STUDIES IN THE GESNERIACEAE OF THE OLD WORLD XXX: ANATOMICAL CHARACTERS IN THE TRIBE TRICHOSPOREAE

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The tribe *Trichosporeae* has long been accepted as a natural group comprising those genera of Old World Gesneriaceae that are distinguished by their seeds having capillary appendages at either end. Associated with this feature is the climbing or epiphytic habit, to which there are only a few exceptions. Nevertheless, *Aeschynanthus*, with relatively small thick leaves produced in equal-sized pairs, is strikingly different from *Agalmyla* which has much larger, thinner leaves with, however, one member of each pair reduced to a small stipule-like structure.

SECT. POLYTRICHIUM		
1. A. marmoratus T. Moore	C 4590	Malay Peninsula
SECT. DIPLOTRICHIUM		
2. A. maculatus Lindl.	C 3779	N. E. India
SECT. HAPLOTRICHIUM		
3. A. evrardii Pellegrin	C 2002	"Indo-China"
4. A. hosseusii Pellegrin	C 4589	"Thailand"
5. A. aff. hosseusii	C 1644	"Indo-China"
6. A. longiflorus (Bl.) DC	C 4923	"Malaysia"
7. A. perakensis Ridl.	C 4043	Malay Peninsula
SECT. HOLOCALYX		
8. A. tricolor Hook.	C 4595	Sarawak
9. A. obconicus C.B.Cl.	C 4591	Malay Peninsula
10. ,,	C 4516	Sarawak
11. ,,	C 4859	,,
12. A. lamponga Miq.	C 3941	"Malaysia"
13. A. pulcher (Bl.) G. Don	C 3780	"Java"
14. A. praelongus Kraenzlin	C 4593	Sarawak
15. A. parvifolius R. Br.	C 3341	
16. ,,	C 4866	Malay Peninsula
17. ,,	C 4869	Sarawak
18. ,,	C 4592	,,
19. ,,	C 4870	,,
20. ,,	C 4872	,,
21. A. radicans Jack	C 4594	,,
22. ,,	C 4878	,,
23. ,,	C 4883	,,
24. A. aff. parvifolius	C 4602	,,
SECT. MICROTRICHIUM		
25. A. ellipticus Lauterb. & K. Schum.	C 4041	New Guinea
26. A. kermesinus Schlechter	C 4597	,,
27. A. nummularius (Burk. & S. Moore) K. Schum.	C 3781	,,
28. A. aff. nummularius	C 4598	,,
29. A. pachyanthus Schlechter	C 4599	,,
30. A. sp.	C 4600	,,
31. A. sp.	C 4601	,,
HYBRIDS		
32. A. x splendidus T. Moore	C 3720	garden origin
33. ,,	C 3793	A. parasiticus x speciosus.

TABLE I. Materials of *Aeschynanthus*.

Within *Aeschynanthus* the arrangement of the species into sections depends, at present, almost entirely on the details of the seed appendages and the lobing of the calyx.

Between *Agalmyla* (sensu stricto) and the closely related genera *Tetradema* and *Dichrotrichum* the morphological distinctions were known (Burtt, 1962, 209) to be very unsatisfactory.

There were thus three problems to which an anatomical survey might contribute some useful data: the relationship of *Aeschynanthus* to the *Agalmyla* group, the subdivision of *Aeschynanthus*, and the generic limits of *Agalmyla*.

In the event it has proved convenient to deal with the taxonomic problem of *Agalmyla* before presenting the anatomical data in detail and this has been done in a separate paper (Burtt, 1968). It has thus been possible to disentangle the taxonomy and the anatomy and to use the revised nomenclature here.

The first part of this paper (by Dr. Rosser) presents the anatomical data, the second part (jointly) discusses their implications in considering the inter-relationships of the genera.

