



Testa and seed appendage morphology in *Aeschynanthus* (Gesneriaceae): phytogeographical patterns and taxonomic implications

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The current sectional classification of the genus *Aeschynanthus* Jack, essentially based on seed morphology, presents some problems of species placement. A comparative SEM survey of seed and seed appendages was undertaken in order to assess the value of this classification. Seeds of 99 taxa (that is about two-thirds of the estimated total) were examined and found to fall into two types, A and B. Type A has spiral testa cell orientation, papillae formed from a single cell and short smooth appendages. Type B is recognized by the straight orientation of the testa cells, combined with the presence of papillae formed from the raised ends of two adjacent cells on the long hair-like appendages and usually on the testa. Only six of the investigated species did not fall into either category. Three have \pm straight testa cell orientation combined with single-cell papillae and short smooth appendages; the papillae and appendage characters place them in type A. Three have spiral testa cell orientation and short smooth appendages but the testa cells have slightly raised ends; these are also placed in Type A. The three subtypes in Type A are equivalent to the sections *Haplotrichium s.s.*, *Microtrichium* and *Aeschynanthus*, but the divisions are less clear than those within Type B. However, other morphological characters support sectional separation. Type B subdivides into three: two subtypes equivalent to sections *Polytrichium* and *Diplotrichium*, and a third encompassing section *Xanthanthos* together with part of the current sect. *Haplotrichium*, and here referred to as sect. *X*. There is sufficient morphological correlation with seed type to make the sectional position of many species clear without recourse to seed, particularly in sects *Polytrichium*, *Diplotrichium*, *Haplotrichium s.s.* and *Aeschynanthus*. There is strong correlation between seed type and geographical distribution. Sects. *Microtrichium* and *Aeschynanthus*, with Type A seed, are essentially Malesian. Groups with Type B seed are largely confined to mainland south and south-east Asia, except for sect. *Polytrichium* which is more widespread, possibly due to the greater effectiveness of a coma of hairs in wind dispersal. It is suggested that Type A seed, probably sect. *Microtrichium*, is the least determined and Type B sect. *Polytrichium* the most derived seed type. Based on these findings a revised key to the sections is provided

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ADDITIONAL KEYWORDS: morphology – phylogeny – phytogeography – sectional delimitation – SEM survey – taxonomy.

INTRODUCTION

The genus *Aeschynanthus* (Gesneriaceae; subfamily Cyrtandroideae; tribe Trichosporeae) consists of approximately 150 species which are mostly epiphytic subshrubs with thick leathery leaves and tubular, usually brightly coloured, strongly protandrous flowers producing copious nectar, suggesting pollination by birds. They are distributed from the Himalayas and

southern India east to southern China, and throughout south-east Asia and Malesia to the Solomon Islands (Fig. 1). Although the genus is widespread, there is a high degree of local endemism at the species level. Within the Old World subfamily Cyrtandroideae, which is characterized by the development of unequal cotyledons soon after germination, the tribe Trichosporeae possess seeds with at least one, often hair-like appendage, at each end, to which the name refers. *Aeschynanthus* fruits are long slender capsules containing many anatropous ovules, with the hilar end pointing towards the apex of the capsule and the apical

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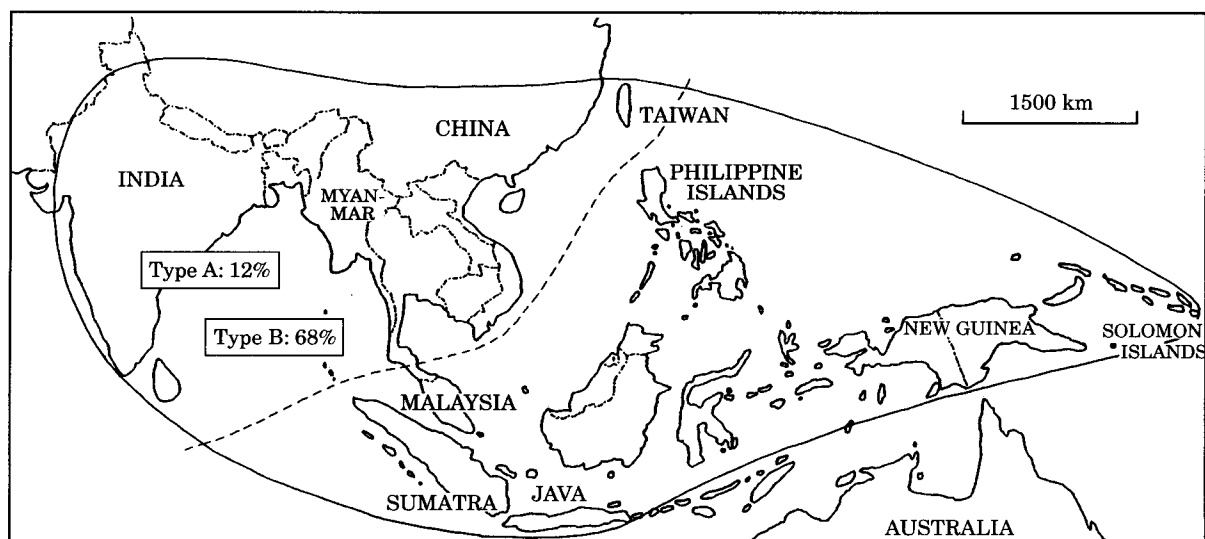


Figure 1. Map showing the distribution of the genus *Aeschynanthus*, and, of the species examined, the % occurrence of the two seed types. For species with Type A seed, only 12% occur on mainland Asia (8 out of 65 spp.) while 88% are Malesian (57 out of 65 spp.). For species with Type B seed, 68% (23 out of 34 spp.) are mainland Asian while 32% (11 out of 34 spp.) are Malesian; 5 of the 11 are in sect. *Polytrichium*.

end towards the base. The number and type of hilar appendage has been used to subdivide the genus into sections. Bentham (1876) recognized four sections, all with a single appendage at the apical end: *Polytrichium*, with many appendages at the hilar end; *Diplotrichium*, with two appendages at the hilar end; *Haplotrichium*, with a single appendage at the hilar end combined with a deeply divided calyx; and *Holocalyx* (now sect. *Aeschynanthus*) with a single appendage at the hilar end and a shallowly lobed calyx. Clarke (1883) added a fifth section, *Microtrichium*, with a short flat triangular appendage at each end; he also noted the 'bubble cells' at the base of the hilar appendage in members of sect. *Aeschynanthus*. Schlechter's 1923 section *Anisocalyx* was reduced to sect. *Microtrichium* by Burt & Woods (1975). An additional section, *Xanthanthos*, based not on seed appendages but on corolla colour and shape, was created by Wang (1984) to accommodate a single Chinese species. He also divided sect. *Haplotrichium* into two series, *Bracteati* and *Novograciles*. The current classification is summarized in Table 1.

The seed of many species is not known, so their assignment to sections is only tentative. There is some correlation with other taxonomic characters, but this is not always reliable and has in the past resulted in some inaccurate placements. Clarke (1883), for instance, placed *A. arfakensis* C.B. Clarke (sect. *Polytrichium*), and *A. leptocladus* C.B. Clarke and *A. philippinensis* C.B. Clarke (both now known to be in sect. *Microtrichium*) all in sect. *Haplotrichium*. In addition, some species cannot be placed with certainty

Table 1. Current classification of *Aeschynanthus* (sections in alphabetical order)

Sect. <i>Aeschynanthus</i> (=sect. <i>Holocalyx</i> Benth.); type species <i>A. volubilis</i> Jack
Sect. <i>Diplotrichium</i> Benth.; type species <i>A. parasiticus</i> (Roxb.) Wall.
Sect. <i>Haplotrichium</i> Benth.; type species <i>A. bracteatus</i> [Wall. ex] DC. series <i>Bracteati</i> W.T. Wang; type species as for section series <i>Novograciles</i> W.T. Wang; type species <i>A. novogracilis</i> W.T. Wang (= <i>A. gracilis</i> [Parish ex] C.B. Clarke)
Sect. <i>Microtrichium</i> C.B. Clarke (including sect. <i>Anisocalyx</i> Schltr.); type species <i>A. microtrichus</i> C.B. Clarke
Sect. <i>Polytrichium</i> Benth.; type species <i>A. longicaulis</i> [Wall. ex] R.Br.
Sect. <i>Xanthanthos</i> W.T. Wang; type species <i>A. denticuliger</i> W.T. Wang

in any one section on seed appendages alone. For example, Mendum (1999) placed *A. argentii* Mendum in sect. *Haplotrichium* on the basis of long appendages, but the present study clearly shows it to be in sect. *Microtrichium*. The demarcations particularly between sections *Microtrichium*, *Haplotrichium* and *Aeschynanthus* are not clear. This study attempts to clarify the sections, and the sectional position particularly of those species with seeds having intermediate characters. It also discusses the implications of seed morphology in terms of distribution patterns and sectional relationships.

Seeds of as many species of *Aeschynanthus* as possible were examined under the SEM, and morphologies of both the seed testa and appendages were compared. Previous studies (Ivanina, 1966; Beaufort-Murphy, 1983) did not examine the structure of the appendages, which in this study was found to be of equal importance. However, they were working with a limited number of species in the context of a much wider survey of seed morphology across the whole family.

MATERIAL AND METHODS

Ripe seed was extracted from capsules on herbarium specimens and from plants which had been selfed in the living collection at RBGE and HBV. Some inter-sectional hybridization was also attempted in order to investigate sterility barriers. Measurements of seed and seed appendages were taken before mounting on aluminium stubs using either Tempfix or carbon discs (E), or double-sided tape (WU), coating with gold palladium for 2 × 2 minutes in an Emscope SC500 sputter coater, and examining with a Zeiss DSM962 scanning electron microscope (E) or a JEOL JSM T-200 (WU). Several factors had to be taken into consideration when extracting seed. Appendage length may vary somewhat, in particular it is shorter towards the ends of the capsule and therefore, wherever possible, seeds were extracted from near the middle. When ripe the seeds and their appendages are free, but when unripe they are difficult to separate and so are unsuitable for SEM work. However, depending on the stage of development of the seed, it may be possible to see sufficient detail for classification. In old dehiscent capsules a few seeds may remain but these are sometimes undeveloped, in which case they are tiny and have very short appendages; these were not used. Preliminary ontogenetic studies show that appendages grow early in seed development and so even infertile, collapsed seed is still valuable. Density of testa papillae may vary slightly between different collections of the same species and even between seeds in the same capsule.

Seeds of 89 named and 10 unidentified taxa (Appendix 2) were examined and grouped according to testa and appendage characters. Species in the resulting groups were compared, and distributions noted. Seed of one species each of *Agalmyla* and *Lysionotus* (both in tribe Trichosporeae) were examined for comparison.

