angola, Zambia, Zimbabwe, Malawi and Madagascar.

Recently (ORTIZ & PAIVA, 1995) we demonstrated the high pappus shape variability in *A. chinensis* [the following specimens beloging to the subsp. *chinensis* but with extremely reduced or absent pappi, complete the rank of variability shown in that article: Zaire, *Symoens 7642* (K); Zaire, *Symoens 10134* (K); Angola, *Pearson 2787* (K); Angola, *Henriques 975* (COI, K); Angola, *Gossweiler 3338* (K) and Angola, *Baum 877* (K)]. As mentioned above, pappus morphology has frequently been used as a discriminant character, despite showing very considerable variability even between otherwise similar specimens. One result of this practice has been that much material belonging in our opinion to the subspecies *chinensis* has been incorrectly assigned to other taxa.

In view of these considerations, we assign to this variety all perennial forms (and certain robust annual forms), regardless of whether the pappus is short with equal scales, with unequal scales or absent. Forms with short equal-scaled pappi were assigned by WILD (1964) to *A. gracilis*, though by LISOWSKI (1989) to *A. chinensis*. Forms with unequal-scaled pappi were assigned by WILD (1964) to *A. chinensis* or to *A. orbicularis*. Forms lacking pappi have in the past generally been assigned either to *A. lastii* subsp. *welwitschii* (despite the fact that the type specimen is clearly of the subspecies *buchwaldii*), *A. alticola* (its type specimen presents characters transitional to *A. chinensis* subsp. *buchwaldii*) or, less commonly, to *A. chinensis*.

1.1.2. Anisopappus chinensis subsp. **chinensis** var. **rupestris** (DC.) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. nov.**

≡ *Epallage rupestris* DC., Prodr. 6: 4 (1838) [basion.]; *E. dentata* var. *rupestris* (DC.) Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 109 (1923)

= *Epallage minima* Baker in J. Linn. Soc., Bot. 20: 189 (1884)

= *Epallage dissitifolia* Baker in J. Linn. Soc., Bot. 22: 494 (1887)

= *Epallage imbricata* Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 107, 300 (1923)

= *Epallage dentata* var. *incisa* Humbert in Mém. Soc. Normandie, Bot. 25: 109 (1923)

= *Epallage boinensis* Humbert in Mém. Soc. Normandie, Bot. 25: 110, 299 (1923); *E. dentata* var. *boinensis* (Humbert) Humbert, Fl. Madagascar, Composées 2: 605 (1962); *A. boinensis* (Humbert) Wild in Kirkia 4: 72 (1964)

= *Epallage nuda* Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 111, 300 (1923)

= *A. rhombifolius* Wild in Kirkia 4: 69 (1964)

Occurring in Angola, Zambia, Zimbabwe, and Madagascar.

In our opinion, annual forms of *A. chinensis* subsp. *chinensis* with membranaceous leaves, capitula less than 1 cm wide and peduncles generally less than 1 mm wide should be considered as a variety comprising both forms with pappus [as assigned by WILD (1964) to *A. dentatus*] and forms without pappus [as assigned by WILD (1964) to *A. lastii* subsp. *lastii*, *A. rhombifolius* or *A. boinensis*].

1.2. Anisopappus chinensis subsp. **buchwaldii** (O. Hoffm.) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. nov.**

≡ *Sphacophyllum buchwaldii* O. Hoffm. in Bot. Jahrb. Syst. 24: 473 (1898) [basion.]

1. Perennial (and certain robust annual plants); leaves not membranaceous; capitula more than 1 cm wide; peduncles generally more than 1 mm wide ..... var. **macrocephala**

1'. Annual; leaves membranaceous; capitula less than 1 cm wide; peduncles generally less than 1 mm wide ..... var. **dentata**

1.2.1. Anisopappus chinensis subsp. **buchwaldii** var. **macrocephala** (Humbert) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. nov.**

≡ *Epallage dentata* var. *macrocephala* Humbert, Fl. Madagascar, Composées 2: 605 (1962) [basion.]