The materials used are listed in Tables I and IV. The reference numbers are those under which voucher specimens are preserved in the Edinburgh herbarium: C. numbers refer to cultivated material. In the text, species are referred to by name only, except when a particular specimen needs to be distinguished: the number in the left hand column of the tables is then quoted. The tables show the geographical origin of the material. Where this appears within quotation marks it means that the precise wild origin is uncertain, the region indicated being that of the species. The source of the remainder of the material is known.

Part I. Anatomical Survey (By E. M. Rosser)

1. The genus Aeschynanthus

A. The leaf.

Leaves of *Aeschynanthus* were examined by means of hand sections and by embedding in paraffin wax and sectioning with a rotary microtome. Sections were stained in safranin and fast green. Mounts of the epidermis were made in safranin glycerine jelly.

A general description of the *Aeschynanthus* leaf is given next, followed by details of the individual characters, many of them being explanatory to the tabulation of characters in Table II.

All *Aeschynanthus* leaves are dorsi-ventral. The upper cuticle varies from thin to thick or very thick. The upper epidermis is small-celled with or without glandular hairs and clothing hairs but in all cases without stomata. Beneath this lies the water-storage tissue of large thin-walled cells. The palisade consists, except in *A. tricolor*, of a single layer of cells only, with numerous chloroplasts and usually druses. Beneath this is a transitional layer of cells intermediate in form between cells of the palisade and spongy mesophylls. Cells of the spongy mesophyll are large and rounded and connect with each other by means of tapering peg-like outgrowths. In some species of section *Holocalyx* only there are sclereids in the spongy mesophyll.