RESULTS

CHARACTERS RECOGNIZED

The characters found to be significant during the course of this investigation are the orientation of the seed testa cells and the presence (or absence) and structure

of papillae on the testa and on the seed appendages. Orientation of the testa cells (looking along the length of the seed and away from the viewer) may be either straight or spiral, the latter either clockwise or in the majority of species anticlockwise (Figs 2, 4–6). Papillae are present on the testa in most species, and on the appendages in about a third of the species; in very few cases none occur. The papillae were found to be of two types: A, formed from a raised portion of a single cell (Figs 3A–C, 7, 8, 14); and B, formed from the raised ends of two adjacent cells and thus being divided by a straight or sinuous anticlinal cell wall (Figs 3D–F, 10–12, 15, 16). Seeds were grouped according to these characters. There is a strong correlation between spiral testa cell orientation, papillae formed by protrusions from single cells, and short smooth appendages (Fig. 2B–D), and straight orientation of the testa cells, the presence of papillae formed from two adjacent cells, and long hair-like appendages (Fig. 2E–G). Of the 99 taxa examined for this study (Appendices 1 and 2), only six did not fit into one of these groups. All of the six have short smooth appendages; three have seed with ± straight cell orientation combined with single-cell papillae (Figs 2A, 19), and three have spiral cell orientation but the testa cells are raised at the edges (Figs 3D, 9). On this basis, *Aeschynanthus* species may be split into two groups: those with spiral cell orientation and one-cell papillae (Type A), and those with straight cell orientation and two-cell papillae (Type B) (Figs 2, 3). The six anomalous species are also placed with Type A species. Type A seed, with a single appendage at each end and found in members of sects. *Haplotrichium* s.s., *Aeschynanthus* and *Microtrichium*, may be further subdivided on the basis of the direction of the spiral orientation of the testa cells and on the length, shape and bubble cell development of the appendages. Type B seed may be further subdivided on the basis of the number of appendages ('hairs') present at the hilar end of the seed (all have a single appendage at the apical end), and on features of the testa. Sections *Polytrichium* and *Diplotrichium* are readily recognizable on seed characters alone, and other morphological characters also link the species within these sections. Those Type B members of the current sect. *Haplotrichium* (hereafter referred to as sect. *X*) and sect. *Xanthanthos* both have seed with a single long appendage at the hilar end; the sections cannot be separated on seed morphology but require corolla characters. Sect. *X*, separated from sect. *Haplotrichium* s.s. whose members have Type A seed, cannot be adequately circumscribed until further morphological studies are complete. The results are summarized in Table 2, and are discussed in greater detail below.

Seed characters do appear to be sufficient for sectional separation of all but sect. *Xanthanthos*, and with

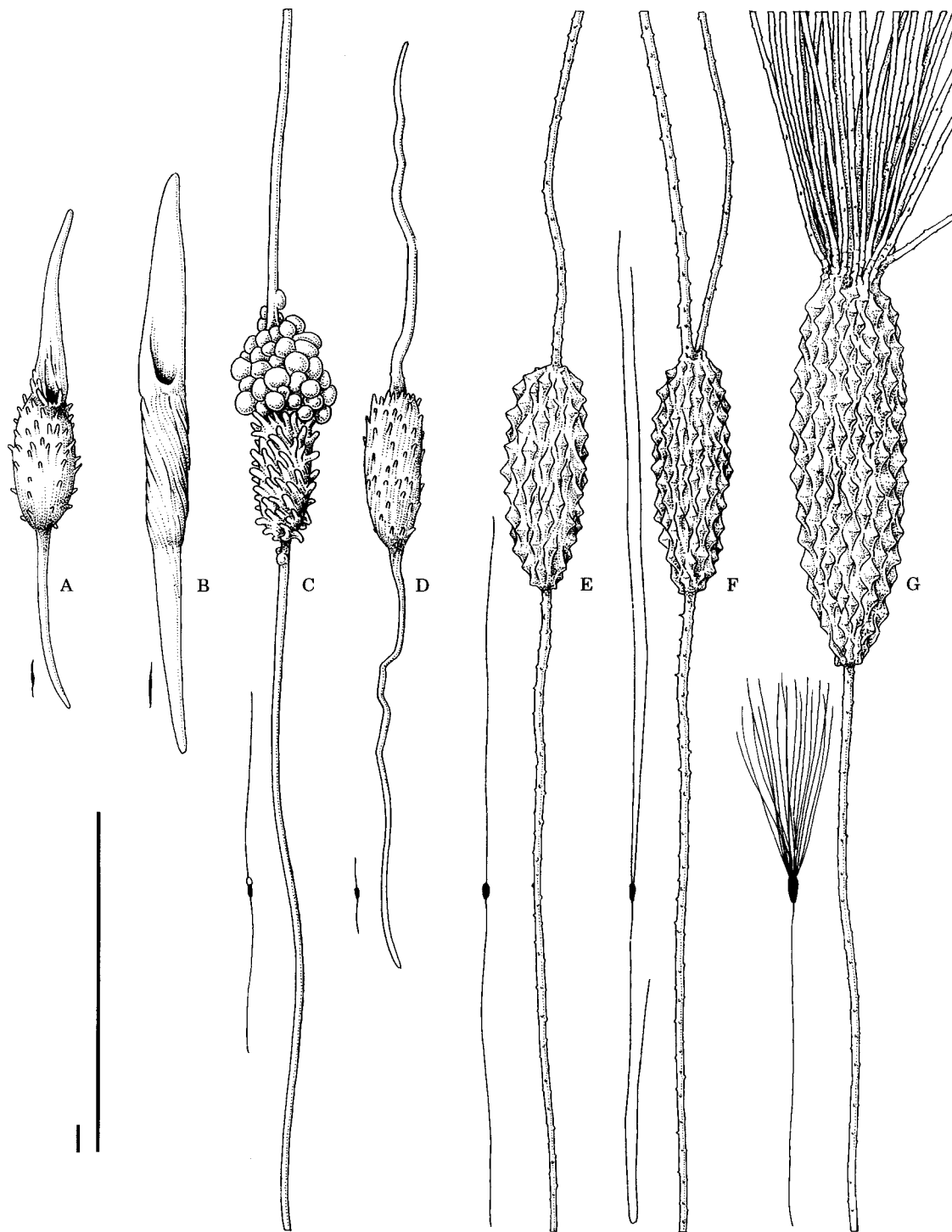


Figure 2. *Aeschynanthus* seeds, smaller scale to show relative length of appendages; subtypes in parentheses. A, *A. garrettii* [A1]; B, *A. musaensis* [A2a]; C, *A. curtisii* [A2c]; D, *A. bracteatus* [A3b]; E, *A. longiflorus* [B1]; F, *A. sikkimensis* [B2]; G, *A. arfakensis* [B3]. Scale bars = 2 mm. Seeds shown in functional orientation, with hilar end uppermost.

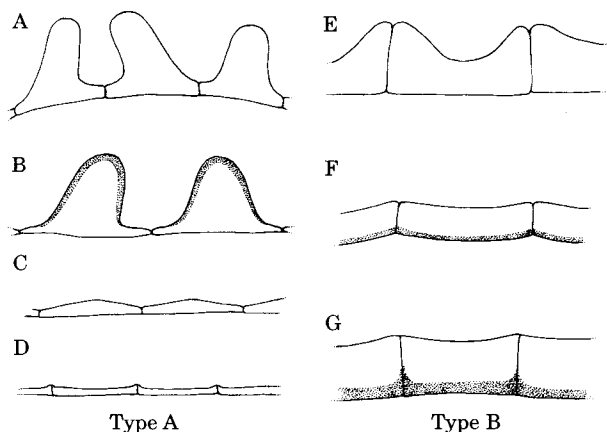


Figure 3. Diagrammatic TS testa. Type A single-celled papillae: A, unthickened, e.g. *A. parvifolius*; B, with thickened central band, e.g. *A. tricolor*; C, hardly developed, e.g. *A. oxychlamys*; D, possibly transitional between Type A & Type B testa, e.g. *A. moningeriae*. Type B two-celled papillae: E, pronounced, e.g. *A. albidus*; F, undulate with a little thickening at the base, e.g. *A. evardii*; G, almost smooth with greater thickening at the base, e.g. *A. humilis*.

the addition of calyx characters to distinguish sect. *Aeschynanthus*. The seed types and subtypes recognized, with sectional affiliations, are summarized in Appendix 1.

TYPE A

(Figs 2A–D, 3A–D, 4, 6–9, 13–14, 17–23, 24–27)

Orientation of testa cells spiral, in a few species clockwise and in the majority anticlockwise, with three species having \pm straight cell orientation. Papillae, formed from a protrusion of the outer periclinal wall of a single cell (Figs 3A–C, 7, 8) and either central or displaced towards the hilar end of the cell, are present on the seed testa of most species and usually concentrated towards the hilar end of the seed; in some cases the papillae have a thickened band running through the middle of the surface (outer periclinal wall (Figs 3B, 8). In three species the testa cells have raised margins (Figs 3D, 9). Appendages single at each end of the seed, in almost all species without papillae, giving a 'smooth' appearance visible under the light microscope. When papillae are present they are formed by a protrusion from the wall of a single cell (Fig. 14). Seed 0.6–1.2 mm with almost all species less than 1 mm, narrowly ovate to \pm cylindric. Appendages 0.7–15 mm long; length and shape fairly constant within species, but between species ranges from long and filiform (the longest at 15 mm overlaps slightly the shortest Type B appendage of 10 mm) to short and thick (0.6 mm and c. 0.25 mm at the base), and they

