NOTES ON THE INFRAGENERIC CLASSIFICATION OF AGAPETES, WITH FOUR NEW TAXA FROM NEW GUINEA

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ABSTRACT. The taxonomic position of the oceanic species of *Agapetes*, considered by some to be better maintained as a separate genus, *Paphia*, is re-evaluated using morphological and simple anatomical data. These species form a distinct entity within *Agapetes* and are accommodated in a new subgenus, *Paphia*; within this subgenus *A. scortechinii* remains in a monotypic section, *Pseudagapetes*. Four new taxa of *Agapetes* are described from New Guinea: *A. prostrata*, *A. shungolensis*, *A. sleumeriana* and *A. brassii* Sleum. ssp. *serratifolia*.

INTRODUCTION

Seemann (1864) described a new genus in the Ericaceae, *Paphia*, based on a single species, *P. vitiensis*, from Fiji. He separated *Paphia* from *Pentapterygium* Klotzsch (= *Agapetes* D. Don) because the latter had a winged calyx tube, and from both *Epigynium* Klotzsch (= *Vaccinium* L.) and *Pentapterygium* because they had less tubular corollas. Many more species are known today, and the differences mentioned cannot be considered as sufficient to segregate genera. Sleumer (1939) made new combinations in *Agapetes* for species from New Guinea with names in *Paphia* and placed all the New Guinea species he recognised (with the exception of *A. helenae*, which was placed in *Agapetes* series *Longifiles* Airy Shaw) in series *Graciles* Airy Shaw. Later (1960) he remarked "not a single character found in *Paphia* . . . differs from those found in the Asiatic species of *Agapetes*". However, Copeland (1931) and Airy Shaw (1948a, 1959) both thought that differences would be found between *Agapetes* sensu stricto and the Malaysian species also included in that genus. Airy Shaw (1959) placed *A. scortechinii*, from Malaya, in a monotypic section, *Pseudagapetes*, since he thought that it formed a link between *Agapetes* and the genera occurring farther to the east—*Paphia*, *Dimorphanthera* F.v.M. and *Costera* J. J. Sm.

The characters of external morphology obviously allow of no clear-cut decision, and during a general survey of the family (Stevens, 1971), it appeared that some anatomical characters might be of help in a re-examination of the problem. The most useful of these are the presence or absence of an hypodermis and of thickened cells adjacent to the abaxial epidermis and also the position of the phellogen.

The first part of the paper is a re-evaluation of the taxonomic position of these species over which there has been discussion; it is found that the morphological and anatomical evidence partly vindicates both views mentioned above. In the second part, three new species and one new subspecies of *Agapetes* recently collected in New Guinea are described.

TAXONOMIC POSITION OF AGAPETES IN THE AREA FROM MALAYA TO FIJI

Materials and Methods. The anatomical observations in this paper are derived from the examination of leaf and stem anatomy of sixty-four species of *Agapetes*. Forty-nine species of *Agapetes* from the Himalayan-Siam

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region have been examined, including members of all series and subseries recognised by Airy Shaw (1959) except for the monotypic series *Fasciculiflorae* Airy Shaw; this group of species will be referred to as 'continental *Agapetes*'. Twelve of the sixteen species of *Agapetes* recognised from the Malayan/Oceanic region (see Sleumer 1939, 1967), as well as three previously undescribed species from this area, have also been examined anatomically; these will be referred to as 'oceanic *Agapetes*'. Specimens examined are listed at the end of this paper: in addition, these specimens and material of most other species of the genus have been studied morphologically.

The anatomical data have been obtained for the most part from herbarium material. Leaves and portions of the stem have been boiled and softened, and hand sections cut at different points along the stem, petiole, leaf midrib and leaf margin. Wherever possible the nodal region of the young stem and an older stem where secondary thickening had started were examined, but limitations of the specimens quite frequently made this impossible. All data on xylem anatomy and pith type are given with reservation; more detailed studies may prove of interest.

Variation within Agapetes. The variation of most of the characters discussed is summarised in Table 1.

Oceanic *Agapetes* has very thick, coriaceous leaves with short, black hairs on the leaf margin and usually on the underside of the leaf as well. These hairs have heads which can hardly be differentiated from the stout stalks. *A. scortechinii* has hairs with long, slender stalks and an abruptly expanded head similar to those found on the leaf and elsewhere on some species of continental *Agapetes*. Some species of continental *Agapetes* have glandular spots near the base of the lamina margin; these are modified hairs.

In gross appearance the flowers of both groups of *Agapetes* are similar. Shape, size and texture of the calyx and corolla are comparable between the two groups, both also have some species with a winged calyx and/or corolla. The larger flowered species of continental *Agapetes* may have red-banded corollas which are curved in only four species: the corolla tubes of oceanic *Agapetes* are plain-coloured and are often, but not always, curved. Continental *Agapetes* sometimes has stamens weakly connate by anther thecae or tubules; despite the often considerable length of the thin tubules, the length of the terminal split is restricted. In oceanic *Agapetes* there is a tendency for the filaments to be connate, and the extent of the anther split is often considerable (less so in *A. scortechinii* and *A. vitiensis*). The falsely 10-locular ovary of continental *Agapetes* is formed by the inpushing of the wall of a 5-locular ovary, oceanic *Agapetes* is 5-locular; for diagrams of the various types, see Fig. 1, A-D.

The only previous work on the anatomy of the genus is that by Niedenzu (1890) on the leaf anatomy of a few species of continental *Agapetes*. It has been found in the course of this work that species of continental *Agapetes* which have been segregated as different genera at one time or another (in *Caligula* Klotzsch, *Corallobotrys* Hook. f., *Desmogyne* King & Prain and *Pentapterygium*) are all similar in leaf and stem anatomy. Within oceanic *Agapetes* there is also substantial agreement in anatomical details, although *A. scortechinii* is a little different (see Table 1).