= *Telekia africana* Hook. f. in J. Linn. Soc., Bot. 7: 201 (1864) [basion.]; *A. africanus*

(Hook. f.) Oliv. & Hiern in Oliv., Fl. Trop. Afr. 3: 369 (1877); *A. chinensis* subsp. *africanus* (Hook. f.) S. Ortiz & Paiva in J. Linn. Soc., Bot. 117: 44 (1995)

= *Sphacophyllum stuhlmannii* O. Hoffm. in Engl., Planzenw. Ost-Afrikas, C: 412 (1895)

= *Sphacophyllum welwitschii* O. Hoffm. in Bol. Soc. Brot. 13: 27 (1896); *A. lastii* subsp. *welwitschii* (O. Hoffm.) Wild. in Kirkia 4: 68 (1964)

= *Sphacophyllum buchwaldii* O. Hoffm. in Bot. Jahrb. Syst. 24: 473 (1898); *Epallage buchwaldii* (O. Hoffm.) Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 108 (1923); *A. buchwaldii* (O. Hoffm.) Wild in Kirkia 4: 60 (1964)

= *Sphacophyllum helenae* Buscal. & Muschl. in Bot. Jahrb. Syst. 49: 506 (1913)

= *Epallage africana* S. Moore. in J. Bot. 55: 123 (1917); *A. rogersii* G. Tayl. in J. Bot. 71: 165 (1923)

= *Sphacophyllum tenerum* S. Moore in J. Linn. Soc., Bot. 47: 274 (1925); *A. tenerus* (S. Moore) Brenan in Mem. New York Bot. Gard. 8(5): 478 (1954)

= *A. inuloides* Hutch. & Burtt in Rev. Zool. Bot. Africaines 23: 41 (1932)

= *A. suborbicularis* Hutch. & Burtt in Rev. Zool. Bot. Africaines 23: 41 (1932)

= *A. iodiotrichus* Brenan in Mem. New York Bot. Gard. 8(5): 477 (1954); *A. buchwaldii* subsp. *iodotrichus* (Brenan) Wild in Kirkia 4: 60 (1964)

= *A. exellii* Wild in Kirkia 4: 57 (1964)

= *A. discolor* Wild in Kirkia 4: 62 (1964)

In accordance with taxonomic treatment showed in this paper, the epithet *buchwaldii* is priority for this subspecies against the epithet *africanus*, used by us before (Ortiz & Paiva, 1995).

Occurring in French Guinea, Sierra Leone, Ghana, Cameroon, Nigeria, Ethiopia, Sudan, Kenya, Uganda, Tanzania, Rwanda, Burundi, Zaire, Angola, Zambia, Zimbabwe, Malawi, Mozambique and Madagascar.

Our reasons for considering species *A. africanus* to be a subspecies of *A. chinensis* have been published previously (Ortiz & Paiva, 1995). Although the two taxa –*A. chinensis* subsp. *chinensis* and *A. chinensis* subsp. *buchwaldii*– are sympatric throughout much of Africa, they show distributional differences: only the subspecies *chinensis* is present in Asia, while only the subspecies *buchwaldii* is present in northeastern and east Africa (Ethiopia, Kenya, Tanzania and Mozambique). However, we have examined material from the Philippines [*Merrill 514* (K)] which presents the typical characters of the subspecies *buchwaldii*, and material from Thailand [*Kerr 8926* (K); *Sorensen, Larsen & Hansen 6263* (K)] which displays intermediate morphology.

We have also seen Tanzanian material which is apparently intermediate between *A. chinensis* subsp. *chinensis* and *A. davyi* subsp. *davyi* (see below).

Apart from the characters cited in the key, the following are also useful for discriminating between the subspecies *chinensis* and *buchwaldii*. The subspecies *chinensis* generally has nonreticulate leaves and receptacular paleae of about 4 mm in length. The subspecies *buchwaldii* generally has reticulate leaves and receptacular paleae of about 6 mm in length. Note, however, that these differences are generally only useful for discriminating between perennial forms.

As with the subspecies *chinensis*, we assign to the subspecies *buchwaldii* var. *macrocephala* all perennial forms (and certain robust annual forms), regardless of whether the pappus is short with equal scales, unequal or absent. Forms with short equal-scaled pappi were generally assigned by Wild (1964) to *A. buchwaldii*, forms with unequal-scaled pappus to *A. africanus*, *A. exellii* or *A. discolor*, and forms without pappus to *A. lastii* subsp. *welwitschii* or, in some cases, *A. africanus*.

Two species described by Wild (1964), *A. exellii* and *A. discolor*, do not appear to differ from *A. chinensis* subsp. *buchwaldii* to an extent which justifies their consideration as separate taxa. *Anisopappus exellii* differs from *A. chinensis* subsp. *buchwaldii* solely in the presence on some leaves of one or two additional lobes separate from the lamina. In a

type specimen from COI examined by us, only 10 of the 40 leaves showed this character. Similarly, *A. discolor* differs from *A. chinensis* subsp. *buchwaldii* solely in that the petiole is slightly longer with respect to the lamina, and in that the leaves are sometimes fasciculate. Discolor leaves (often cited as a distinguishing characteristic of *A. discolor*) are in fact not uncommon in *A. chinensis*.