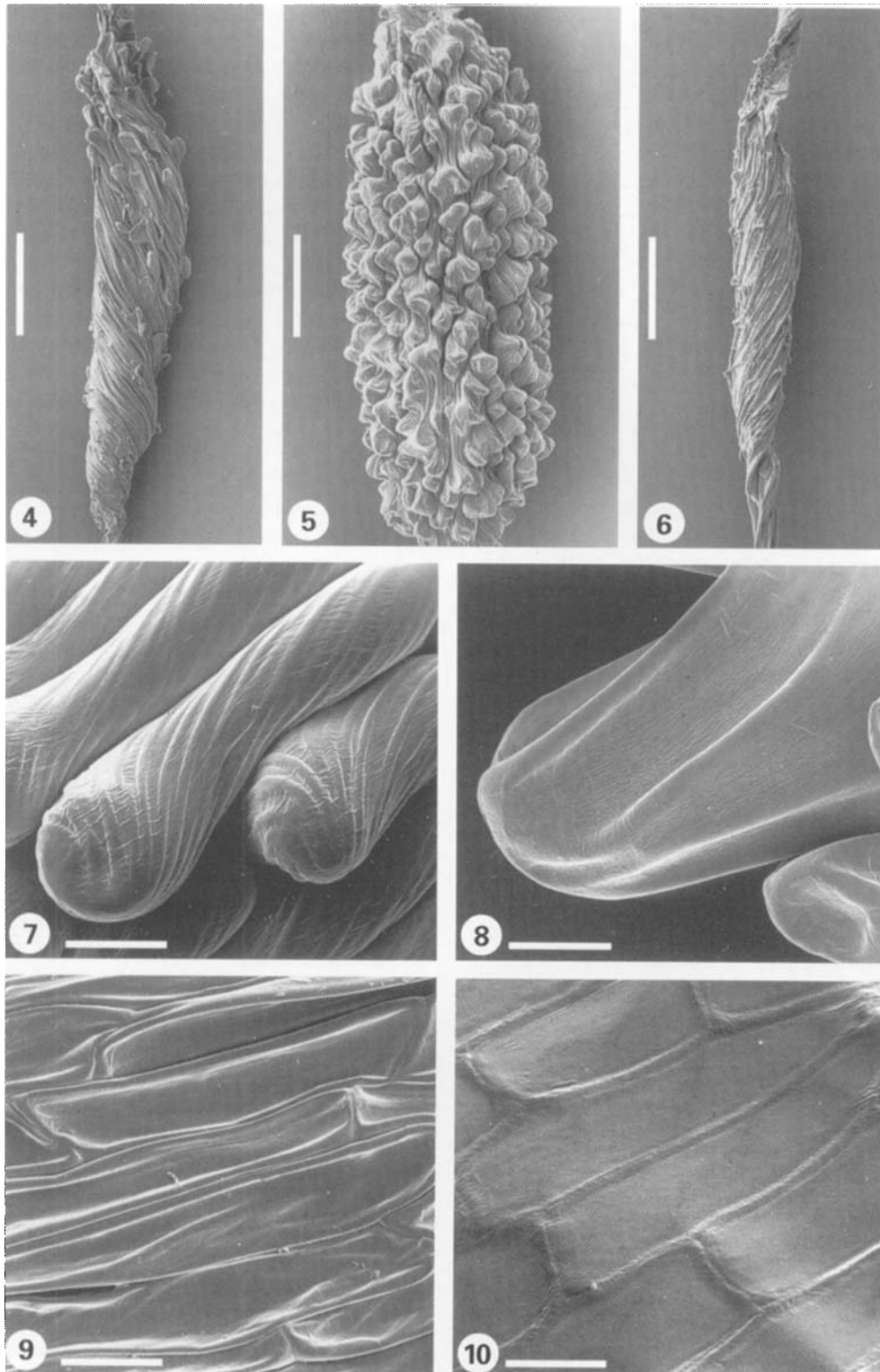
break at the base rather than along their length. Greater length is usually associated with the presence of prominent clusters of bubble cells at the base of the hilar appendage (Figs 21, 22), and sometimes also some bubble cell development at the base of the apical appendage. Less discrete clusters of smaller bubble cells also occur in a few species, associated with shorter thicker appendages (Fig. 20), and the shortest appendages are very broad and triangular. Species with Type A seeds are more numerous and morphologically much more diverse than those with Type B. They comprise all members of sect. *Microtrichium* and *Aeschynanthus* so far examined, together with about three-fifths of species thought to be in sect. *Haplotrichium* as previously understood.

Subtype A1: Testa cells with \pm straight orientation

Seed 0.8–1 mm long, narrowly oval; testa moderately to strongly papillose, cell orientation \pm straight; appendages 0.7–1 mm long, broad-based, conspicuous cavity leading to micropyle (Figs 2A, 19, 24). Three species examined: *A. buxifolius*, *A. garrettii*, *A. longicalyx*. Sect. *Microtrichium pro parte*? Appendages appear to be typical *Microtrichium* (Group A2a), but the testa is markedly different. Cell orientation is straight, or even very slightly clockwise in *A. garrettii*, and the testa is moderately to densely papillose especially towards the hilar end. Two of the species, *A. buxifolius* and *A. garrettii*, have in common a twiggy habit, warty stems, small divided calyces, corollas hairy inside the tube and exerted stamens; the former occurs in China and North Vietnam and the latter in Thailand and Vietnam. The third species, *A. longicalyx*, is from Peninsular Malaysia and has a 5 cm partly divided calyx and corolla to 8.7 cm, glabrous inside and stamens not exerted; it has many morphological similarities with *A. magnificus* and *A. vinaceus* (Group A2c).

Subtype A2: testa cells with slight to strong anticlockwise orientation

Group A2a. Seed 0.6–1.2 mm long, testa slightly to strongly spiral, papillae absent to moderate (in most species spiral moderate and papillae few); appendages 0.7–4.5 mm long (in most species between 1 and 2.5 mm), broad at base, bubble cells absent (Figs 2B, 4, 13, 17, 25). Twenty-six species examined: *A. argentii*, *A. calanthus*, *A. cardinalis*, *A. crassifolius*, *A. guttatus*, *A. horsfieldii*, *A. irigaensis*, *A. leptocladus*, *A. aff. leptocladus*, *A. microtrichus*, *A. miniaceus*, *A. montisucris*, *A. musaensis*, *A. oxychlamys*, *A. pachyanthus*, *A. philippinensis*, *A. pullei*, *A. ramosus* (ined.), *A. roseoflorus*, *A. solomonensis*, *A. sp. 1–6*. Sect. *Microtrichium pro parte typica*. The shortest hilar appendages are the broadest at the base and with a conspicuous cavity leading to the micropyle (Fig. 17), apical appendages



Figures 4–10. Testis surface details. Scale bars 4–6 = 200 μm , 7–10 = 20 μm . Fig. 4. Anticlockwise orientation of testis cells. *A. guttatus*, Woods 215 [A2a]. Fig. 5. Straight orientation of cells. *A. hookeri*, RBGE 19892128 [B2]. Fig. 6. Clockwise orientation of cells. *A. superbus*, King's collector s.n. [A3b]. Fig. 7. Cylindrical single-celled papillae. *A. longicalyx*, RBGE 19672365 [A1]. Fig. 8. Flattened single-cell papillae. *A. gibbsiae*, Clemens 28329 [A2c]. Fig. 9. Testis cell orientation clockwise, surface somewhat tessellated, approaching Type B surface. *A. moningeriae*, Liang 64183 [A3a]. Fig. 10. Hard thick testa, cells forming reticulate surface pattern. *A. andersonii*, RBGE 19970465 [B1a].

Table 2. Synopsis of types and subtypes

1a. Papillae when present 1-celled; appendages short, smooth; testa cell orientation spiral, rarely straight...	Type A
2a. Testa cells with \pm straight orientation; appendages short and broad	Subtype A1
2b. Testa cells with slight to strong anticlockwise orientation; appendages slender to short & broad...	Subtype A2
2c. Testa cells with slight to moderate clockwise orientation	Subtype A3
1b. Papillae 2-celled; appendages long and filiform, papillose; testa cell orientation straight.....	Type B
3a. Hilar appendage 1.....	Subtype B1
3b. Hilar appendages 2.....	Subtype B2
3c. Hilar appendages a coma of 5–60.....	Subtype B3

are less broad, e.g. *A. musaensis* and *A. philippinensis*. Longer appendages are more slender e.g. *A. argentii*. One collection of *A. pachyanthus* has slightly raised bumps arising from the centres of a few appendage cells. The size and number of testa papillae varies between species and to a lesser extent between seed even in the same capsule. Habit varies from stiff and twiggy to flexuous, and in contrast to the other sections the calyx shape ranges from tubular or even spathaceous to most commonly deeply divided. Flower colour ranges from greenish to purple with the majority red, and in only a few species are the stamens exerted. The pattern of distribution of hairs inside the corolla is significant for species recognition but appears not to bear any relation to seed morphology. Of the 26 species examined, one each occurs in Java, Seram, the Solomon Islands and Borneo, five in the Philippines, and 17 in New Guinea.

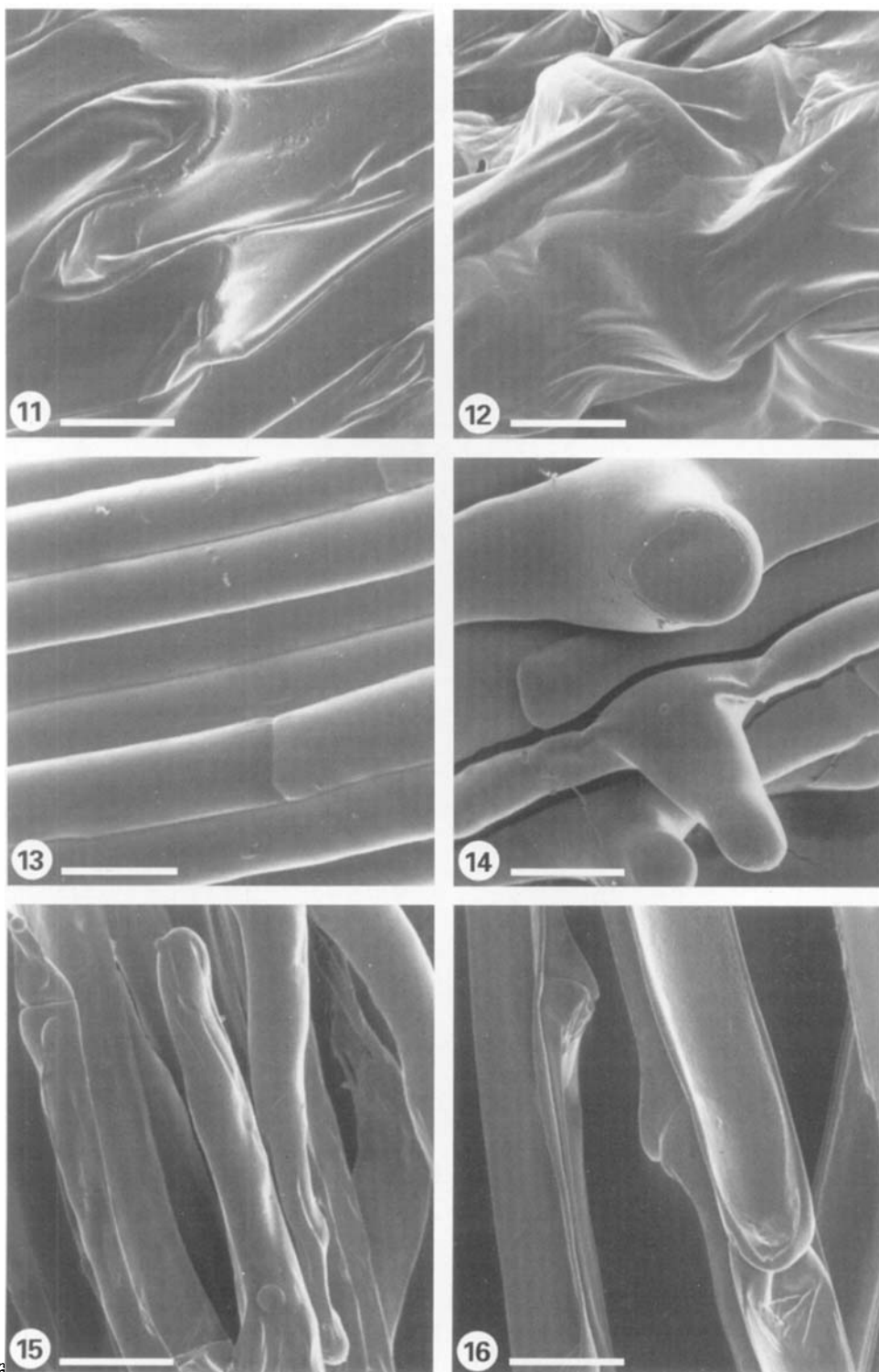
Group A2b. Seed 0.7–0.9 mm long, testa with moderate spiral orientation and few papillae; appendages 0.9–1.6 mm long, often broader than the seed at their bases, bubble cells absent but cells rounded giving a 'foamy' appearance and irregular outline, especially of the hilar appendage, cavity leading to micropyle conspicuous (Figs 18, 25). Four species examined: *A. brachyphyllus*, *A. ellipticus*, *A. forbesii*, *A. nummularius*. Sect. *Microtrichium pro parte*. The small rounded cells of the appendages make them very distinct but still apparently in sect. *Microtrichium*. All have flexuous pendulous growth, small divided calyces and corollas strongly gibbous at the base, and are from New Guinea.