	Vaccinium section *Epigynium*	Subgenus *Agapetes*	*Agapetes* Subgenus *Paphia* Section *Paphia*	Subgenus *Paphia* Section *Pseudagapetes*
Differential and diagnostic characters				
Leaves coriaceous	±	— or +	+	+
Multicellular leaf hairs	usually short stalked	—, or long stalked	short stalked	long stalked
Multicellular stem hairs	usually long stalked, or —	long stalked, or —	short stalked, or —	long stalked
Inflorescence >15-flowered	+	—, rarely +	—	—
Corolla <1 cm.	+	—, rarely +	—	—
Stamen fusion	anthers, or —	anthers, or —	filaments, or —	filaments
Ovary falsely 10-locular	+	+	—	— (see text)
Hypodermis present	—	—	+	+
Abaxial spongy tissue lignified	—	—	+	interrupted
Phellogen superficial	+	+	—	—
Non-differential characters				
Calyx and/or corolla winged	—	+, —	+, —	+
Stamens: filaments shorter than thecae	+	+, —	+, —	+
Petiole bundle closed	+	+, —	+	+
Lamina bundle bifacial	+	+, —	—	—

Table 1: Variation of some characters in *Vaccinium* section *Epigynium* and *Agapetes*

No species of continental *Agapetes* has an hypodermis, but it is present in all oceanic species and is often lignified (the number of layers in the hypodermis in these species is listed in the Appendix). The thickening and lignification of the spongy mesophyll next to the abaxial epidermis is restricted to their inner periclinal and anticlinal walls; in *A. vitis-idaea* all the spongy mesophyll tends to have thickened and lignified walls (see Fig. 1, E–L). Continental *Agapetes* does not have comparable tissue, although one species, *A. leptantha*, has some lignified cells in the body of the spongy mesophyll and a few species, e.g. *A. miranda* and *A. forrestii*, have rather thick-walled, rigid, but unlignified spongy mesophyll. Details such as the distribution of the sclereids in the petiole and midrib and the behaviour of the vascular bundle in its course through petiole and lamina are similar in the two groups. However, in small-leaved species of continental *Agapetes*, and also some big-leaved species like *A. moorei* and *A. macrostemon*, the vascular tissue of the petiole bundle is arcuate (open); in other large-leaved species it is circular (closed). In oceanic *Agapetes* the petiole bundle is always closed, despite the small size of the leaf in some species. Expanded vein endings, c. 60–120 μm in diameter, have been observed in some species of oceanic *Agapetes*.

In the stem of oceanic *Agapetes* the phellogen is initiated just inside the ring of fibres surrounding the phloem, i.e. in a deep-seated position; around the persistent leaves the phellogen becomes superficial. All species of continental *Agapetes* examined have a superficial phellogen initiated just below the epidermis. Some other characters of stem anatomy need more study; the occurrence of broader rays and broader vessels in the xylem of oceanic *Agapetes* is not an absolute difference, since there is overlap with continental *Agapetes* in both these characters. The thickening and lignification of the pith cell walls is irregular in a number of species in oceanic *Agapetes*; although some cells have very thick walls whilst others remain thin-walled there does not seem to be any size disparity in the cells. Thickening and lignification are not irregular in continental *Agapetes*.

Although it is difficult to observe the distribution of floral stomata from the fleshy flowers of *Agapetes*, the data obtained suggest that there is no difference between the two groups. Testa anatomy is poorly known, but in those species of continental *Agapetes* whose seeds were examined the testa cells were large and somewhat elongated, with variable wall thickening. In some species the testa becomes mucilaginous on wetting (see also Airy Shaw, 1968); these seeds have a green embryo. Oceanic *Agapetes* does not have elongated testa cells and the anticlinal and inner periclinal walls of the testa cells are considerably thickened; the embryo is white.

Evaluation of the variation in Agapetes. The variation pattern within *Agapetes* can be best appreciated by comparing it with the closely related genus *Vaccinium*. One or two species form links between mainland *Agapetes* and SE Asian sections of *Vaccinium*; *V. bulleyanum* (Diels) Sleum. and *A. pilifera* Hook. f. have been shuttled backwards and forwards between the two genera (e.g. see Sleumer, 1941; Airy Shaw, 1959). The sections of *Vaccinium* closest to mainland *Agapetes* are *Epigynium* (Kl.) Hook. f. and, to a slightly lesser extent, *Galeopetalum* J. J. Sm. and *Conchophyllum* Sleum. (nomenclature of sections follows Sleumer, 1941). Although the actual position of the dividing line between *Agapetes* and *Vaccinium* is somewhat