1.2.2. Anisopappus chinensis subsp. **buchwaldii** var. **dentatus** (DC.) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. nov.**

≡ *Epallage dentata* DC., Prodr. 6: 4 (1838) [basion.]; *A. dentatus* (DC.) Wild in Kirkia 4: 63 (1964)

= *Sphacophyllum lastii* O. Hoffm. in Engl., Pflanzenw. Ost-Afrikas, C: 412 (1895) [basion.]; *A. lastii* (O. Hoffm.) Wild in Kirkia 4: 67 (1964)

Occurring in Uganda, Tanzania, Mozambique, Angola, Zambia, Zimbabwe, Malawi and Madagascar.

Annual forms of *A. chinensis* subsp. *buchwaldii* with membranaceous leaves, capitula less than 1 cm wide and peduncles generally less than 1 mm wide should be considered as a variety comprising both forms with pappus [as assigned by WILD (1964) to *A. dentatus*] and forms without pappus [as assigned by WILD (1964) to *A. lastii* subsp. *lastii*].

1.3. Anisopappus chinensis subsp. **oliveranus** (Wild) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. & stat. nov.**

≡ *A. oliveranus* Wild in Kirkia 4: 66 (1964) [basion.]; *Astephania africana* Oliv. in Hook., Icon Pl. 16, tab. 1506 (1886); *Sphacophyllum africanum* (Oliv.) O. Hoffm. in Abh. Preuss. Akad. Wiss., Phys.-Math. Kl. 1894: 58 (1894)

Occurring in Kenya and Tanzania.

The taxon referred to by WILD (1964) as *A. oliveranus* appears to actually be an extreme variant of the *A. chinensis* group, with close affinities to the subspecies *buchwaldii*. Transitional forms between the subspecies *buchwaldii* and *oliveranus* were referred to by WILD (1964) as *A. buchwaldii* (whose type differs from other forms of *A. chinensis* subsp. *buchwaldii)* solely in possessing short equal-scaled pappus. Pappus-lacking but otherwise typical forms of the subspecies *buchwaldii* can also be viewed as transitional form. Examples are: Tanzania, *Linder 3717* (K); Tanzania, *Carmichael 674* (K); Tanzania, *Lema 36* (K) and Tanzania, *Harvey & Newbould 42025* (K).

Specimens of the subspecies *oliveranus* generally lack pappus, but this is not always the case, as for example: Tanzania, *Semsei 4080* (K); Tanzania, *Haarer 1496* (K) and Tanzania, *Faulkner 1049* (K). Long petioles, often cited as characteristic of this subspecies, may also be observed in the subspecies *buchwaldii*, as for example in specimens previously referred to as *A. discolor*, in which the lamina is less than 3 cm wide. Other features which appear to characterize this subspecies well are the receptacular paleae, generally flat and narrow, and the leaves, generally more than 4 cm wide. However, these distinguishing characters are in our opinion insufficient to justify separate species status; indeed, WILD (1964) does not cite these characters as a basis for differentiation from related taxa.

1.4. Anisopappus chinensis subsp. **lobatus** (Wild) S. Ortiz & Paiva in Bot. J. Linn. Soc. 117: 46 (1995)

≡ *A. dentatus* subsp. *lobatus* Wild in Kirkia 4: 64 (1964)

Generally considered to be restricted to the 'kopjes' (granite outcrops) of Zimbabwe, although we have also seen specimens from Zambia [*E.A. Robinson 4547* (K); *Hooper & Townsend 689* (K); *Richards 16435* (K)].

The following specimens present characteristics intermediate between this subspecies and *A. chinensis* subsp. *buchwaldii:* Zimbabwe, *Chase 8387* (COI); Zambia, *Hooper & Townsend 689* (K) and Zambia *Richards 16435* (K). As discussed below, some specimens show morphological similarities to *A. abercornensis* subsp. *abercornensis*.

1.5. Anisopappus chinensis subsp. **paucidentatus** (Wild) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. & stat. nov.**

≡*A. paucidentatus* Wild in Kirkia 4: 55 (1964) [basion.]

Endemic on quartzites in the Chimanimani Mountains, in Zimbabwe and Mozambique.