Group A2c. Seed 0.7–1.1 mm long, testa with strongly spiral cell orientation and slightly to moderately papillose; appendages 2.5–3.5 mm long, broadening somewhat towards base, bubble cells present but small and forming a less discrete feature than in A2e species (Figs 20, 25). Two species examined: *A. magnificus*, *A. vinaceus*. Sect. *Microtrichium pro parte*. There is a little bubble cell development in *A. magnificus* and considerably more in *A. vinaceus*, but appendages are

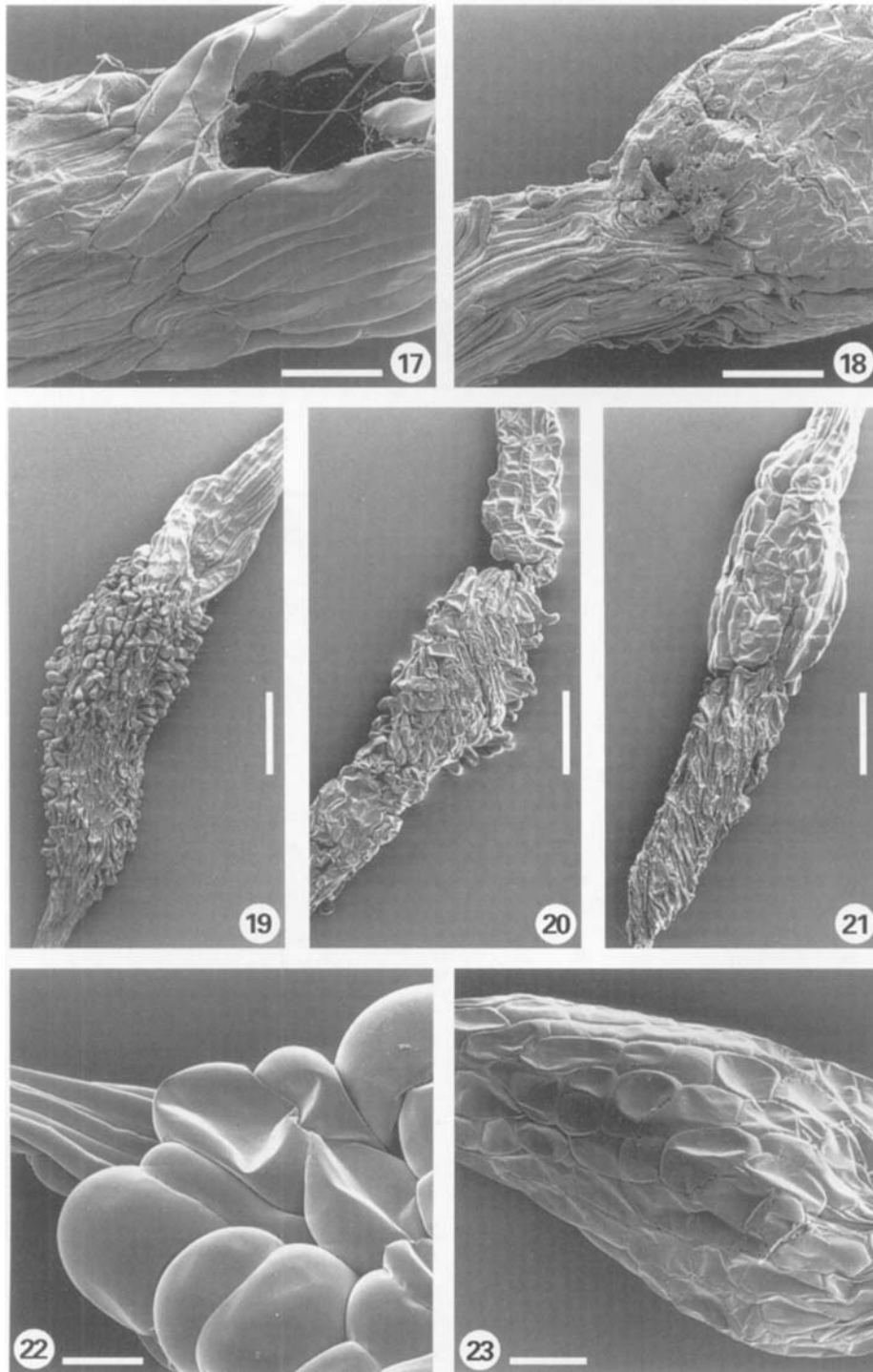
not slender to the base. Both these Bornean species have asymmetric partly divided calyces which do not detach from the pedicel, robust arching growth, large leaves and stamens not exerted.

Group A2d. Seed 0.7 mm long, testa with moderate spiral orientation and few papillae; appendages 2.8–3.5 mm long, thickening slightly towards base, with pronounced bubble development at the base of the hilar appendage and often a little at the base of the apical appendage (Figs 21, 26). One species examined: *A. chrysanthus*. Sect. *Aeschynanthus pro parte?* *A. chrysanthus* is a Sumatran species which has a calyx detaching from the pedicel but tubular to about halfway then divided somewhat asymmetrically into linear, pointed lobes, a shape more usually associated with species in sect. *Haplotrichium* (in this paper sect. X) (Woods, 1991). It is a robust large-leaved species with bright yellow flowers, a very uncommon colour in *Aeschynanthus*, and is only known from the type collection. Further data are required to clarify the position of this species.

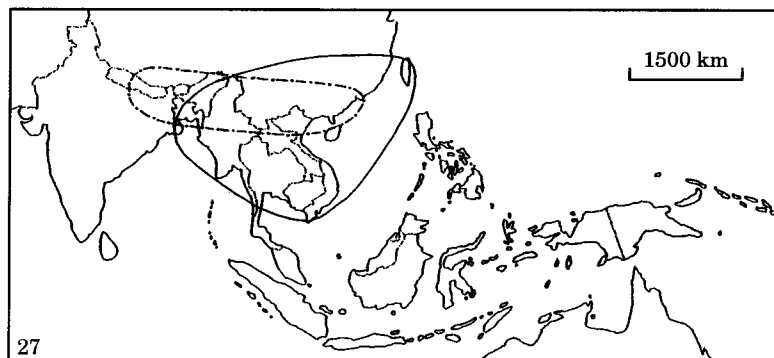
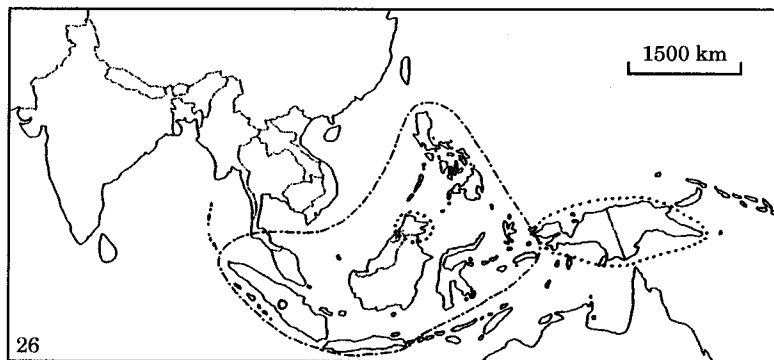
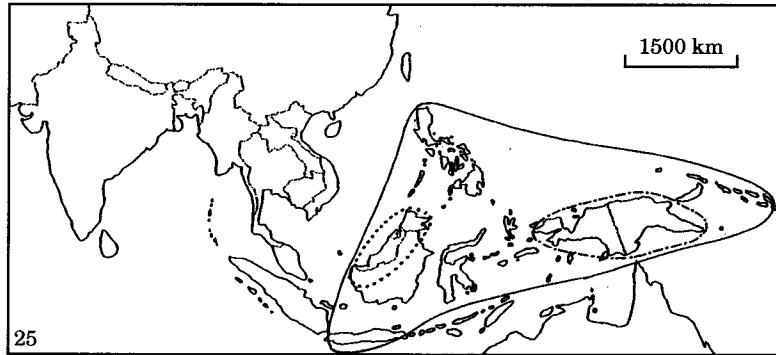
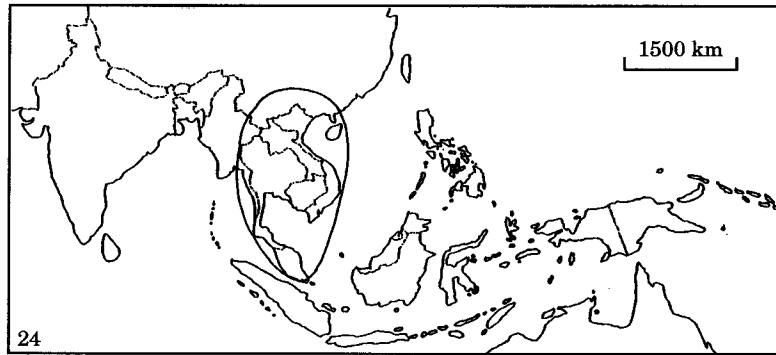
Group A2e. Seed 0.5–1.2 mm long, \pm cylindrical, testa with slight to moderate spiral cell orientation, moderately to strongly papillose, papillae often with a thickened central band; appendages slender to the base, 3.5–15 mm (Figs 2C, 8, 22, 26). Twenty-two species examined: *A. arctocalyx*, *A. beccarii*, *A. curtisii*, *A. flavidus*, *A. gibbsiae*, *A. hians*, *A. javanicus*, *A. lanceolatus*, *A. loheri*, *A. obconicus*, *A. parvifolius*, *A. pulcher*, *A. radicans*, *A. radicans* var. *robustior*, *A. rhodophyllus*, *A. teysmannianus*, *A. tricolor*, *A. truncatus*, *A. sp.* 7–10. Sect. *Aeschynanthus pro parte typica*. Seed in most species c. 0.8 mm long, appendages c. 10 mm, the hilar appendage usually slightly longer than the apical. Most have considerable development of bubbles at the base of the hilar appendage, some have very few bubbles, and a few none, but the range is continuous. A few of the species with pronounced hilar bubble development also have a little bubble development at the base of the apical appendage. Species are linked morphologically by the possession of a



Figures 11–16. Testis and appendage details for some species. Fig. 11. Testis papillae sinuate, papillae 2-celled with sinuous junctions. *A. angustifolius*, Anderson S30783 [B1c]. Fig. 12. Testa papillae more prominent, junctions straight-walled. *A. arfakensis*, Clemens 1287 [B3]. Fig. 13. Cells of appendage smooth, papillae absent. *A. argentii*, Argent 1444 [A2a]. Fig. 14. Appendage papillae clearly formed from centres of single cells. *A. bracteatus*, Kingdon Ward 6370 [A3b], the only Type A species seen with papillose appendages. Fig. 15. Appendage papillae formed from extensions of cell ends. *A. humilis*, RBGE 19850473 [B1a]. Fig. 16. Appendage papillae formed from the junction of raised cell ends. *A. albidus*, RBGE 19841169 [B3].