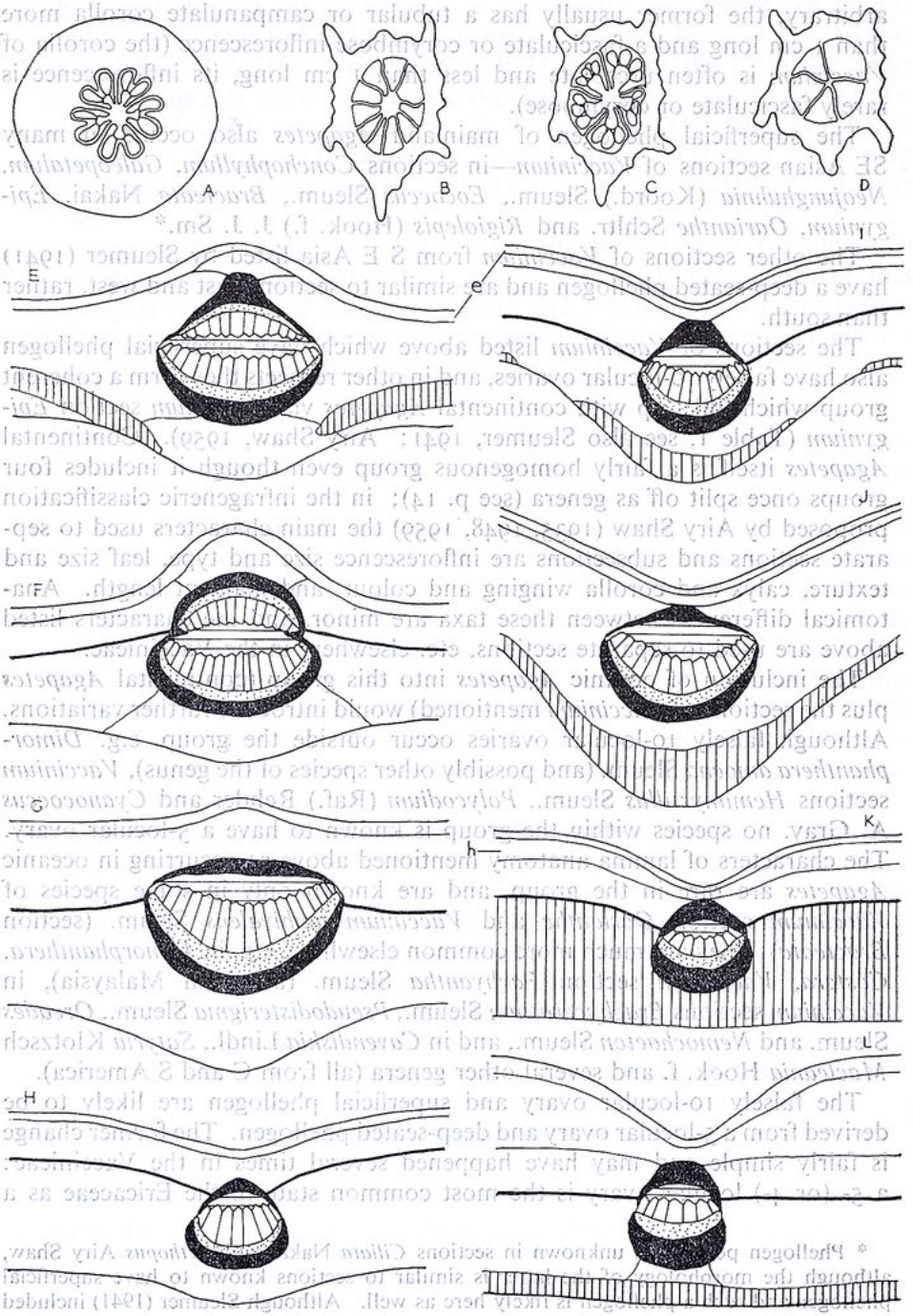

FIG. 1. Ovary and leaf anatomy in *Agapetes*. Transverse section ovary, A, *A. buxifolia*, × 5; B–D, *A. scortechinii*, × 2½, at the top, middle and base. Leaf anatomy, diagrammatic transverse section of the midrib region, E, *A. leptantha*, ×75; F, *A. odontocera*, × 66; G, *A. moorei*, × 66; H, *A. lacei*, × 50; I, *A. scortechinii*, × 25; J. *A. neo-caledonica*, × 40; K, *A. vitis-idaea*, × 33; L, *A. prostrata*, × 66. (e = epidermis + cuticle, h = hypodermis, heavy black line marks limit of palisade tissue where this is known, vertical ruling denotes lignified spongy mesophyll, solid black denotes fibres ± enclosing vascular bundles).

arbitrary, the former usually has a tubular or campanulate corolla more than 1 cm long and a fasciculate or corymbose inflorescence (the corolla of *Vaccinium* is often urceolate and less than 1 cm long, its inflorescence is rarely fasciculate or corymbose).

The superficial phellogen of mainland *Agapetes* also occurs in many SE Asian sections of *Vaccinium*—in sections *Conchophyllum*, *Galeopetalum*, *Neojunghuhnia* (Koord.) Sleum., *Eococcus* Sleum., *Bracteata* Nakai, *Epigynium*, *Oarianthe* Schltr. and *Rigiolepis* (Hook. f.) J. J. Sm.*

The other sections of *Vaccinium* from S E Asia listed by Sleumer (1941) have a deep-seated phellogen and are similar to sections east and west, rather than south.

The sections of *Vaccinium* listed above which have superficial phellogen also have falsely 10-locular ovaries, and in other respects they form a coherent group which links up with continental *Agapetes* via *Vaccinium* section *Epigynium* (Table 1, see also Sleumer, 1941; Airy Shaw, 1959). Continental *Agapetes* itself is a fairly homogenous group even though it includes four groups once split off as genera (see p. 14); in the infrageneric classification proposed by Airy Shaw (1935, 1948, 1959) the main characters used to separate sections and subsections are inflorescence size and type, leaf size and texture, calyx and corolla winging and colour, and filament length. Anatomical differences between these taxa are minor, and the characters listed above are used to separate sections, etc. elsewhere in the Vaccinieae.

The inclusion of oceanic *Agapetes* into this group (continental *Agapetes* plus the sections of *Vaccinium* mentioned) would introduce further variations. Although falsely 10-locular ovaries occur outside the group, e.g. *Dimorphanthera amoena* Sleum. (and possibly other species of the genus), *Vaccinium* sections *Hemimyrtillus* Sleum., *Polycodium* (Raf.) Rehder and *Cyanococcus* A. Gray, no species within the group is known to have a 5-locular ovary. The characters of lamina anatomy mentioned above as occurring in oceanic *Agapetes* are rare in the group, and are known only in some species of *Vaccinium* section *Oarianthe* and *Vaccinium ambivalens* Sleum. (section *Bracteata*); they are much more common elsewhere, e.g. in *Dimorphanthera*, *Costera*, *Vaccinium* section *Pachyantha* Sleum. (all from Malaysia), in *Vaccinium* sections *Brachyceratium* Sleum., *Pseudodisterigma* Sleum., *Oreades* Sleum. and *Nemochaeton* Sleum., and in *Cavendishia* Lindl., *Satyria* Klotzsch *Macleania* Hook. f. and several other genera (all from C and S America).

The falsely 10-locular ovary and superficial phellogen are likely to be derived from a 5-locular ovary and deep-seated phellogen. The former change is fairly simple and may have happened several times in the Vaccinieae: a 5- (or 4-) locular ovary is the most common state in the Ericaceae as a

* Phellogen position is unknown in sections *Ciliata* Nakai and *Aëthopus* Airy Shaw, although the morphology of the latter is similar to sections known to have superficial phellogen and such a phellogen is likely here as well. Although Sleumer (1941) included fourteen SE Asian species with the circumboreal *V. vitis-idaea* L. in section *Vitis-idaea* (Moench) Koch, *V. vitis-idaea* itself, with its deep-seated phellogen, anthers dehiscing by pores, 4-locular ovary, etc., is properly placed in a monotypic section most similar to some N American sections. The other species (excluding *V. paucicrenatum* Sleum. which was transferred to section *Aëthopus*, Airy Shaw, 1948b), probably all belong to section *Conchophyllum*. Section *Pachyantha*, from New Guinea, has deep-seated phellogen, a 5-locular ovary (see below) and a different stamen type and will be excluded from the discussion for the time being.

whole and there is no evidence of a 10-locular ovary being the original condition; in *Dimorphanthera* and oceanic *Agapetes* there are intermediate states between the two types (Fig. 1, B–D). Within the Ericaceae superficial phellogen is unknown outside the taxa mentioned which belong to a demonstrably fairly advanced tribe, the Vaccinieae. This tribe has inferior ovaries with compressed vasculature, (Palser, 1961), its stamen morphology is specialised, it lacks anther endothecium, etc.—all derived character states.