Plants of this taxon are chamaephytic, highly ramified and with numerous flowers; morphologically, this subspecies is very close to *A. chinensis* subsp. *chinensis*, from which it differs solely in its leaves, which are largely obovate and crenate-dentate in their distal half; as recognized by WILD (1964, 1980), however, the leaves may also be ovate or elliptical, similar to those of typical specimens of *A. chinensis* subsp. *chinensis*.

1.6. Anisopappus chinensis subsp. **scrophulariifolius** (Baker) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. & stat. nov.**

≡*Temnolepis scrophulariifolia* Baker in J. Linn. Soc., Bot. 22: 495 (1887) [basion.]; *Epallage scrophulariifolia* (Baker) Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 110 (1923); *A. scrophulariifolius* (Baker) Wild in Kirkia 4: 65 (1964)

=*Epallage dentata* var. *disciformis* Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 109, 300 (1923)

≡*Epallage dentata* var. *homogama* Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 109, 300 (1923)

Known only from Madagascar.

As recognized by HUMBERT (1962), plants of this subspecies have very similar external morphology to the annual forms of *A. chinensis* subsp. *buchwaldii*, although the leaves are somewhat more sinuate and the corymbs more dense. The ray florets are rudimentary or absent, as in other species of this genus (*A. athanasioides*, *A. pinnatifidus*, *A. pseudopinnatifidus*); this character (though highly variable, even within the same individual) clearly distinguishes this taxon from the other subspecies of *A. chinensis*. The populations described by HUMBERT (1923) as *Epallage dentata* var. *disciformis* (with rudimentary ray florets) and *E. dentata* var. *homogama* (without ray florets) appear to be transitional forms between this subspecies and *A. chinensis* subsp. *buchwaldii*.

2. Anisopappus davyi S. Moore in J. Linn. Soc., Bot. 47: 275 (1925)

1. Leaves narrowly oblanceolate, 1.5-6 mm wide, flat, rarely revolute ..... **2.1.** subsp. **davyi**
1'. Linear leaves, 0.8-1.5(2) mm wide, generally revolute ..... **2.2.** subsp. **pumilus**

2.1. Anisopappus davyi S. Moore subsp. **davyi**.

=*A. petitianus* Lisowski in Bull. Jard Bot. Belg. 56: 202 (1986)

=*A. robynsianus* Lisowski in Bull. Jard. Bot. Belg. 56: 369 (1986)

=*A. lejolyanus* Lisowski in Bull. Jard. Bot. Belg. 56: 370 (1986)

=*A. upembensis* Lisowski in Bull Jard. Bot. Belg. 56: 371 (1986)

Known from Tanzania, Zaire and Zambia.

In the present revision we have taken a conservative approach and maintained *A. davyi* as a separate species. However, *A. davyi* subsp. *davyi* shows clear morphological similarities to *A. chinensis* subsp. *chinensis*, and in fact *A. davyi* subsp. *davyi*, with very narrow leaves generally inserted on the lower half of flowering stems, may simply be an extreme variant of this latter taxon. Intermediate specimens include: Tanzania, *Milne-Redhead & P.G. Taylor 9842* (K); Tanzania, *Milne-Redhead & P.G. Taylor 9365* (K); Zambia, *Cruse 347* (K); Zambia, *Richards 5763* (K); Angola, *Silva 3473* (K) and Angola *Baum 877* (COI, K). Specimens previously referred to as *A. lejolyanus* likewise appear to be intermediates between this subspecies and *A. chinensis* subsp. *chinensis*.

2.2. Anisopappus davyi subsp. **pumilus** (Hiern) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. & stat. nov.**

≡*Sphacophyllum pumilum* Hiern, Cat. Afr. Pl. Welw. 1(3): 573 (1898) [basion.]

1. Flowering stems 6-10 cm long; leaves 3-5(8) mm long, some highly revolute, others only with slightly revolute borders ..... **2.2.1.** var. **pumilus**

1'. Flowering stems 15-45 cm long; leaves 5-13 mm long, generally, all highly revolute .... **2.2.2.** var. **bampsianus**

2.2.1. Anisopappus davyi S. Moore subsp. **pumilus** var. **pumilus** (Hiern) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. & stat. nov.**

≡ *Sphacophyllum pumilum* Hiern, Cat. Afr. Pl. 1(3): 573 (1898) [basion.]; *A. pumilus* (Hiern) Wild in Kirkia 4: 65 (1964)

Known only from Angola.