Figures 17–23. Testa and appendage details. Scale bars 17, 18 = 100 μm ; 19–21 = 250 μm ; 22, 23 = 50 μm . Fig. 17. Base of hilum appendage (right) showing cavity leading to micropyle. *A. musaensis*, RBGE 19630372 [A2a]. Fig. 18. Base of hilum appendage (right) showing rounded ‘foamy’ cells. *A. forbesii*, van Royen, Sleumer & Schram 7685 [A2b]. Fig. 19. Seed of *A. buxifolius*, RBGE 19970164 [A1] showing \pm straight testa cell orientation combined with short thick appendages. Fig. 20. Seed of *A. vinaceus*, Burt & Martin 5058 [A2c] showing anticlockwise testa cell orientation and some development of bubble cells at the base of the short thick appendages. Fig. 21. Seed of *A. chrysanthus*, RBGE 19810535 [A2d] showing anticlockwise testa cell orientation and pronounced bubble cell development. Fig. 22. Base of hilum appendage of *A. obconicus*, RBGE 19621297 [A2c] showing large discrete bubble cells. Fig. 23. Base of hilum appendage of *A. obovatus*, Haviland & Hose 3528K [A2f] showing smaller flatter bubble cells.



Figures 24-27. Sectional distribution of examined species. Fig. 24. Sect. *Microtrichium*, subtype A1. Fig. 25. Sect. *Microtrichium*, subtype A2: group A2a (28 spp.) —; A2b (4 spp.) ---; A2c (2 spp.) Fig. 26. Sect. *Aeschynanthus*, subtype A2: group A2d (1 sp.) —; A2e (22 spp.) ---; A2f (1 sp.) Fig. 27. Sect. *Haplotrichium* s.s., subtype A3: group A3a (3 spp.) —; A3b (3 spp.) ---.

shallowly lobed calyx which is either tubular, campanulate or saucer-shaped, a fact recognized by Bentham (1876) when he created sect. *Holocalyx* to include these species. Clarke's 1883 modification of Bentham's definition of the section, citing the presence of bubble cells, excludes those species which have no bubble cells, such as *A. gibbsiae* and *A. tricolor*, and so is not useful. Species have a trailing, often flexuous habit, stamens not or hardly exerted, and the calyx has an abscission layer at the base and detaches when the flower is old or pollinated. This group of species occurs throughout Malesia, with one species extending to S. Thailand and possibly another to Great Nicobar Is. (South Andamans).

Group A2f. Seed 0.5 mm, testa with strongly spiral cell orientation, papillae absent; appendages 6.5–8.5 mm, slender to base with bubble cell development at base of hilar appendage, individual bubble cells small and relatively flat (Figs 23, 26). One species examined: *A. obovatus*. Sect. *Aeschynanthus pro parte*. *A. obovatus*, from Borneo and New Guinea has, in common with group A2e species, a tubular calyx which readily detaches from the pedicel when the flower is old and would seem to be a member of sect. *Aeschynanthus*, despite possessing exerted stamens. It is the only member of this section so far known from New Guinea, and the only New Guinea species so far that is not endemic.

Subtype A3: Testa cells with slight to moderate clockwise orientation

Seed 0.6–1.3 mm long; appendages 1.2–3.5 mm long (Figs 2D, 3D, 6, 9, 14). Six species examined. On testa morphology they may be subdivided into two groups:

Group A3a. Testa cells sunken in the centre, edges slightly raised to give a somewhat tessellated appearance to the seed (Fig. 3D, 9). Three species examined: *A. acuminatus*, *A. moningeriae*, *A. superbus*.

Group A3b. Testa cells strongly papillose. Three species examined: *A. bracteatus*, *A. stenosepalus*, *A. wardii*. This subtype (Fig. 2D) defines sect. *Haplotrichium*. The testa surface of A3a species is superficially similar to that of Type B1a species but the cells are thin and delicate, whereas the appearance of B1a testa is due to thickening of the cells which masks the two-celled papillae. A3a testa could be considered as transitional between Type A and Type B, as the cell ends are undoubtedly raised. The papillae on the testa of *A. bracteatus* (A3b) are towards the ends of the cells and in a few instances touch; they could be considered precursors of two-celled papillae. *A. bracteatus* is the

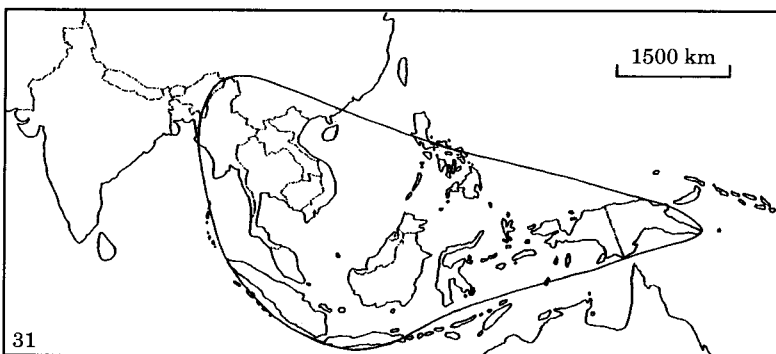
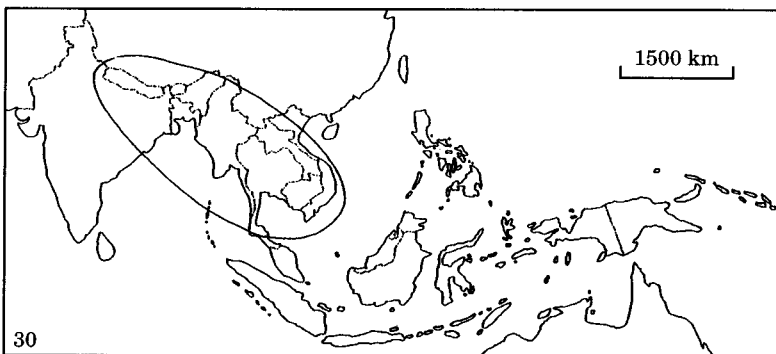
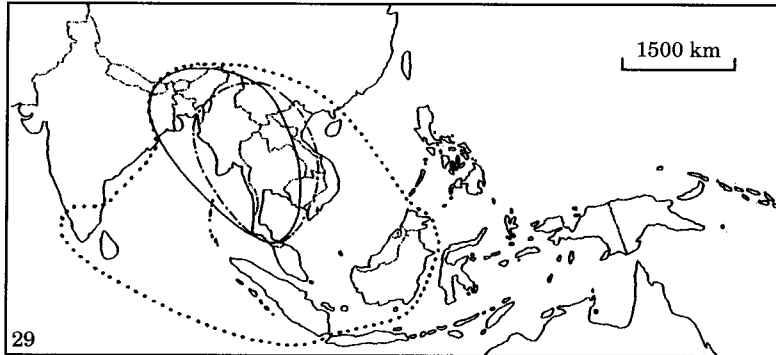
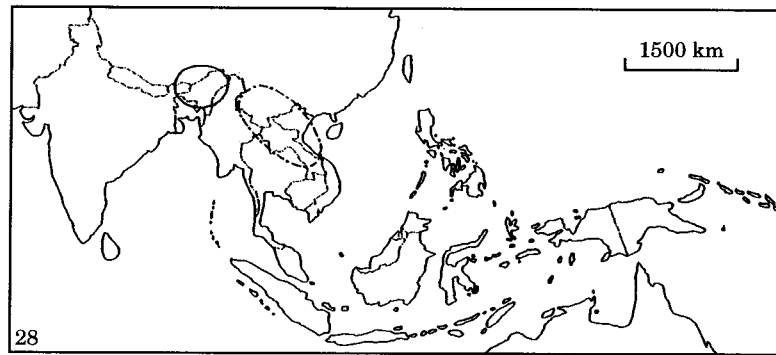
only Type A species seen in this study to have a few papillae on the appendages, (*A. pachyanthus* 19623299, seed type A2a, has slightly raised bumps) but these are clearly derived from the centres of single cells and not from the junction of two raised cell ends (Fig. 14); a few of the papillae are quite long, approaching the length of the structures on the appendages of B1a and B1b species. Subtype A3 seed is possibly morphologically transitional between the simpler Type A and the more complex Type B seed. All six species have other morphological features in common, such as pedunculate inflorescences, often large and usually persistent bracts, and exerted stamens. They occur from northern India to China and in Indo-China (Fig. 27).

When Bentham (1876) defined sect. *Haplotrichium* (calyx divided, lobes acute or rarely obtuse, seed with one hair at each end), he listed *A. acuminatus*, *A. bracteatus* and *A. superbus* as members, but also *A. andersonii*, *A. gracilis*, *A. longiflorus*, *A. perrottettii*, and *A. speciosus*, all of which have type B seed and are here placed in sect. X. Burt & Woods (1975) made *A. bracteatus* the lectotype of sect. *Haplotrichium*, commenting on the pedunculate inflorescences. Wang (1984) made *A. bracteatus* the type of series *Bracteati*, within sect. *Haplotrichium* but the series level is superfluous because the other series, *Novograciles*, has as its type *A. Novogracilis* (= *A. gracilis*), a member of sect. X.

SEED TYPE B

(Figs 2E–G, 3E–G, 5, 10–12, 15, 16, 28–31)

Orientation of testa cells straight and appendages always papillose. Papillae, whether on testa or appendages or both, formed from raised ends of two adjacent cells (Fig. 3D–F). In most species the testa papillae are divided by straight or sinuous cell walls (Figs 11, 12). A few species possess a somewhat reticulate testa with slightly raised papillae, and rarely the seed surface is reticulate and almost smooth (Fig. 10). Appendages are long and filiform ('hairs') with papillae formed from the raised ends of adjacent cells; less often one of the two cells extends to form a longer almost hook-like projection (Figs 15, 16). The appendages have a 'jointed' appearance which can be seen under the light microscope; they also break easily. Seed length ranges from 0.8 to 2.5 mm with almost all species over 1 mm; appendage length ranges from 10 to 45 mm with almost all species between 15 and 40 mm. This is an apparently natural group comprising all members of sections *Polytrichium* and *Diplotrichium* so far examined, together with about two-fifths of the known members of section *Haplotrichium* as previously defined (in this paper sect. X), and two members of sect. *Xanthanthos*.



Figures 28–31. Sectional distribution of examined species. Fig. 28. Sect. *Xanthanthos*, subtype B1: group B1a (1 sp.) —; B1c (1 sp.) - - -. Figure 29. Sect. *X*, subtype B1: group B1a (2 spp.) —; B1b (3 spp.) - - -; B1c (11 spp.) ····. Fig. 30. Sect. *Diplotrichium*, subtype B2 (7 spp.). Fig. 31. Sect. *Polytrichium*, subtype B3 (9 spp.).