Hence mainland *Agapetes* has derived states in two of the characters separating oceanic from mainland *Agapetes*; the original states of these characters are found in oceanic *Agapetes* and a number of Vaccinieae from Malaysia and C and S America, and these similarly agree in a number of details in leaf anatomy (Stevens 1971: pp. 42–43).

Taxonomic position of oceanic Agapetes. The similarities between continental *Agapetes* and some SE Asian sections of *Vaccinium* are suggestive, yet there is only one morphological character which separates oceanic *Agapetes* from all continental *Agapetes*—the ovary type. Hair type is a useful supporting character, but *A. scortechinii* differs from the rest in this. There are also three anatomical differences separating the two: the hypodermis, the lignified spongy mesophyll next to the abaxial hypodermis and the deep-seated phellogen. The other characters discussed above, which are of inconstant occurrence within one group but which do not occur at all in the other, increase confidence in the separation of the two groups. In view of the distribution of the character states, as discussed above, it seems that oceanic *Agapetes* is best placed as subgenus *Paphia*, whilst subgenus *Agapetes* contains the continental species.

Within subgenus *Paphia* the monotypic section *Pseudagapetes* contains the very distinct *A. scortechinii*. The calyx tube of *A. scortechinii* is continuous with the pedicel (i.e. not articulated; *A. neo-caledonica* is the only other species like this) and has very prominent wings, and the calyx limb is longer than in the other species (c. 14 mm, as against less than 6 mm). Its ovary, as mentioned above, is 10-locular at the very top. Its anthers (Fig. 2, J) are bent inwards at the tubule-theca junction and dehisce by a slit of limited extent; this is somewhat different from the other species, although those of *A. sclerophylla* are not greatly dissimilar. *A. scortechinii* differs also in general facies and indumentum, and in lamina anatomy it differs in that the abaxial layer of lignified spongy cells is only poorly developed (see Table 1).

As mentioned above *A. neo-caledonica* also has a non-articulated calyx tube. In calyx, ovary, corolla, stamens, indumentum and anatomy it is like the other species of subgenus *Paphia* rather than *A. scortechinii*, and hence it is included with these species in section *Paphia*.

Agapetes D. Don ex G. Don, Gen. Syst. 3: 862 (1834).

Subgenus **Agapetes** (for a sectional and infrasectional classification see Airy Shaw, 1959, and references therein; not including section *Pseudagapetes*).

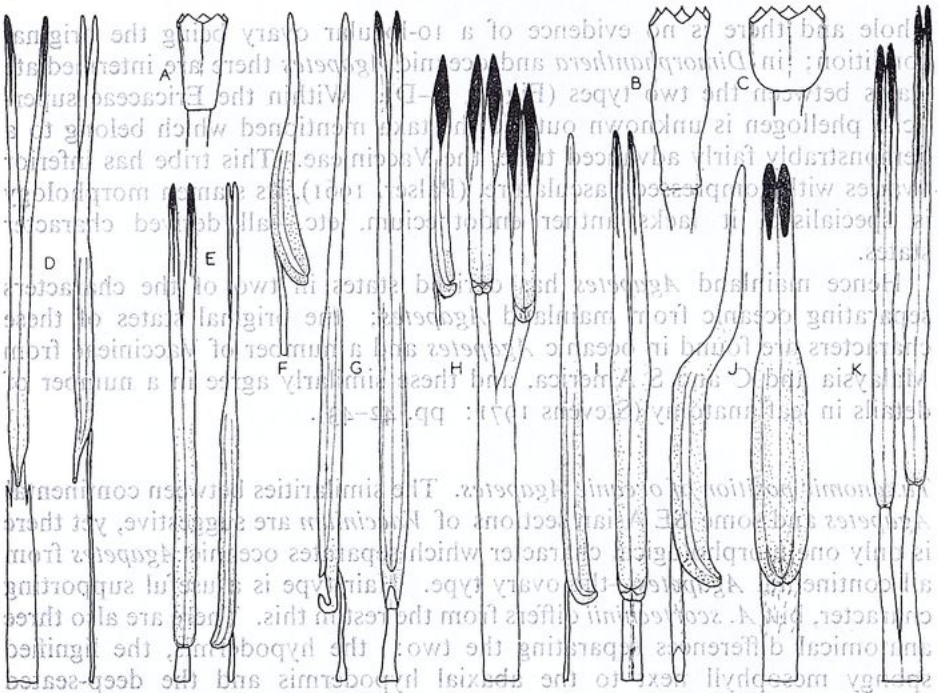

FIG. 2. Stamens and ovary of *Agapetes* subgenus *Paphia*. Ovary, × 3, A and C, *Agapetes stenantha*; B, *A. shungolensis*. Stamens, D, *A. shungolensis*. × 2½; E, *A. stenantha*, × 2½; F, *A. sclerophylla*, × 5; G, *A. vitiensis*, × 2½; H, *A. vitis-idaea*, × 5; I, *A. prostrata*, × 2½; J, *A. scortechinii*, × 5; K, *A. costata*, × 2½.

Subgenus **Paphia** (Seem.) Stevens, **comb. et stat. nov.**
Syn. *Paphia* Seem. in Journ. Bot. London 2: 77 (1864).
Sect. **Paphia** (Seem.) Stevens, **stat. nov.**
18 species: New Guinea, Australia, New Caledonia and Fiji. Type: *A. vitiensis* (Seem.) Drake.
Sect. **Pseudagapetes** Airy Shaw in Kew Bull. 3: 511 (1959).
1 species: Malaya. Type: *A. scortechinii* (King & Gamble) Sleum.