WILD (1964) states that plants of this taxon have stems shorter than 15 cm; in fact, only the flowering stems are short. In general, these stems arise from a thick rhizome. However, some specimens [Angola, *Silva 1023* (COI)] are more than 1 m high, and the flowering stems arise above soil level.

2.2.2. Anisopappus davyi subsp. **pumilus** var. **bampsianus** (Lisowski) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. & stat. nov.**

≡ *A. bampsianus* Lisowski in Bull. Jard. Bot. Belg. 56: 199 (1986) [basion.]

= *A. lawalreanus* Lisowski in Bull. Jard. Bot. Belg. 56: 200 (1986)

Reported from Zaire, Zambia and Angola.

Clear morphological transitions exist between this variety and *A. davyi* subsp. *davyi*. Such specimens have mostly flat leaves of width greater than 1.5 mm, though with some highly revolute leaves of width less than 1.5 mm, see for example: Zambia, *Richards 10972, 4025, 1508* (K). Specimens referred to as *A. petitianus* likewise appear to be intermediates between these two taxa.

The two varieties of the subspecies *pumilus* are sympatric, at least around Humpata in the Huila region of Angola. Although there has been very little herborization in Angola, some intermediate specimens have been found [Angola, *Welwitsch 4064* (COI)].

LISOWSKI (1986a, 1986b, 1988), in his description of the various species included by us in the synonymy of one or the other of the subspecies of *A. davyi*, uses only a very limited set of discriminant characters, namely the presence or absence of pappus, fine details of pappus morphology, and achene pubescence. In a later publication (LISOWSKI, 1989), this author uses these same characters as a basis for separating these taxa from other species occurring in Zaire. As discussed previously (PAIVA & ORTIZ, 1995) and in the present revision, pappus morphology varies greatly within the same species, and is thus of little discriminant value unless the morphology in question is consistently accompanied by some other reliable discriminant character. Lisowski attaches considerable importance to the lack of achene pubescence (for example, as a discriminant character of *A. upembensis* and *A. lejolyanus*), and indeed the achene is usually pubescent in most species of the genus. In many such species, however, glabrous achenes are not infrequent: Tanzania, *Harley 4205* (K); Nigeria, *Chapman 5027* (K); Nigeria, *Daramola 6245* (K); Nigeria, *Heppen 1709* (K); Zaire, *Leonard 3038* (K); Zaire, *Rogers 10909* (K) and Zaire, *Symonsen 14169 (K)*. All these specimens are of subspecies of *A. chinensis*, with morphology in all other respects typical of the subspecies in question. We thus consider Lisowski's putative species are simply reflections of the internal variability of *A. davyi*.

3. Anisopappus grangeoides (Vatke & Höpfner ex Klatt) Merxm. in Mitt. Bot. Staatssamml. München 9: 415 (1945)

≡ *Anthemis grangeoides* Vatke & Höpfner ex Klatt in Bull. Herb. Boissier 4: 465 (VI?-1896)

= *Sphacophyllum pinnatifidum* O. Hoffm. in Bol. Soc. Brot. 13: 26 (XII-1896)

= *Sphacophyllum gossweileri* S. Moore in J. Linn. Soc., Bot. 47: 273 (1925)

Known from Angola and Namibia.

We feel that this taxon with irregularly sinuate leaves should be maintained as a distinct species, although it clearly shows considerable morphological similarity to the *A. chinensis* group, particularly to that which has been called *Sphacophyllum pratense*, with lanceolate leaves and without pappus. Furthermore, intermediates between *A. grangeoi-*

des and *A. chinensis* are known [Zimbabwe, *Wild 5710* (K)]. Despite these qualifications, *A. grangeoides* is characterized by its linear, unfolded receptacular paleae of 0.2-0.3 mm in width, together with the consistent absence of pappus.

4. Anisopappus abercornensis G. Taylor in J. Bot. 71: 164 (1933)

1. Annual; leaves pinnatipartite with 1-3 lateral pinnae; peduncles less than 0.6 mm wide; capitula less than 8 mm wide; pappus scales generally equal, 0.1-0.3 mm long ..... 4.1. subsp. **abercornensis**

1'. Generally perennial; leaves pinnatipartite, usually with more than 3 lateral pinnae; peduncles more than 0.6 mm wide; capitula more than 6 mm wide; pappus scales generally unequal, 0.2-1.5 mm long ..... 4.2. subsp. **anemonifolius**

4.1. Anisopappus abercornensis G. Taylor subsp. **abercornensis**

= *A. annuus* Lawalrée in Bull. Jard. Bot. État 19: 220 (1949)

= ? *A. burundensis* Lisowski in Bull. Jard. Bot. Belg. 58: 259 (1988)

Known only from the Abercorn district of northeastern Zambia, though possibly also present in Burundi and other areas close to Lake Tanganyika.