Subtype B1: hilar appendage 1

Seed 0.8–2 mm, broadly to narrowly cylindrical, sometimes tapered, testa almost smooth to papillose; hilar appendage one, papillose and sometimes with longer projections towards the base. This subtype encompasses members of both sect. *Xanthanthos* and sect. *X*. There is considerable variation in the size and shape of the seed itself between species, but there are no clear divisions across the range. There does seem to be an association between seed size, testa thickness and surface smoothness, and the number and size of projections on the appendages. Species with the largest and least papillose seed have appendages with the greatest number of and longest projections. Seed can be approximately grouped as follows:

Group B1a. Seed 1.2–1.8 mm long, broadly cylindrical, testa wall thick and quite hard, surface almost smooth, the cells giving a reticulate pattern; appendages 1.3–2.5 cm, with long projections formed from ends of some cells, particularly towards the base (Figs 3G, 10, 15, 28 [*A. chiritoides*], 29). Three species examined: *A. andersonii*, *A. chiritoides*, *A. humilis*. All are from north India, Indo-China or China. *A. andersonii* and *A. humilis* (sect. *X*) have a stiff twiggy habit, a 3–4 mm deeply divided calyx and 1.7–2.5 cm orange-red corollas with exerted stamens. *A. chiritoides* (sect. *Xanthanthos*) however has a flexuous and trailing habit, white corollas and included stamens. The thickened testa wall makes the surface appear smooth, masking the two-celled papillae but they are clearly seen in cross-section (Fig. 3F). This may be an adaptation assisting avoidance of desiccation. *A. humilis* is described (as *A. hildebrandii*) as growing in rather dry open woodland with its root system spreading under the bark (Burt & Woods, 1975), again possibly providing protection from desiccation.

Group B1b. Seed 1.5–2 mm long, cylindrical and somewhat tapering towards apical end, testa cells with slightly raised papillae giving an undulate surface; appendages 2.5–4.4 cm, some cells with long projections (Figs 3F, 29). Three species examined: *A. evardii*, *A. fulgens*, *A. macranthus*. The testa wall is somewhat thickened, partly masking the papillae; again this may be an adaptation related to desiccation tolerance. These species are all in sect. *X*, and have a stiff, spreading habit, a 1.5–2 cm narrowly campanulate calyx with small triangular lobes, and 5–7 cm orange-red corollas narrow at the base. This group occurs from India and Indo-China to China.

Group B1c. Seed 0.8–1.6 mm long, cylindrical, testa papillose; appendages 1.3–4.5 cm, some cells extended into long projections (Figs 2E, 11, 28 [*A. denticuliger*], 29).

Twelve species examined: *A. angustifolius*, *A. austroyunnanensis*, *A. ceylanicus*, *A. denticuliger*, *A. fruticosus*, *A. gracilis*, *A. lepidospermus*, *A. longiflorus*, *A. micranthus*, *A. perrottettii*, *A. pseudohybridus*, *A. speciosus*. 11 species in sect. *X* and one member of sect. *Xanthanthos* belong here. Of the species from Sino-Himalaya and Indo-China, *A. austroyunnanensis*, *A. gracilis* and *A. micranthus* (sect. *X*) and *A. denticuliger* (sect. *Xanthanthos*) have a trailing habit and 3.5–5 mm deeply divided calyx. *A. austroyunnanensis* and *A. micranthus* have 2–2.7 cm red corollas with lobes not spreading and exerted stamens. *A. denticuliger* and *A. gracilis* have very small leaves, a small deeply divided calyx and short broad corollas, but *A. denticuliger* has a yellow corolla with included stamens and *A. gracilis* a red corolla with slightly exerted stamens. The six species examined from West Malesia also have B1c seed but form two species groups morphologically unlike the Indo-Chinese species. One group is the apparently closely related *A. angustifolius* and *A. fruticosus*, with small leaves in whorls, a 4–5 mm deeply divided calyx and 1.5–2.2 cm corollas. The second consists of *A. longiflorus*, *A. pseudohybridus* and *A. speciosus*, linked by arching, spreading habit, large leaves, deeply divided calyx and 6–9 cm corollas narrow at the base. Flowers of *A. lepidospermus* are not known. The two south Indian/Sri Lankan species, *A. perrottettii* and *A. ceylanicus*, also have B1c seed but the papillae on testa and particularly appendages are very well-developed. Both have a 5–8 mm deeply divided calyx and 2.5–3.5 cm corollas.

About 1% of the seed of *A. micranthus* 19821966 showed development of a second appendage at the hilar end, as did a few seeds of *A. gracilis* 19802575.

Sect. *Xanthanthos* is defined by the possession of a conspicuously bilabiate yellow or white corolla with stamens not exerted. There do not appear to be any seed or appendage characters separating the two members from the other species with subtype B1 seed. This section is Sino-Himalayan and Indo-Chinese (Fig. 28).

Sect. *X*: on seed characters alone the species in this section belong with those in sect. *Xanthanthos*, but morphologically most are very different and none fit sect. *Xanthanthos* as currently understood. At present it is difficult to define this section until more information becomes available. There are considerable morphological differences between species groups but no more than in the very variable sect. *Microtrichium* and it may be that the definition of sect. *Xanthanthos* will require modification to accommodate sect. *X* species.

Wang (1984) makes *A. novogracilis* W.T. Wang (= *A. gracilis*) the type of series *Novograciles*, within sect. *Haplotrichium* but this group of species are not in sect. *Haplotrichium* s.s. Indeed B.L. Burt (pers. comm.)

has suggested that *A. gracalis* belongs in sect. *Xanthanthos*.

Subtype B2: hilar appendages 2

Seed 0.8–1.3 mm long, narrowly ovate, testa moderately to strongly papillose; hilar appendages 2, papillose but without projections (Figs 2F, 5, 30). Seven species examined: *A. hookeri*, *A. lineatus*, *A. maculatus*, *A. mimetes*, *A. parasiticus*, *A. parviflorus*, *A. sikkimensis*. This subtype defines sect. *Diplotrichium*. Hilar appendages range between 1.7 and 3.5 cm with one usually slightly longer than the other, and the apical appendage varies from 2 to 4 cm, depending on the species. Seed and appendage lengths are consistent within species, which in this section are markedly similar in habit and floral characters. Stems are stiff and spreading to pendulous. The calyx is partly divided or less commonly entirely divided, with the lobes acute. The corolla is narrow from the base then flaring and curving quite sharply, red to pale orange with median dark stripes on all lobes, and with exserted stamens. Inflorescences are pseudoterminal, rarely lateral, and the twigs are often swollen at the sites of old inflorescences. This section has a restricted distribution from northern India throughout Indo-China to China and is not known from Malesia.

One collection of *A. parasiticus* (JDH 1069) had a few seeds with a third hilar appendage developed.

Subtype B3: hilar appendages a coma of 5–60

Seed 1.4–2.5 mm long, spindle- or top-shaped, testa moderately to strongly papillose; appendages to 3 cm, papillose but without long projections, hilar appendages a coma with the bases forming a collar around the micropyle (Figs 2G, 3E, 12, 16, 31). Nine species examined: *A. albidus*, *A. arfakensis*, *A. asclepioides*, *A. batakiorum*, *A. fecundus*, *A. infraflavus*, *A. longicaulis*, *A. myrmecophilus*, *A. poilanei*. This subtype defines sect. *Polytrichium*. Coma appendages vary in number but over a narrow range for any one species, from 5–8 in *A. myrmecophilus*, to 40–60 in *A. albidus*. Appendage length is also variable within the coma, the longest seen at 2.1 cm is in *A. batakiorum*. The apical appendage is longer than the hilar appendages, reaching 3 cm in *A. fecundus*. Seeds themselves are large for the genus. There seems to be an association between greater numbers of coma hairs and a strongly papillose testa. Species in this small section (c. 10 members) occur at low altitude and have spreading twiggy stems and leaves large relative to the rather inconspicuous green, yellowish, dull orange or dull red corollas. Sectional range is from Burma to New Guinea; four species occur in southern Asia and Peninsular Malaysia, and the other five in Malesia.

Hybrids

The sections of *Aeschynanthus* are not thought to be separated by sterility barriers (Burt & Woods, 1975). Examples of garden-raised intersectional hybrids are *A. pulcher* (sect. *Aeschynanthus*) × *A. ellipticus* (sect. *Microtrichium*), and *A. × splendidus* T. Moore (*A. parasiticus*, sect. *Diplotrichium*, × *A. speciosus*, sect. *X*) which was raised in 1851 and is still in cultivation. This has subsequently been further crossed with *A. longicaulis* (sect. *Polytrichium*) to give rise to the cultivar 'Black Pagoda'. The only known Type A × Type B seed cross is *A. pulcher* (sect. *Aeschynanthus*) × *A. macranthus* (sect. *X*) (Saylor, 1973). Further intersectional crosses have been attempted. Some failed while others produced poorly-developed non-viable seed. Hybrids of known parentage, and the results of this study, would suggest that there is a degree of sterility not necessarily between sections, but between species with type A seed and those with type B seed. It will be necessary to see the results of many more intersectional crosses in order to either support or disprove this hypothesis.

Agalmyla and Lysionotus

Seed of one species of each genus was examined for comparison. The seed itself is tiny (0.6–0.7 mm), with a single short (c. 1.6 mm) smooth appendage at each end, broadening slightly towards the base. The appendages are brown and hyaline, unlike the white appendages in *Aeschynanthus*. The testa surface in *Agalmyla* sp. is somewhat reticulate with slightly raised cell ends and occasional small tubercles; that of *L. heterophyllus* is slightly reticulate, with scattered small tubercles mostly on the cell margins. Cell orientation is ± straight. Testa and appendage morphology in both are unlike that of *Aeschynanthus*.

DISCUSSION

There is a high degree of correlation between seed type, existing sectional classification, and distribution patterns within the genus *Aeschynanthus*. Species with Type A seed (testa cell orientation usually spiral, papillae formed from a single cell, and short smooth appendages) are in sects. *Aeschynanthus*, *Microtrichium* and *Haplotrichium s.s.* Type B seed (testa cell orientation straight, papillae formed from two adjacent cells, and long slender papillose appendages) is characteristic of members of sects. *Polytrichium*, *Diplotrichium*, *Xanthanthos* and sect. *X*. There is also good correlation between seed type and other morphological characters, particularly in sects. *Polytrichium*, *Diplotrichium* and *Aeschynanthus* (see Results).

Of the 89 named and 10 unidentified taxa examined, those with Type A seed are predominantly Malesian

(Figs 1, 24–27) while those with Type B seed have a predominantly Sino-Himalayan and Indo-Chinese distribution (Figs 1, 28–31). The eastern Type A group is by far the largest; with the exception of the six members of sect. *Haplotrichium* s.s. and two members of sect. *Microtrichium*, the rest (56 species) are Malesian. The Indo-Chinese members of sect. *Microtrichium* (*A. buxifolius* and *A. garrettii*) are two of the three with straight testa cell orientation (subtype A1), otherwise the seed is 'typical' *Microtrichium*. The centre of development of sect. *Microtrichium* appears to be New Guinea with 21 of the examined species, five from the Philippines, three from Borneo, and one each from Java, Seram, the Solomon Islands, and Peninsular Malaysia (this last with subtype A1 seed). Of the 23 species in sect. *Aeschynanthus* examined, 13 are from Borneo. A few of these also occur in West Malesia and one, *A. radicans*, extends as far as S. Thailand. One, *A. obovatus*, is in Borneo and New Guinea. A few other species are West Malesian, and four are from the Philippines, where there are several other putative members whose seed is not yet known.