NEW SPECIES AND SUBSPECIES OF AGAPETES IN NEW GUINEA

The majority of the species of *Agapetes* subgenus *Paphia* occur in New Guinea; of the sixteen species previously recognised, eleven are endemic there. Of the other five, *A. meiniana* and *A. queenslandica* are endemic to Queensland, Australia, *A. neo-caledonica* to New Caledonia, *A. vitiensis* to Fiji and *A. scortechinii* to Malaya. Thirteen out of the fourteen New Guinea species presently known are found on the mountains between Mt Shungol (6° 50′ S, 145° 45′ E) and Mt Victoria (8° 55′ S, 147° 35′ E), a distance of only some 250 km. *A. rubrocalyx* is the only exception, being known only from the mountains of the Huon Peninsula and the Western Highlands District. *A. stenantha* and *A. vitis-idaea* also occur elsewhere (*A. stenantha* grows on Mt Maneau, Mt Dayman and Goodenough Island, *A. vitis-idaea* is found in the Saruwageds and the Western and Eastern Highlands Districts); all the other species are apparently endemic to this small area. No other angiosperm genus in New Guinea is known with such a concentration of species in the south-east.

Agapetes brassii Sleum. ssp. **serratifolia** Stevens, **subspecies nova.**

Folia 2·8–5·4 × 1·3–2·5 cm, ovata, apice breviter acuminata, marginibus serratis, ad apicem serraturarum pilis crassis nigris glanduliferis praedita, in pagina inferiore pilis nullis. *Flores* 2–4 fasciculati; pedicellus 1·2–2·7 cm, apice pilis crassis nigris praeditus. *Calyx* glaber, 10–11·5 mm longus in toto, limbo circa 2 mm, lobis 1 mm. *Corolla* 2·7–3·3 cm, albida, plus minusve glabra. *Filamenta* apice pilis parvis in marginibus praedita. Aliter velut in ssp. *brassii*.

Papua. Central district, Tapini subdistrict, Mt Strong, summit ridge, 3445 m, (11,300 feet), 2 v 1971, *P. F. Stevens & M. J. E. Coode* LAE 51411 (holo. LAE) (Edge of subalpine forest. Small shrub, stems more or less arching, rooting at the base. Height 60 cm (2 feet); leaves dark green above, paler below, venation clear and reticulated above, only main laterals visible below. Flowers: calyx limb and pedicel purplish-green, corolla pale purplish-dirty white, slightly curved, anthers yellow, style green). Specimens sent to L, CANB, A, K, & E were seen before distribution. Ibid., 3475 m (11,400 feet), *P. F. Stevens & M. J. E. Coode* LAE 51342: LAE!, duplicates sent to L, BRI, CANB, A, K, E, BO, & SING were seen before distribution.

A. brassii ssp. *brassii* has larger leaves up to 12 cm long which are more or less oblong in shape and with a longer acumen; there are always dark, glandular hairs on the underside of the leaf, although they vary in density. Ssp. *brassii* has only 1–2 flowers together; these flowers have a calyx limb only up to 8 mm in all, and are pink or red in colour. Ssp. *brassii* has short white hairs on the corolla and the upper part of the pedicel. The pedicel of ssp. *serratifolia* lacks these hairs, but although the corolla also appears to be glabrous at least sometimes very minute hairs are visible under a × 20 lens. Ssp. *brassii* has not yet been collected above 2835 m, but it occurs in the same area as ssp. *serratifolia*.

Agapetes prostrata Stevens, **species nova** (Figs. 2I; 3).

Fructiculus sempervirens prostratus, usque ad 15 cm; rami teretes, pilis unicellularibus et paucis fuligineis multicellularibus glanduliferis praediti. *Folia* non aggregata; petiolus 2–3 mm, pilis unicellularibus et multicellularibus glanduliferis praeditus; lamina 1–2·4 × 0·7–1·8 cm, ovata vel elliptica, coriacea, 0·5 mm crassa, apice rotundata, apiculata, basi cuneata, integra, margine anguste revoluto, ad marginem et supra pilis unicellularibus caducis supra prope costam et subtus ubique pilis multicellularibus glanduliferis persistentibus praedita, costa supra impressa subtus elevata, venatione camptodroma obscura. *Inflorescentia* subfasciculata, floribus 1–2 in axillis defoliatis crescentibus, pedunculo 1–3 mm longo; pedicellus 4–5 mm crassiusculus, pilis unicellularibus et multicellularibus hic apice numerosioribus praeditus, bractea basali 1 mm, ovata, apice acuta, bracteolis 2 oppositis 1 mm supra basin pedicelli, ovatis, apicibus acutis, 1–1·75 mm. *Calyx* pilis unicellularibus praeditus, tubo 4 mm leviter 5-angulato, basi truncato cum pedicello articulato, limbo 4·5 mm erecto, lobis 5 circa 2·75–3 mm. *Corolla* tubularis, 30 × 5 mm, carnosa, extra pilis unicellularibus praedita, intus glabra, tubo rubro, lobis 5 acutis, 2·5 mm ochroleucis. *Stamina* 10, fere isomorpha; filamenta glabra, circa 3 mm, libera; antherae 23 mm, thecis 13–14 mm, granulatis, basi acutis leviter incurvatis, tubulis