In his description of *A. burundensis*, Lisowski (1988) only details differences between this species and *A. lastii* (*A. chinensis* subsp. *buchwaldii* var. *dentatus* in the present study), from which it does indeed clearly differ (as confirmed by our examination of type specimens in K). Later (Lisowski, 1989), this author mentions the morphological similarities between *A. burundensis* and *A. abercornensis* subsp. *abercornensis*, from which it differs solely in displaying pappus-lacking glabrous achenes; as discussed above, both characters tend to show high within-species variability. In our opinion, these are insufficient grounds for considering *A. burundensis* as a separate species. Furthermore, like *A. abercornensis* susbp. *abercornensis*, the putative *A. burundensis* specimens were all found close to Lake Tanganyika, although at the opposite, northern side. Despite these arguments, caution is necessary, since very little *A. burundensis* material has been collected.

Certain populations of *A. abercornensis* subsp. *abercornensis* show morphological similarities to *A. chinensis* subsp. *lobatus*, occurring on granite outcrops, in Zambia and Zimbabwe.

4.2. Anisopappus abercornensis subsp. **anemonifolius** (DC.) S. Ortiz, Paiva & Rodr.-Oubiña, **comb. & stat. nov.**

≡ *Epallage anemonifolia* DC., Prodr. 6: 4 (1838) [basion.]; *A. anemonifolius* (DC.) G. Taylor in J. Bot. 71: 165 (1933)

= *A. angolensis* O. Hoffm. in Bol. Soc. Brot. 10: 176 (1892)

= *Sphacophyllum pusillum* S. Moore in J. Bot. 44: 147 (1906); *Epallage pusilla* (S. Moore) Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 105 (1923)

= *Epallage anemonifolia* var. *confluens* Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 110, 299 (1923)

= *Epallage calva* Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 110, 299 (1923); *E. anemonifolia* var. *calva* (Humbert) Humbert, Fl. Madagascar, Composées 2: 610 (1962)

Occurring in Zambia, Angola and Madagascar.

Wild (1964) considered the two subspecies of *A. abercornensis* to be separate species, and differentiated between them largely on the basis of capitulum size. In a later publication (Wild, 1980), this author stressed the great morphological similarity between the two taxa, although he maintained their status as separate species.

The characters detailed in the above key permit the two taxa to be discriminated; however, there is no abrupt discontinuity between them. Some specimens which would otherwise be assigned to the subspecies *abercornensis* have clearly unequal pappus (Zambia, *Richards 18092, 4518* (K)). Likewise, some specimens which would otherwise be assigned to the subspecies *anemonifolius* have short equal pappus [Zambia, *Pope, A.R. Smith*

& Goyder 2167 (K); Zambia, *Hutchinson & Guillet 4072* (K); Zambia, *Fanshawe 9251* (K)]. Furthermore, some specimens with *anemonifolius*-type morphology are annuals, though of robust appearance [Zambia, *Pope, A.R. Smith & Goyder 2167* (K); Zambia, *A.R. Richards 9289* (K)]. Finally, in the Abercorn district of Zambia (to which the subspecies *abercornensis* is considered endemic), populations of the subspecies *anemonifolius* also occur [*Richards 16365* (K)]. In view of these observations, we consider subspecies rank to be the most appropriate for these two taxa.

5. Anisopappus corymbosus Wild in Kirkia 4: 61 (1964)

Known only from Angola.

This species, described by WILD (1964), appears to be well characterized by its sessile or subsessile membranaceous leaves extending to the base of the capitulum, and by its capitula which are arranged in composite corymbs and whose peduncles are generally shorter than 1(1.5) cm (fig. 2).

6. Anisopappus longipes (Comm. ex Cass.) Wild in Kirkia 4: 65 (1964)

≡ *Buphthalmum longipes* Comm. ex Cass. in Bull. Soc. Philom. Paris 1822: 144 (1822)

= *Epallage humifusa* Baker in J. Linn. Soc., Bot. 20: 189 (1883)

= *Epallage humifusa* var. *minor* Humbert in Mém. Soc. Linn. Normandie, Bot. 25: 108 (1923)

= *Aspilia alterniflora* Klatt in Ann. Naturhist. Hofmus. 7: 298 (1892)

Known only from Madagascar.