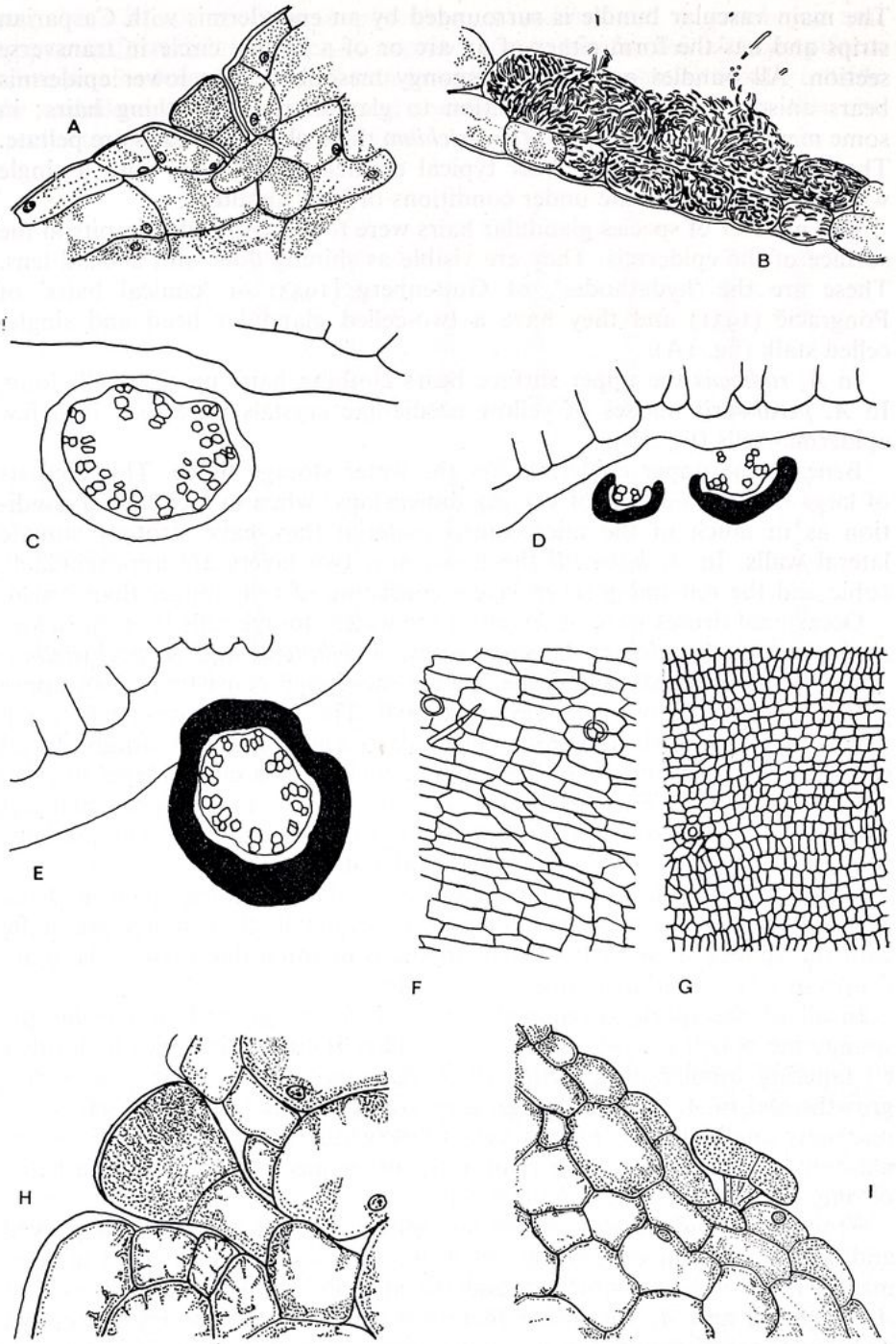

FIG. 1. A. *Aeschynanthus obconicus*, glandular hair immersed in pit on lower leaf surface, X 300. B. *Aeschynanthus perakensis*, crystals in cells of epidermis and hypoderm, X 300. C. *Aeschynanthus longiflorus*, T. S. vascular bundle of leaf midrib showing xylem and phloem, X 72. D. *Aeschynanthus obconicus*, T.S. vascular bundle of leaf midrib showing xylem, phloem and crescents of sclerenchyma (black), X 72. E. *Aeschynanthus evrardii*, T.S. vascular bundle of leaf midrib showing xylem, phloem and sclerenchyma sheath (black), X 72. F. *Aeschynanthus* sect. *Microtrichium*, epidermis, X 72. G. *Aeschynanthus kermesinus*, epidermis of tesselated type, X 72. H. *Aeschynanthus radicans* (No. 21), glandular hair in pit, X 300. I. *Aeschynanthus nummularius*, peltate glandular hair in shallow pit, X 300.

The main vascular bundle is surrounded by an endodermis with Casparian strips and has the form either of an arc or of a hollow circle in transverse section. All bundles occur in the spongy mesophyll. The lower epidermis bears anisocytic stomata in addition to glandular and clothing hairs; in some members of the section *Microtrichium* these glandular hairs are peltate. The margins of the leaves bear typical epithem hydathodes with a single water pore; these guttate under conditions of high humidity.

In a number of species glandular hairs were found embedded in pits in the surface of the epidermis. They are visible as shining dots with a hand lens. These are the 'hydathodes', of Guttenberg (1943) or 'conical hairs' of Pongračič (1931) and they have a two-celled glandular head and single-celled stalk (fig. 1A).

In *A. radicans* the upper surface bears clothing hairs up to 7 cells long. In *A. perakensis* masses of yellow needle-like crystals were seen in a few epidermal cells (fig. 1B).

Beneath the upper epidermis lies the water storage tissue. This consists of large thin-walled cells of varying dimensions; when in a collapsed condition as in much of the microtomed material they have strongly sinuate lateral walls. In *A. hosseusii* the uppermost two layers are approximately cubic and the remaining seven layers consisting of cells longer than broad.

Occasional druses were observed in the water storage cells in *A. hosseusii*, *A. lamponga*, *A. pulcher*, *A. marmoratus*, *A. ellipticus* and *A. pachyanthus*.