In contrast, the distribution of species with Type B seed is predominantly northern and western. The only exception seems to be the small sect. *Polytrichium* (Type B3) which has a range from Indo-China and China, through Malesia to New Guinea (Fig. 31); this may reflect the greater effectiveness of a coma of long hairs in seed dispersal. Neither sect. *Diplotrichium* nor sect. *Xanthanthos* has been recorded from Malesia. A few species of sect. *X* with subtype B1 seed reach as far east as Borneo with a possible record (*A. angustifolius*) from Sulawesi. Overall, of the 34 species examined with Type B seed, 23 appear to be restricted to the Asian mainland and Sri Lanka (but excluding Peninsular Malaysia) with a further two also in Peninsular Malaysia. Of the Malesian species the easternmost, in the Philippines, Seram and New Guinea, are all in sect. *Polytrichium*.

There is both morphological and molecular evidence that the condition of more than one hilar appendage is derived, and that it arose from Type B1 seed, with two-celled papillae and a single long papillose hilar appendage. All other genera in tribe Trichosporeae (*Agalmyla* [including *Dichrotrichum*], *Loxostigma*, *Lysionotus*) are reported to have seed with a single hilar appendage, and by far the majority of *Aeschynanthus* species also have a single hilar appendage. Seed of the doubtful genus *Micraeschynanthus*, presumed to be in the Trichosporeae, is not known. Preliminary studies of seed ontogeny (Saueregger & Mühlbauer, unpubl.; current studies by Christie & Mendum) show that, in sect. *Polytrichium*, one appendage begins to develop a little before the others and remains somewhat longer and stouter, possibly corresponding to the single appendage of other species. A small percentage of seeds,

of two species in sect. *X* and one in sect. *Diplotrichium*, shows development of an additional shorter hilar appendage. It is suggested that Type B1 seed itself could have evolved from Type A3. The testa cells of *A. acuminatus*, *A. moningeriae* and *A. superbus* have raised margins and appear to be transitional between Type A and Type B. The papillae on both testa and appendages of *A. bracteatus* are clearly single-celled but not central and sometimes meet, and could be considered precursors of two-celled papillae. It would thus seem probable that seed with single-cell papillae and short appendages is the most primitive condition, giving rise to sects. *Haplotrichium* s.s., *X*, *Diplotrichium* and *Polytrichium* in the western end of the range, while in Malesia sect. *Microtrichium* speciated and also, with the elaboration of longer appendages often with bubble cells, gave rise to sect. *Aeschynanthus*. This suggestion is strongly supported by the molecular studies of Denduangboripant & Cronk (pers. comm. and 2000), who sequenced 23 *Aeschynanthus* species and found two distinct clades which closely correlated with seed types A and B. The exceptions were seed types A1 and A3 which were basal to the seed type B clade, A1 being basal to A3, suggesting that sect. *Microtrichium* may be paraphyletic with respect to the other sections.

Long filiform appendages combined with tiny seeds are very effective for wind dispersal but less effective in the wet, so may be more suited to seasonal climates such as occur in mainland south-east Asia. A few of these species show thickening of the seed testa wall, presumably an adaptation to a drier climate. The appendages possibly also aid attachment to a substrate. Seeds with shorter appendages do not drift so readily on slight air currents, and fall to the ground more quickly. The bubbles present on the hilar appendages in some members of sect. *Aeschynanthus* enable them to stay airborne longer, and also appear to absorb water thus helping to anchor the seed to a substrate. The above results allow a revised key to the sections (see Table 3)

CONCLUSIONS

On the basis of the morphology of the seed testa and seed appendages, the genus *Aeschynanthus* may be informally divided into two groups, those with Type A and those with Type B seed. The former contains sects *Aeschynanthus*, *Haplotrichium* s.s. and *Microtrichium*; the latter sects *Polytrichium*, *Diplotrichium*, *Xanthanthos*, and those members of the existing sect. *Haplotrichium* (in this paper sect. *X*) possessing Type B seed. Wang's 1984 division of the existing sect. *Haplotrichium* into series *Novograciles* and *Bracteati* takes account of this but is superfluous. While there are no seed or appendage characters separating species in sect. *X* from those in sect. *Xanthanthos*, they do not

Table 3. Revised key to the sections

1a. Seed with a single appendage at hilar end	2
1b. Seed with more than 1 appendage at hilar end	6
2a. Appendage short, not papillose	3
2b. Appendage long, slender, papillose	5
3a. Testa cell orientation anticlockwise, rarely straight; inflorescences rarely pedunculate; bracts small, not persistent	4
3b. Testa cell orientation clockwise, inflorescences long pedunculate, bracts large, usually persistent.....sect. <i>Haplotrichium s.s.</i>	
4a. Appendages not slender to base; calyx without abscission layer at base, usually deeply divided, rarely tubular or spatheous.....	sect. <i>Microtrichium</i>
4b. Appendages slender to base, bubble cells often present; calyx with abscission layer at base, tubular or cup-shaped, lobes rounded, rarely pointed	sect. <i>Aeschynanthus</i>
5a. Corolla white or yellow, stamens not exerted	sect. <i>Xanthanthos</i>
5b. Corolla orange, red or green, stamens usually exerted	sect. <i>X</i>
6a. Seed with 2 appendages	sect. <i>Diplotrichium</i>
6b. Seed with a coma of several to many appendages	sect. <i>Polytrichium</i>

belong in that section as currently defined on corolla characters. Thus sect. *X* is left without circumscription pending further studies. There is good correlation between seed characters and other morphological features, making sectional placement for many species possible without recourse to seed.

Those species with Type A seed are almost all Malasian; the main exception being sect. *Haplotrichium s.s.* which is Indo-Chinese and Sino-Himalayan. Those with Type B seed have a predominantly western distribution within the range of the genus.

Any discussion of evolutionary aspects is highly speculative, but it would seem probable that *Microtrichium*, or possibly *Haplotrichium s.s.*, is the least and *Polytrichium* the most derived seed type. Either one of *Microtrichium* or *Haplotrichium* could have given rise to the other and to sect. *Aeschynanthus* on one side, and to sects *X*, *Xanthanthos*, *Diplotrichium* and *Polytrichium* on the other.

NOTE ADDED IN PROOF

A paper in the *Bangladesh Journal of Plant Taxonomy* 6(2) 1999, has recently come to the attention of the first author. Rashid MH, Jong K, Mendum M: Seed morphological and taxonomic studies in the genus *Aeschynanthus* (Gesneriaceae) was published without any prior knowledge of either Mendum or Jong.

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PNH, U, US and WU for permission to remove seed from herbarium sheets, to B. L. Burttt and Q. C. B. Cronk for discussion and advice, and to the horticultural staff, especially S. Scott at RBGE, and at the Botanical Garden Vienna (HBV). Thanks are also due to E. Vogel at Leiden Botanic Garden, and especially W. Cherry at the Royal Botanic Gardens Sydney, who arranged for living material critical to this study to be sent to Edinburgh. AW acknowledges financial support by the 'Fonds zur Förderung der wissenschaftlichen Forschung' (project numbers: P 8166-B, P 6969-B, and P 7984-BIO).

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APPENDIX 1: SEED TYPES EXAMINED

sect. *Microtrichium*

A1
A. buxifolius
A. garrettii
A. longicalyx
A2a
A. argentii
A. calanthus
A. cardinalis
A. crassifolius
A. guttatus
A. horsfieldii
A. irigaensis
A. leptocladus
A. aff. leptocladus
A. microtrichus
A. miniaceus
A. montisucris
A. musaensis
A. oxychlamys
A. pachyanthus
A. philippinensis
A. pullei
A. ramosus (ined.)
A. roseoflorus
A. solomonensis
A. sp. 1
A. sp. 2
A. sp. 3
A. sp. 4
A. sp. 5
A. sp. 6
A2b
A. brachyphyllus
A. ellipticus
A. forbesii
A. nummularis
A2c
A. magnificus
A. vinaceus

sect. *Aeschynanthus*

A2d
A. chrysanthus
A2e
A. arctocalyx
A. beccarii
A. curtisii
A. flavidus
A. gibbsiae
A. hians
A. javanicus
A. lanceolatus
A. loheri
A. obconicus
A. parvifolius
A. pulcher
A. radicans
A. radicans var. *robustior*
A. rhodophyllus
A. teysmannianus
A. tricolor
A. truncatus
A. sp. 7
A. sp. 8
A. sp. 9
A. sp. 10
A2f
A. obovatus

sect. *Haplotrichium*

A3a
A. acuminatus
A. moningeriae
A. superbus
A3b
A. bracteatus
A. stenosepalus
A. wardii

sect. *Xanthanthos*

B1a
A. chiritoides
B1c
A. denticuliger

sect. *X*

B1a
A. andersonii
A. humilis
B1b
A. evrardii
A. fulgens
A. macranthus
B1c
A. angustifolius
A. austroyunnanensis
A. ceylanicus
A. fruticosus
A. gracilis
A. lepidospermus
A. longiflorus
A. micranthus
A. perrottetii
A. pseudohybridus
A. speciosus

sect. *Diplotrichium*

B2
A. hookeri
A. lineatus
A. maculatus
A. mimetes
A. parasiticus
A. parviflorus
A. sikkimensis

sect. *Polytrichium*

B3
A. albidus
A. arfakensis
A. asclepioides
A. batakiorum
A. fecundus
A. intraflavus
A. longicaulis
A. myrmecophilus
A. poilanei