This taxon shows morphological similarities to the *A. chinensis* group, of which it is probably a derivative. It is well characterized by its prostrate radicant stems.

7. Anisopappus holstii (O. Hoffm.) Wild in Kirkia 4: 69 (1964)

≡ *Sphacophyllum holstii* O. Hoffm. in Engl., Pflanzenw. Ost-Afrikas, C: 412 (1895)

Occurring in Uganda, Kenya and Tanzania.

Though sometimes of similar general appearance to *A. chinensis* subsp. *buchwaldii* var. *dentatus*, *A. holstii* can be readily discriminated by its highly acuminate involucral bracts. We have always found this character to be accompanied by a lack of pappus. In addition, the anthers are exsert with 0.3-0.4 mm long tails; this aids discrimination from the most similar taxa, in which the anthers are not exsert and have tails of 0.1-0.2 mm in length.

8. Anisopappus marianus Lawalrée in Bull. Jard. Bot. Belg. 44(1/2): 188 (1974)

Known only from Zaire.

9. Anisopappus kirkii (Oliv.) Brenan in Mem. New York Bot. Gard. 8(5): 478 (1954)

≡ *Sphacophyllum kirkii* Oliv. in Hook., Icon Pl. 15, tab. 1451 (1884)

= *Sphacophyllum flexuosum* Hutch. in Bull. Misc. Inform. Kew 1906: 246 (1906); *A. flexuosus* (Hutch.) Brenan in Mem. New York Bot. Gard. 8(5): 478 (1954)

Occurring in Zimbabwe, Malawi and Mozambique.

10. Anisopappus sylvaticus (Humbert) Wild in Kirkia 4: 71 (1964)

≡ *E. sylvatica* Humbert in Mém. Linn. Soc. Normandie, Bot. 25: 106, 300 (1923)

Known only from Madagascar.

11. Anisopappus salviifolius (DC) Wild in Kirkia 4: 66 (1964)

– *Epallage salviifolia* DC., Prodr. 6: 3 (1838) ["salvifolia"]; *Sphacophyllum bojeri* Benth. in Hook, Icon Pl. 12, tab. 1135 (1876), nom illeg.; *S. madagascariense* Benth. in Hook, Icon Pl. 12: 33 (1876), nom illeg.

= *Epallage salviifolia* subsp. *andohahelensis* Humbert, Fl. Madagascar, Composées 2: 600 (1962)

Known only from Madagascar.

12. Anisopappus pinnatifidus (Klatt) O. Hoffm. ex Hutch. in Bull. Misc. Inform. Kew 1917: 115 (1917)

≡ *Matricaria pinnatifida* Klatt in Bull. Herb. Boissier. 3: 437 (1895)