Below the water storage tissue lies the mesophyll consisting of an upper palisade layer and lower spongy mesophyll. The palisade consists of small rectangular cells with numerous chloroplasts and sometimes druses. In all species but *A. tricolor*, where the palisade consists of a double layer of cells, the layer is single. The number of palisade cells to each hypodermal cell varies with the species, and is tabulated in Table II as item 5. The presence or absence of druses also varies: this is tabulated as item 6.

Below the palisade lies a transitional zone of cells intermediate in shape between those of the palisade and spongy mesophyll; these merge gradually with the spongy mesophyll so that no sharp dividing line exists. There are druses in this transitional zone in *A. tricolor*.

In all of the species examined except *A. lamponga* and *A. tricolor* the spongy mesophyll consists of large rounded cells connecting with each other by tapering tubular outgrowths. In *A. lamponga* the cells lack these outgrowths and in *A. tricolor* though they are present the cells themselves are markedly smaller than in other species of the genus. In *A. radicans* the spongy mesophyll is a narrower layer than in the other species examined, consisting of only a few of the large rounded cells.

Around the mid-rib the spongy mesophyll cells are more closely packed and lack the tubular outgrowths. In *A. hosseusii* starch grains occur in large masses in spongy mesophyll around the mid-rib. Around the main vein in *A. lamponga* and *A. parvifolius* there are druses in the spongy mesophyll and druses are distributed in the spongy mesophyll of A. 5. In *A. perakensis* masses of yellow needle-like crystals occur in some cells of the spongy mesophyll.

Just beneath the lower epidermis in some species of Section *Holocalyx* there occur in the spongy mesophyll cubic or elongated uniformly thickened or hippocrepiform sclereids with strongly pitted walls. The cubic or rec-

tangular sclereids occur in *A. obconicus*, *A. pulcher* and *A. praelongus* and hippocrepiform sclereids in *A. tricolor*. In *A. tricolor* the hippocrepiform sclereids also form a partial sheath around the main vascular bundle outside the endodermis. Thus the cortical sheath of the stem appears in this one species to be continued into the leaf.

	1. Cuticle	2. Hairs in pits	3. Hypoderm layers	4. Hypoderm shape	5. Palisade hypoderm	6. Druses in palisade	7. Mid-rib
1. marmoratus	A	+	4	0	5	++	A
2. maculatus	B	0	7	+	5	+	A
3. evrardii	A	+	7	+	5	++	C
4. hosseusii	B	0	9	+	7	++	C
5. sp.	B	0	7	+	4	++	A
6. longiflorus	B	+	3	0	3	+	A
7. perakensis	A	0	4	0	7	++	C
8. tricolor	A	0	6	+	7	++	C
9. obconicus	B	+	4	0	8	++	A
12. lamponga	A	+	4	0	4	++	C
13. pulcher	A	+	5	+	5	+	C
14. praelongus	B	0	6	0	6	0	A
15. parvifolius	A	+	5	0	5	++	C
19. ,,	B	+	4	0		+	A
21. radicans	A	+	5	+	5	++	C
24. sp.	B	+	5	0	6–7	0	A
25. ellipticus	A	+	3	0	3	++	A
26. kermesinus	A	+	3	0	3	++	A
27. nummularius	A	0	1	0	3	+	A
28. sp.	A	+	3	+	3–4	++	A
29. pachyanthus	A	+	4	+	6–7	++	A
30. sp.	B	+	5	+	3–4	0	A
31. sp.	A	0	4	+	4	++	A
32. x splendidus		+	7	+	4	0	A

TABLE II. Tabulation of leaf characters of *Aeschynanthus*. Explanations of symbols: cuticle, A = thin, B = thick; hairs in pits, presence (+) or absence (0) of glandular hairs in pits on upper surface; hypoderm layers, number; hypoderm shape, cells longer than broad (+) or not (0); palisade hypoderm, number of palisade cells to each hypodermal; druses in palisade, in all cells (++) or some (+) or absent (0); mid-rib, forming an arc in t.s. (A) or a circle (C).