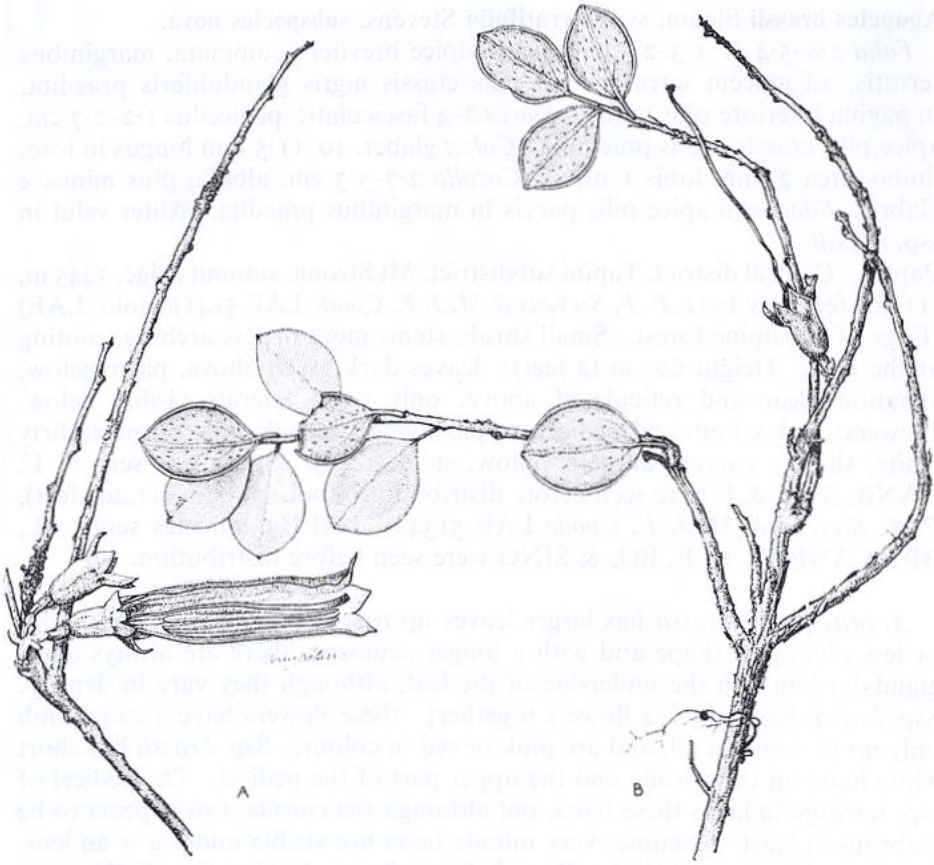

FIG. 3. *A. prostrata* Stevens (from *N.G.F.* 17925, natural size). A, inflorescence and opened flower; B, young fruit and leafy twigs. Only the side branches come above the moss, the two main axes eventually root (there are a few small roots on B).

laevibus per rimas elongatas aperientibus. *Ovarium* inferum 5-loculare; discus glaber; stylus 29 mm, stigmate truncato. *Bacca* juvenilis 7·5 × 7 mm (limbo calycis excluso), seminibus numerosis brunneis 1·5 × 0·6 mm, aliquantum complanatis; cellulae testae plus minusve rhombicae, parietibus exterioribus periclinalibus exceptis incrassatis.

Territory of New Guinea. Morobe district, S of Wau, Mt Amungwiwa, 7° 30′, long. 140° 40′ E, 11,400 feet (3,474 m), 3 xi 1963, *J. S. Womersley* NGF 17925 (holo. LAE). (Alpine shrubbery, prostrate among moss, height 6 inches (15 cm). Flowers red, corolla tips cream; anthers all same length). Morobe District, Mt Amungwiwa, 3352 m, x 1963, *Rosenberg* 44B, LAE! (A mixed collection; collected with *A. vitis-idaea*).

A. prostrata is a very distinct and interesting species. *A. helenae* has similarly small leaves and a corolla hairy on the outside, but differs from *A. prostrata* in having flowers borne in the upper leaf axils on 1·3 cm pedicels, a larger corolla (3·5–4 cm) which apparently has hairs on the inside, stamens with filaments 1·3 cm long and a smaller calyx limb only 3 mm long.

A. prostrata is distinguishable from all other members of the genus whose anatomy has been studied in having a 3-layered hypodermis; this is about

200 μm tall. In other species, the hypodermis may become locally 3-layered owing to an extra anticlinal division of an hypodermal cell; one collection of *A. stenantha* (LAE 50457) has an entirely 3-layered hypodermis but this is only about 100 μm tall. Most species of *Agapetes* have epidermal cells 25–40 (–50) μm across, but in *A. prostrata* (and *A. rubrocalyx*) they are 35–85 μm across. Although *A. rubrocalyx* has a 2-layered hypodermis, the hypodermal cells are large and similar to those of *A. prostrata*; the two species are also similar in facies, habit, inflorescence and indumentum. *A. rubrocalyx* has longer, acuminate leaves and a smaller, densely pubescent corolla; its stamens are smaller, but otherwise similar.

A. shungolensis Stevens, **species nova** (Figs. 2B, D; 4).

Arbor sempervirens usque ad 6·5 metra; ramuli teretes, glabri; gemmae axillares perulis 2 elongatis, 1–2 mm, brunneolis, anguste lanceolatis compositae. *Folia* non aggregata, prima folia incrementi novi multo minora; petiolus 0·4–0·5 cm, glaber; lamina 3·2–4·6 × 1·1–1·7 cm, elliptica vel obovata, brevissime acuminata, coriacea, margine serrulato parum recurvato, pilis crassis nigris glanduliferis apicibus serrularum praedito, costa supra impressa (sed imo elevata), subtus manifeste elevata, nervis lateralibus supra obscuris, infra leviter elevatis, circa 3-jugis, ascendentibus. *Flores* solitarii vel 2-fasciculati in axillis foliatis crescentes; pedicellus 12–15 mm, paulo gracilis sed apicem versus crassior, glaber, bractea 1·5 mm, ovata apice acuta, bracteolis 2 suboppositis, circa 1·5 mm supra basin pedicelli, ovato-lanceolatis, apicibus acutis, 2–2·5 mm. *Calyx* glaber, tubo 5·5 × 2·5 mm, tereti, aliquantum angustato apicem basinque versus, cum pedicello articulato, limbo 1·2 mm, effuso, lobis circa 0·9 mm. *Corolla* tubularis, 3–3·2 × 0·3 cm, leviter curvata et apicem versus aliquantum dilatata, carnosa, glabra, lobis 5, 1·2–1·5 mm, acutis. *Stamina* 10, fere isomorpha; filamenta glabra, 8–10 mm, per majorem partem longitudinum connata; antherae 22–24 mm, thecis 10–12 × 0·5 mm, granulatis, basi in processus 2 acutos deorsum intendentes attenuatis, tubulis laevibus per rimas elongatas aperientibus. *Ovarium* inferum, 5-loculare; discus glaber; stylus 32–35 mm, curvatus, tandem exsertus, stigmate truncato. *Fructus* non visi.

Territory of New Guinea. Morobe district, Mt Shungol, c. 5 miles (8 km) S of Wagau, c. 7,000 feet (2287 m), 17 xii 1963, *C. D. Sayers* under *T. G. Hartley* 12561 (holo. LAE). (Tree about 20 feet × 2 inches (6m × 5 cm) in lower moss forest. Outer bark silvery grey, with very shallow longitudinal fissures; inner bark orange brown). Duplicates sent from A to CANB, L, K, BRI, US, RSA.

A. shungolensis is clearly allied to, but distinct from *A. stenantha*. It is easily separable by its longer filaments (10–12 mm, as against 1–3 mm), anthers with downwardly, and not inwardly, pointing processes (Fig. 2, E, D,) and a longer and relatively much narrower calyx tube which is quite unribbed (Fig. 2, A–C). No multicellular hairs were seen on the abaxial surface of the leaf, although in *A. stenantha* these are always present and are very numerous (often over 1,000).