APPENDIX 2: TAXA EXAMINED

- A. acuminatus* [Wall. ex] DC.: Keenan *et al.* 3431 (E); Lin 314 (E); SKN 1929 (PNH); Smuts 047 (BM); ?coll. 9.v.1959 (KUN).
- A. albidus* (Blume) Steud.: Argent 84/17, cult. RBGE 19841169 (E); Argent 84/18, cult. RBGE 19841170 (E); Burt & Woods 2352 (E); HB 5077 (U, as *A. motleyi* C.B. Clarke var. *ceramensis* C.B. Clarke); Noteboom 1346 (L).
- A. andersonii* C.B. Clarke: Anderson 22.ix.1868 (CAL); Cherry 638, cult. RBGE 19970465 (E).
- A. angustifolius* (Blume) Steud.: Anderson s30783 (E); Backer 25909 (U); Bünnemeijer 4493 (U); King's coll. 4738 (K, as *A. stenophyllus* Ridl.).
- A. arctocalyx* Mendum & Madulid: Argent GAM 21, cult. RBGE 19922776 (E).
- A. arfakensis* C.B. Clarke: Carr 12809 (BM, as *A. hartleyi* P. Woods); Clemens 1287 (L); Hartley 10344 (A, as *A. hartleyi*); Spies s.n., cult. RBGE 19770654 (E, as *A. hartleyi*); Takeuchi 11353 (E); Wiakabu 73382 (LAE).
- A. argentei* Mendum: Argent 1444 (E).
- A. asclepioides* (Elmer) B.L. Burt & P. Woods: Ramos Bur. Sci. 1484 (BM, as *A. dolichosepalum* Merr.); Ramos 39496 (BM).
- A. austroyunnanensis* W.T. Wang: Reid & Fernie 004, cult. RBGE 19951561 (E).
- A. batakiorum* Mendum: Mendum *et al.* 25354 (E).
- A. beccarii* C.B. Clarke: Beccari 796 (FI).
- A. brachyphyllus* S. Moore: Boden Kloss s.n. (BM); Robbins 933 (CANB); Vink 16398 (L).
- A. bracteatus* [Wall. ex] DC.: Forrest 9271 (E); Forrest 17192 (E); Kingdon Ward 6370 (E); Lace, Oct. 1902 (E); Native Collector, Khasia Hills (E); Wallace 583/90 (NSW); Xu G15427 (E).
- A. buxifolius* Hemsl.: Cherry 135, cult. RBGE 19970164 (E); Feng 17.viii.1947 (KUN); Feng 4.xi.1947 (KUN); Goodwin & Cherry 384, cult. RBGE 19970178 (E).
- A. calanthus* Schltr.: Jacobs 8643 (L); Sayers NGF19796 (LAE); Woods 185 (E).
- A. cardinalis* ([Copel. ex] Merr.) Schltr.: Elmer 13603 (E).
- A. ceylanicus* Gardner: Burt & Townsend 85 (E).
- A. chiritoides* C.B. Clarke: Poilane 25668 (P).
- A. chrysanthus* P. Woods: Paterson 291, cult. RBGE 19810535 (E).
- A. crassifolius* (Elmer) Schltr.: Elmer 13624 (NSW, as *A. foxworthyi* Kraenzl.).
- A. curtisii* C.B. Clarke: Burt 5132, cult. RBGE 19672135 (E).
- A. denticuliger* W.T. Wang: Poilane 26366 (P).
- A. ellipticus* Lauterb. & K.Schum.: Conn *et al.* 66320 (LAE); Holttum 525-63, cult. RBGE 19661884 (E); Woods 382a, cult. RBGE 19630478 (E).
- A. evardii* Pellegr.: Mus. Nat. d'Hist., cult. RBGE 19550210 (E).
- A. fecundus* P. Woods: Larsen 103, cult. RBGE 19672219 (E); Ridley 13599 (BM).
- A. flavidus* Mendum & P. Woods: Argent s.n., cult. RBGE 19781740 (E).
- A. forbesii* (S.Moore) K. Schum.: Millar 22686 (CANB); van Royen, Sleumer & Schram 7685 (A; K); Stone 10194 (LAE).
- A. fruticosus* Ridl.: Ridley Feb 1921 (K).
- A. fulgens* Wall.: Komes s.n. (E).
- A. garrettii* Craib: Beusekom & Phengklai 2433 (E); Valder 37, cult. RBGE 19750205 (E).
- A. gibbsiae* [S. Moore ex] Gibbs: Clemens 28329 (L).
- A. gracilis* [Parish ex] C.B. Clarke: Grierson & Long 4125, cult. RBGE 19821972 (E); North 13227 (E); Wiehler 2201, cult. RBGE 19802575 (E).
- A. guttatus* P. Woods: Pullen 7735 (CANB); Woods 215 (E).
- A. hians* C.B. Clarke: Burt & Martin 5565, cult. RBGE 19672482 (E); Haviland 2309 (K).
- A. hookeri* C.B. Clarke: KEKE 45, cult. RBGE 19892128 (E).
- A. horsfieldii* R.Br.: Woods 1011 (E); Horsfield, Java (BM).
- A. humilis* Hemsl.: Kerr 515 (BM, as *A. persimilis* Craib); Smitinand s.n., cult. RBGE 19850473 (E).
- A. intraflavus* Mendum: Argent 87/1, cult. RBGE 19880250 (E).
- A. irigaensis* (Merr.) B.L. Burt & P. Woods: Ramos Bur. Sci. 30315 (K); RBG/PNH IS 28, cult. RBGE 19972532 (E).
- A. javanicus* Hook.: Vogel s.n., cult. RBGE 19971334 (E).
- A. lanceolatus* Ridl.: Burt & Woods 1643, cult. RBGE 19621285 (E).
- A. lepidospermus* C.B. Clarke: Beccari 2803 (FI).
- A. leptocladus* C.B. Clarke: Kostermans 2133 (BO); van Royen & Sleumer 8037 (L).
- A. aff. leptocladus*: Brass 12056 (L).
- A. lineatus* Craib: Hilliard & Burt 5592, cult. RBGE 19672590 (E); Wallace, Chambers & Curry 615, cult. RBGE 19970174 (E); Yu 18196 (E).
- A. loheri* Kraenzl.: Reillo 1438 (PNH).
- A. longicalyx* Ridl.: Stone KLU 7194, cult. RBGE 19672365.
- A. longicaulis* [Wall. ex] R.Br.: Burt & Woods B 1724, cult. RBGE 621414 (E); Burt & Woods B 1739, cult. RBGE 621423 (E); Copenhagen Univ., cult. RBGE 19672218 (E).
- A. longiflorus* (Blume) DC.: Blume 124 (BM); Burt & Woods 1644, cult. RBGE 19621286 (E); Korthals s.n. (U); Woods 1055 (NSW).
- A. macranthus* (Merr.) Pellegr.: Seidenfaden s.n., cult. RBGE 19801140 (E).
- A. maculatus* Lindl.: Panigrahi 2551, cult. RBGE 19570009 (E).
- A. magnificus* Stapf: Aberdeen Univ. ABD 28, cult. RBGE 19812962 (E); Burt & Martin 5226, cult. RBGE 19672453 (E); Clemens 26717 (L); Clemens s.n. 31/31 (BM).
- A. micranthus* C.B. Clarke: Clarke 13213 (BM); Cornell University G260 (E); Grierson & Long 3535, cult. RBGE 19821966 (e).
- A. microtrichus* C.B. Clarke: Beccari 6890 (FI).
- A. mimetes* B.L. Burt: Forrest 26299 (E); Henry 12995 (E).
- A. miniaceus* B.L. Burt & P. Woods: Edano PNH 40194 (CANB); Elmer 13529 (E).
- A. moningeriae* (Merr.) Chun: Liang 64183 (E); McClure 9349 (PNH).
- A. montisucris* P. Royen: Brass 31429 (LAE); Iserentant 9465 (BM); Pullen 6049 (CANB).
- A. musaensis* P. Woods: Woods 177 and cult. RBGE 19630372 (E).

- A. myrmecophilus* P. Woods: Weber 19860819-712 (WU); Woods 616, cult. RBGE 19680715 (E).
- A. nummularius* (Burkill & S.Moore) K. Schum.: Brass 23653 (LAE); Cruttwell 388 (E, as *A. microcardia* B.L. Burtt & R.A. Davidson); Foreman & Vinas LAE 60077 (LAE); Glasgow Bot. Gdn. PNG 87, cult. RBGE 19932365 (E); Woods 157, cult. RBGE 19630371 (E).
- A. obconicus* C.B. Clarke: Burtt 1666, cult. RBGE 19621297 (E); Burtt & Woods 2721A, cult. RBGE 19622832 (E); Burtt & Woods 2721B, cult. RBGE 19622833 (E); Burtt & Woods B 2721C, cult. RBGE 19622834 (E).
- A. obovatus* C.B. Clarke: Hartley 10444 (A, as *A. papuanus* [Schltr.] B.L. Burtt); Haviland & Hose 5528K (K, as *A. hoseanus* Kraenzl.); Motley 1158 (K); Streimann & Kairo NGF 39296 (L).
- A. oxychlamys* Mendum: Barker & Lelean LAE 67247 (E); Mendum 92631 (E); Mendum 92646 (E); Mitchell & Smith 187, cult. RBGE 19930953 (E).
- A. pachyanthus* Schltr.: Clunie & Katik LAE 63308 (LAE); Conn & Kairo 137 (CANB); Remarii & Streimann NGF 30871 (E); Takeuchi *et al.* 4337 (CANB); Woods 57A, cult. RBGE 19623299 (E).
- A. parasiticus* (Roxb.) Wall.: Cooper & Bulley 3674 (E); J.D. Hooker 1069 (BM).
- A. parviflorus* (D. Don) Spreng.: Beusekom & Charoenphol 1660 (E); Charoenphol, Larsen & Warncke 4270 (E).
- A. parvifolius* R.Br.: Chai S.30362 (E); Weber 840712-1/3 (WU); Woods s.n., cult. RBGE 19680649 (E).
- A. perrottetii* DC.: Ramamurthy 18193 (E); Wight 656 (E, as *A. planiculmis* (C.B. Clarke) Gamble).
- A. philippinensis* C.B. Clarke: Cuming 813 (K); Ramos Bur. Sci. 1945 (BM); Vidal 3386 (K).
- A. poilanei* Pellegr.: Poilane 7137 (P); Poilane 10389 (P).
- A. pseudohybridus* Mendum: Burtt & Woods 4967, cult. RBGE 19672107 (E); Vogel, Schuiteman & Roelfsema s.n., cult. RBGE 19971340 (E).
- A. pulcher* (Blume) G. Don: Woods 1062, cult. RBGE 19680843 (E).
- A. pullei* Schltr.: Mendum & Argent 92863 (E).
- A. radicans* Jack: Penang Bot. Gdn., cult. RBGE 19651314 (E); Smitinand 698 (E).
- A. radicans* var. *robustior* C.B. Clarke: Teysmann 11207 (K).
- A. ramosus* (ined.): Katik NGF46827 (BRD); Kokori NGF 43570 (LAE); Woods 1151 (NSW).
- A. rhodophyllus* Kraenzl.: Haviland 1513 (K).
- A. roseoflorus* Mendum: Argent 87/14, cult. RBGE 19880263 (E).
- A. sikkimensis* (C.B. Clarke) Stapf: Grierson & Long 3162 and cult. RBGE 19822401(E).
- A. solomonensis* P.Woods: Craven & Schodde 169 (CANB).
- A. speciosus* Hook.: Clemens 10332 (PNH).
- A. stenosepalus* J. Anthony: Kingdon Ward 3494 (E); Yu 19422 (E).
- A. superbus* C.B. Clarke: McGregor 1054 (E); King's coll. s.n. (BM).
- A. teysmannianus* Miq.: Hort. Amstelod. (U).
- A. tricolor* Hook.: Burtt & Woods 2062, Cult. RBGE 19622149 (E); Burtt & Woods 2432A (E); Collenette 2350 (E).
- A. truncatus* (Elmer) Schltr.: Edano PNH 7200 (PNH).
- A. vinaceus* P. Woods: Burtt & Martin 5058 (E).
- A. wardii* Merr.: Kingdon Ward 10170 (BM).
- A. sp. 1*: Balgooy 692 (L).
- A. sp. 2* (T5): Stevens *et al.* LAE 58430 (LAE).
- A. sp. 3* (aff. T5): Brass 27863 (L).
- A. sp. 4*: Brass 22375 (US); Brass 22826 (A).
- A. sp. 5*: Brass 3250 (A).
- A. sp. 6*: Woods 149 (NSW).
- A. sp. 7*: Hennipman 5782 (E).
- A. sp. 8*: MSBG 87-162 (E).
- A. sp. 9*: Nengah Wirawan (BO).
- A. sp. 10*: Mendum *et al.* 25434 (E).
- Agalmyla* sp.: Woods 2027, cult. RBGE 19681844 (E).
- Lysionotus heterophyllus* Franch.: B.J. Wallace 587/90.