Like the upper epidermis the lower epidermis consists of small thin-walled cells but here the epidermis contains stomata and also frequently bears clothing hairs. In *Aeschynanthus kermesinus* it has been found that the wall of the epidermal cells in the mid-rib region is papillate. In *A. perakensis* masses of yellow needle-like crystals occur in a few cells of the lower epidermis in patches. In all species examined glandular hairs are embedded in pits in the lower epidermis. In *A.* 28 (aff. *nummularius*) and *A. pachyanthus* of Section *Microtrichium* these glandular hairs are not of the usual conical form but are peltate.

The stomata are anisocytic. In *A. obconicus* they are grouped in quite large patches visible with a hand lens. Counts of stomata in these groups

showed that the most frequently occurring number in a group was three, the maximum number nine. 100 solitary stomata were found in the same leaf as 172 groups. Grouped stomata in the Gesneriaceae were observed by Solereder in the genus *Napeanthus* (1909) and also occur elsewhere.

In transverse section the main vascular bundle of the leaf may have the form of an arc with the phloem on the lower convex surface; or xylem forms a circle surrounded by phloem (Table II, item 7). In *A. hosseusii* a group of xylem elements lies in the parenchyma within this circle. In A. 5 and A. 30 an additional small bundle lies above the main mid-rib bundle, with xylem and phloem reversed and in *A. obconicus* there is a similar small bundle in which xylem and phloem are orientated in the same way as in the main bundle.

In all species the main bundles are surrounded by an endodermis with Casparian strips. Associated sclerenchyma may be absent as in *A. longiflorus* (fig. 1C) or may take the form of crescents (*A. obconicus*, fig. 1D) or a complete sheath (*A. evrardii*, fig. 1E).

Along the margin of *Aeschynanthus* leaves are epithem hydathodes. Small protrusions from the leaf at this point bear a single water pore, below which the vascular bundle enters obliquely.

B. The stem.

Fresh material was fixed in Formalin Acetic Alcohol. It was impossible to use stems of the same thickness throughout the investigation since stems in the section *Microtrichium* are quite thin and wiry and those in other sections comparatively stout. For this reason therefore, material from at least the seventh internode was considered in addition to young stems. All stems were examined by means of hand sections. The epidermis was studied by means of surface sections taken with a razor. Transverse sections were stained in safranin and fast green and also treated with phloroglucinol and Sudan IV. The surface strips were mounted in safranin glycerine jelly.

In all of the species examined the cuticle is thick and in *A. maculatus* and *A. marmoratus* and *A. evardii* very thick. In *A. perakensis* the cuticle is not only thick but striated.

In section *Microtrichium* (with the exception of *A. kermesinus* and *A.* 30) the epidermal cells were found to be large and rectangular, orientated parallel with the stem axis (fig. 1F). In *A. kermesinus*, A. 30 and the species of other sections examined the cells are of a tesselated type, more or less isodiametric in surface view (fig. 1G). In *A. kermesinus* they are small and almost cubic. The majority of other tesselated species have at least a few cells elongated transverse to the axis of the stem, while in *A. marmoratus* and the hybrid *A. x splendidus* the elongation is parallel to the stem axis. Some of the epidermal cells of *A. kermesinus* have one or more small papillae.

Stomata only occur infrequently on the stems. In some of the stems examined (including all those of sect. *Microtrichium*) none have been observed. It therefore seems worth while to detail cases in which they have been seen. *A. evrardii* showed one normal anisocytic stoma and one anomalous stoma with four subsidiaries. One anisocytic stoma was observed in *A. longiflorus*. In a strip obtained by maceration *A. sp.* (No. 5) showed grouped stomata, namely one patch of six stomata with one of the normal

anisocytic type with three subsidiaries and the remainder anomalous. In *A. maculatus* there are occasional stomata of the anisocytic type with three subsidiaries and other anomalous stomata with up to five subsidiaries. In *A. marmoratus* a stoma of the anisocytic type with three subsidiaries was observed.