A. alberti-eduardi has only a few multicellular hairs on the lower surface of its leaves; and it also differs from *A. shungolensis* in leaf shape, bracteole

FIG. 4. *A. shungolensis* Stevens (from *Hartley* 12561, natural size).

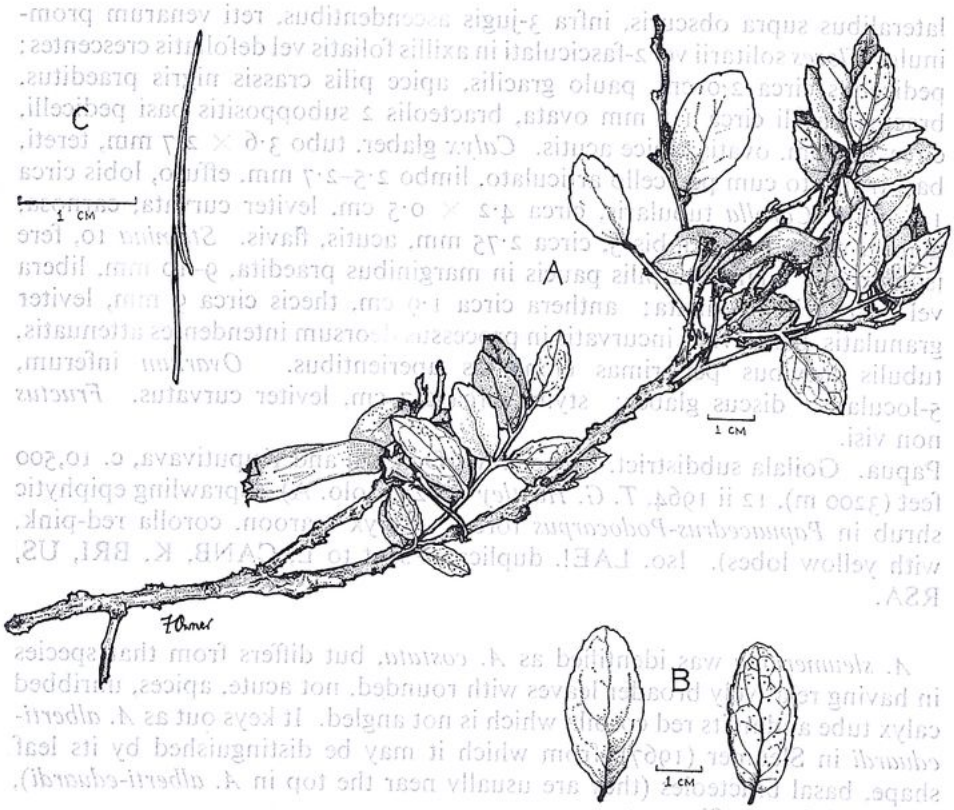

FIG. 5. *A. sleumeriana* Stevens (from *Hartley* 13028) A, shoot; B leaf from above and below; C. stamen from the side.

position, calyx length and stamen type. The calyx tubes of some collections of *A. alberti-eduardi* are similar in shape to those of *A. shungolensis*.

A. shungolensis is distinguishable from most other species in lamina anatomy because the walls of the inner layer of the two-layered hypodermis are so much thickened that the lumina are almost obscured. This also occurs in some, but not all, collections of *A. alberti-eduardi*; three collections from lower altitudes (c. 2775–2900 m) lacked such extremely thickened walls, whilst in two (including the isotype) from higher altitudes (c. 3350–3590 m), the walls were very much thickened. This thickening does not seem simply to become more pronounced with increasing age of the leaf: *A. shungolensis* grows at lower altitudes than any of the collections of *A. alberti-eduardi* studied.

Agapetes sleumeriana Stevens, **species nova.** Fig. 5.

Frutex; ramuli teretes, pilis parvis praediti, glabrescentes; gemmae axillares perulis 1 mm longis compositae. *Folia* non aggregata, prima folia incrementi novi multo reducta; petiolus 1·5–2·5 mm, glaber; lamina 2·2–4·5 × 1–1·6 cm, ovata vel oblonga, apice rotundata vel subacuta, basi plus minusve truncata, coriacea, marginibus leviter recurvatis, serrulatis, pilis crassis nigris glandiferis apicibus serrularum et circa 25–45 in pagina inferiore praeditis, costa supra impressa (sed imo elevatas), infra elevata, nervis

lateralibus supra obscuris, infra 3-jugis ascendentibus, reti venarum prominulo. *Flores* solitarii vel 2-fasciculati in axillis foliatis vel defoliatis crescentes; pedicellus circa 2·0 cm, paulo gracilis, apice pilis crassis nigris praeditus, bractea basali circa 1·2 mm ovata, bracteolis 2 suboppositis basi pedicelli, circa 1·4 mm, ovatis, apice acutis. *Calyx* glaber, tubo 3·6 × 2·7 mm, tereti, basi truncato cum pedicello articulato, limbo 2·5–2·7 mm, effuso, lobis circa 1·2 mm. *Corolla* tubularis, circa 4·2 × 0·5 cm, leviter curvata, carnosa; glabra, rubro-rosea, lobis 5, circa 2·75 mm, acutis, flavis. *Stamina* 10, fere isomorpha; filamenta pilis paucis in marginibus praedita, 9–10 mm, libera vel basi leviter connata; anthera circa 1·9 cm, thecis circa 9 mm, leviter granulatis, basi leviter incurvatis in processus deorsum intendentes attenuatis, tubulis laevibus per rimas elongatas aperientibus. *Ovarium* inferum, 5-loculare; discus glaber; stylus circa 2·7 cm, leviter curvatus. *Fructus* non visi.

Papua. Goilala subdistrict, between Mt Dickson and Kuputivava, c. 10,500 feet (3200 m), 12 ii 1964, *T. G. Hartley* 13028 (holo. A). (Sprawling epiphytic shrub in *Papuacedrus-Podocarpus* forest. Calyx maroon, corolla red-pink, with yellow lobes). Iso. LAE!. duplicates sent to L, CANB, K, BRI, US, RSA.

A. sleumeriana was identified as *A. costata*, but differs from that species in having relatively broader leaves with rounded, not acute, apices, unribbed calyx tube and in its red corolla which is not angled. It keys out as *A. alberti-eduardi* in Sleumer (1967), from which it may be distinguished by its leaf shape, basal bracteoles (they are usually near the top in *A. alberti-eduardi*), and much longer filaments.