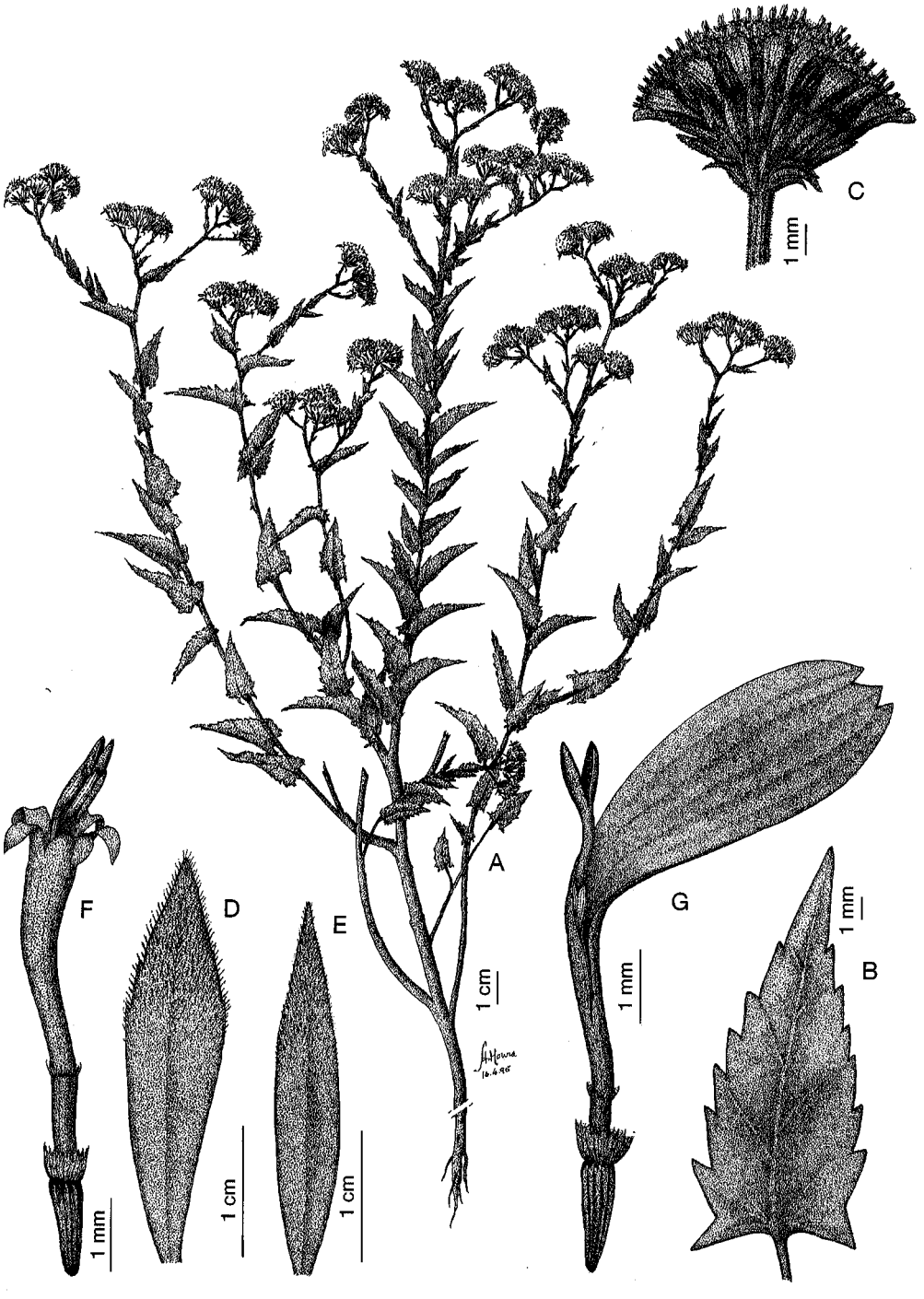

Fig. 2.–*Anisopappus corymbosus* Wild: A, flowering stem; B, leave; C, capitulum; D, receptacular palea; E, involucral bract; F, disc-floret; G, ray-floret. All from *Teixeira 318* (LUAI).

= *Athanasia triloba* Klatt in Bull. Herb. Boissier. 3: 435 (1895); *A. trilobus* (Klatt) O. Hoffm. ex Merxm. in Mitt. Bot. Staatssamml. München 1: 416 (1954)
= *Eenia damarensis* Hiern & S. Moore in J. Bot. 37: 373 (1899)
= *Senecio aschersonianus* Muschl. & Dinter in Repert. Spec. Nov. Regni Veg. 23: 232 (1926), nom. inval.
= *Senecio oreophilus* Muschl. ex Dinter in Repert. Spec. Nov. Regni Veg. 23: 232 (1926), nom. inval.

Known only from Namibia.

13. Anisopappus pseudopinnatifidus S. Ortiz & Paiva in Bot. J. Linn. Soc. 117: 40 (1995)

Known only from Namibia.

14. Anisopappus athanasioides Paiva & S. Ortiz in S. Ortiz & Paiva, Bot. J. Linn. Soc. 117: 40 (1995)

Known only from Angola.

15. Anisopappus junodii Hutch. in Bull. Misc. Inform., Kew 1906: 249 (1906)

Known only from the Transvaal, in eastern South Africa.

16. Anisopappus smutsii Hutch. in Bull. Misc. Inform. Kew 1933: 425 (1933)

Known only from eastern South Africa (Transvaal and Natal) and Swaziland.

17. Anisopappus latifolius (S. Moore) B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 37(2): 295 (1979)
≡ *Anaglypha latifolia* S. Moore in J. Bot. 55: 105 (1917)

Known only from the Transvaal (South Africa).

This plant, initially included in the southern African genus *Anaglypha* DC., lacks receptacular paleae. As pointed out by HILLIARD & BURTT (1979), however, in all other respects its morphology, including pollen morphology, conforms to that of the genus *Anisopappus*. These authors thus argued against assigning this species to a separate genus.

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