	1. Clothing hairs	2. Glandular hairs	3. Cortical sclereids young	4. Cortical sclereids old	5. Druses in cortex	6. Cortical sheath	7. Young pith	8. Old pith
1. marmoratus	0	0	X	X	0	D	D	D
2. maculatus	0	0	X	X,I	0	C	D	
3. evrardii	0	0	X	X,I	X,I	D	D	
4. hosseusii	0	A	0		I	D	D	
5. sp.	0	C	0	0	0	C		
6. longiflorus	8	0	0		X,I	D	D,C	
7. perakensis	0	0	0		0	D	D	
8. tricolor	6	A	I	X,I	0	C		
9. obconicus	0	A	I	I	I	C	D,S	
10. ,,	4–5	B	0	I	I	C	0,S	D,S
11. ,,		B	0	I	0	C	D	0
12. lamponga		B	0		I	C	D	D
13. pulcher	0	A	X	I	0	C		
14. praelongus	5	A	I	X,I	I	C	D	0,S
15. parvifolius	4	B	I	X,I	I	C	0	D
16. ,,	6–7	B	0	I	0	C	D	
17. ,,	5–6	A	0		X,I	C	D,S	
18. ,,		A	I	I	0	C	0	D
20. ,,	3–5	C	0		0	C	D	D
21. radicans	5	A,C	0		I	C	D	D
22. ,,	5	B	0		0	C		
23. ,,	5–7	B	X,I	X,I	0	C	0,S	D
24. sp.	5	A	X,I	X,I	0	C	D	
25. ellipticus	4	A,C	0		0	C	D	0,C
26. kermesinus	5–7	A	0		0	C	0	0,S
27. nummularius	2–5	B,C	0		0	C	D	0,S
28. sp.	2–7	A	0		0	D	D	0
29. pachyanthus	0	A	0		X,I	D	D,S	D
30. sp.	0	B	0		0	C	D	0
31. sp.	0	B	0	I	0	C	0,S	
32. x splendidus	0	0	0		0		D	

TABLE III. Tabulation of some stem charcters of *Aeschynanthus*. Explanation: clothing hairs, number of cells; glandular hairs, absent (0), conical in pits (A), peltate in pits (B), stalked and superficial (C); cortical sclereids, absent (0), in outer cortex (X), in inner cortex (I); druses in cortex, absent (0), in outer cortex (X), in inner cortex (I); pith, druses absent (0), present in some cells (D), starch grains present (S), crystals present (C).

A. obconicus (No. 11) has stomata in groups of two or three as well as solitary stomata on white patches on the stem. Detailed examination has been made of all *Aeschynanthus* stems showing such small white patches, with the following results. White patches, containing one to few stomata and a few hair scars have been found in many species, but sometimes most of the patches lack stomata and a long search was needed before one was

found. The species concerned included *A. evrardii*, *A. obconicus*, *A. lamponga*, *A. tricolor*, *A. parvifolius*, *A. radicans*, *A. pachyanthus*, *A. spp.* (No. 24, 30).

Some species are altogether glabrous, but when clothing hairs are present they vary in length from 3 to 8 cells. Details are given in Table III, item 1.

Many species exhibit glandular hairs in pits, the type which Guttenberg described (1934-35) in leaves of *A. pulcher* as hydathodes. In others the hairs are of the much more familiar stalked type with glandular heads. Since the actual functioning of the glandular hairs has not been observed in *Aeschynanthus* the term glandular hairs will be adhered to for all of them even though it seems probable that hairs of the type in pits are indeed hydathodes.

These hairs vary in frequency in different species and lie in such deep pits that the tops of their heads only are level with the surface (fig. 1H). In most cases they have conical two-celled heads with a one-celled stalk; in some species (e.g. *A. radicans*, No. 22, 23) the heads are peltate and in *A. nummularius* (fig. 1I) and other species, the hairs are peltate with several-celled stalks and lobed several-celled heads and emerge from shallow pits.