AGAPETES SPECIES EXAMINED ANATOMICALLY

Agapetes subgenus Agapetes: A. acuminata D. Don ex G. Don—*Griffith*; A. affinis (Griff.) Airy Shaw—*Hooker & Thomson*, Khasia; A. angulata (Griff.) Hook. f.—*Keenan & al.* 3939; A. angustifolia Knagg—*Kingdon Ward* 5566, *Keenan & al.* 3171; A. auriculata (Griff.) Hook. f.—*Ludlow & Sherriff* 7236; A. brachypoda Airy Shaw—*Kingdon Ward* 3066; A. bracteata Hook. f.—*Lobb*, Moelmin; A. burmanica W. E. Evans—*Farrer* 1912; A. buxifolia Nutt.—Cult, Edinburgh *C.* 751; A. forrestii W. E. Evans—*Forrest* 27755; A. griffithii Clarke—Nullah at 1524 m, (collector unknown); A. hosseana Diels—*Winit* 1342, *Hosseus*, Siam, 19 i 1905; A. hyalocheilos Airy Shaw—*Keenan & al.* 3205; A. incurvata (Griff.) Sleumer—*Lace* 2303, *Ludlow & al.* 7224; A. interdicta (Hand.-Mazz.) Sleumer—*Farrer* 1517; A. lacei Craib—*Forrest* 26990, *Forrest* 21597; A. leptantha Airy Shaw—*Kingdon Ward* 5541; A. linearifolia Clarke—*Kingdon Ward* 8021; A. lobbii Clarke—*Keenan & al.* 3468; A. neriifolia (King & Prain) Airy Shaw—*Keenan & al.* 3368A, *Kingdon Ward* 21302, *Forrest* 9107; A. macrophylla Clarke—*Kingdon Ward* 8032; A. macrostemon Clarke—*Robertson* 131; A. mannii Hemsl.—Cult. Edinburgh; A. megacarpa W. W. Smith—French Consul, Yunnan; A. miniata (Griff.) Hook. f.—Herb. the late East India Company 3475; A. miranda Airy Shaw—*Ludlow & al.* 3718; A. oblonga Craib—*Yü* 20539; *Forrest* 29355; A. obovata (Wight) Hook. f.—Cult. Edinburgh; A. odontocera (Wight) Hook. f.—*Keenan* 3424; A. parishii Clarke—*Lace*, Burma, i 1912, *Kerr* 10364; A. pensilis Airy Shaw—*Yü* 20038; A. pilifera Hook. f.—*Hooker & Thompson*, Khasia; A. praeclara Marquand—*Ludlow & al.* 12262; A. pseuso-griffithii Airy Shaw—*Kingdon Ward* 5551; A. pubiflora Airy Shaw—*Yü* 21058; A. pyrolifolia Airy Shaw—*Kingdon Ward* 5477; A. refracta Airy Shaw—*Cox & Hutchinson* 487; A. salicifolia Clarke—Herb. the late East India Company 3477; A. saligna Hook. f.—*Ludlow and Sherriff* 2926, *Cooper* 3623; A. saxicola Craib—*Sørenson* 2378; A. serpens (Wight) Sleumer—Cult. Edinburgh *C.* 750; A. setigera D. Don—*Griffith*, Khasia, 1844; A. similis Airy Shaw—*Cox & Hutchinson* 550;

A. smithiana Sleumer—Cult. Kew from *Cox & Hutchinson* 413; A. spissa Airy Shaw—*Kingdon Ward* 8479; A. toppinii Airy Shaw—*Keenan & al.* 3409; A. variegata (Roxb.) D. Don ex G. Don—Cult. Edinburgh, *Hooker & Thompson*, Khasia, 4000 feet; A. vernayana Merrill—*Kingdon Ward* 3697; A. wardii W. W. Smith—*Farrer* 829, *Kingdon Ward* 20602.

Agapetes subgenus Paphia (the number in parenthesis after the species name refers to the number of layers of the hypodermis)

Section Paphia

A. alberti-eduardi Sleum. (2)—*Woods* 3018, *Brass* 4380, *Ridsdale* N.G.F. 36823, *Foreman and Wardle* N.G.F. 45508, *van Royen* N.G.F. 30014, *Foreman* N.G.F. 48372; A. brassii Sleum. ssp. brassii (2)—*Hartley* 12820, *van Royen* N.G.F. 20401; Ssp. serratifolia Stevens (2)—*Stevens & Coode* LAE 51342, 51411; A. costata Wright (2)—*Woods* 3001, *van Royen* N.G.F. 30053, *Ridsdale* N.G.F. 36849, *Foreman & Wardle* N.G.F. 45536, *Coode & Stevens* N.G.F. 46304; A. helenae (F. v. M.) F. v. M. ex Sleum. (2)—*MacGregor* Mt. Victoria, 1889; A. meiniana F. v. M. (2)—*Brass* 20145; A. neo-caledonica Guill. (1)—*McKee* 8209; A. prostrata Stevens (3)—*Womersley* N.G.F. 17925, *Rosenberg* 44B; A. rubrocalyx Sleum. (2)—*Pullen* 5032, *Vink* 16023; A. sclerophylla Sleum. (2)—*Woods* 3067, *Hartley* 12769; A. shungolensis Stevens (2)—*Sayers* for *Hartley* 12561; A. sleumeriana Stevens (2)—*Hartley* 13028; A. stenantha (Schltr.) Sleum. (2–3)—*Cruttwell* 523, *Brass* 22272, 22572, 22948, 24775, *Stevens* LAE 50457; A. vitis-idaea Sleum. (2)—*Pullen* 5004, *van Balgooy* 620, *Brass & Collins* 31017, *Rosenberg* 44A, *Pullen* 226, *Gillison* 147, *Womersley* N.G.F. 5189, *van Royen* N.G.F. 18096; A. vitiensis (Seem.) Drake (1)—*Koriveibau & Kuruvoli* Flora of Fiji 13964, *Kuruvoli & Vodonaivalu* Flora of Fiji 15465.

Section Pseudagapetes

A. scortechinii (King & Gamble) Sleum. (1)—*Scortechini* 309, *Burkill* 797, *Melville & Landon* 4822, *Woods* 662.

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