In a few species the stalked glandular hairs often reported in other Gesneriads (see Sachs, 1915) are found. In *A. nummularius* these have a one or two-celled stalk and two-celled heads. *A. ellipticus* has superficial hairs with two-celled heads and six-celled stalks. *A. radicans* (No. 21) has long-stalked glandular hairs with six-celled stalks and two-celled heads, *A. parvifolius* (No. 20) 4–6 celled stalks with 2-celled glandular heads and young shoots of *A.* 5 show short-stalked glandular hairs with two-celled heads which can be seen as shining dots with a lens. These are often over anthocyanin coloured subepidermal cells. Details of occurrence of the 3 types of glandular hairs are given in Table III, item 2. Glandular hairs are absent from the young stems of *A. evrardii*, *A. perakensis*, *A. longiflorus*, *A. maculatus* and *A. marmoratus*.

The cortex provides a variety of characters. In a number of species the outer cortex in the young stems is very closely packed. Some species are characterized by the presence of the cells with lignified horse-shoe thickenings referred to by Solereder and by Metcalfe & Chalk. These sclereids have lignified thickening on the radial and inner walls only and may either be solitary or distributed in occasional groups around the circumference of the stem. Sometimes as in *A. maculatus* these horse-shoe thickenings are very thick and associated with extremely strong development of the cortical sheath which will be described later. The horse-shoe cells are absent from the cortex of all species of the section *Microtrichium* so far examined but present in at least some species of the other sections. They are absent from the hybrid *A. x splendidus*. Another feature of interest is the presence of small druses in cortical cells of some species, sometimes throughout the cortex and sometimes only in the inner cortex.

The presence of these cortical characters in the individual species may now be noted.

The cortex has an outer zone of very closely packed cells in young stems of *A. hosseusii*, *A. perakensis*, *A. obconicus* (No. 9), *A. parvifolius* (No. 15), *A. praelongus*, *A. pulcher*, *A. radicans* (No. 21), and *A. tricolor*. In section *Microtrichium* all except *A. kermesinus* have the inner cortex as well as the outer closely packed in young stems. In old stems the outer cortex was

closely packed in all the species examined, including *A. kermesinus* which in the young stem has a loosely packed cortex.

A summary of the occurrence of horse-shoe cells in outer and inner cortex is given in Table III, items 3 & 4. The following details may be added. In young stems horse-shoe cells occur in the outer cortex in *A. evrardii* (in groups); in *A. maculatus* (very thick and in groups—fig. 2A); in *A. marmoratus* (thick, solitary or grouped); in *A. pulcher* (solitary). They occur throughout the cortex in *A.* 24, *A. parvifolius* (No. 15), *A. radicans* (No. 23) and in the inner cortex alone in *A. obconicus* (No. 9), *A. praelongus* (numerous groups), *A. tricolor* (occasional), *A. parvifolius* (No. 18) (numerous solitary). It is noteworthy that the extent of development of horse-shoe cells in old and young stems of the same species may differ considerably (compare items 3 and 4 in Table III). Generally they are more extensively developed in the older stem and this reaches an extreme in *Aeschynanthus evrardii* for in that species while the young stem contains small groups of horse-shoe sclereids in the cortex the old stem contains large groups of sclereids, only the outer members of the group being of the horse-shoe type, the inner thickened all round.

Aeschynanthus praelongus was the only material cut in which the situation was seemingly reversed and sclereids were more abundant in the young stem than in the older stem. A stem of *A. praelongus* nineteen internodes long was therefore sectioned. It was found that sclerification was only complete in the oldest internodes, which have abundant horse-shoe sclereids in the cortex. The frequency of horse-shoe sclereids in internodes between the first and the seventh varied considerably from few to many. Thus there were many in the second and few in the sixth. Another long stem sectioned in the same way showed no horse-shoe sclereids at all in the youngest internodes, numerous sclereids in the 23rd and few to many in internodes between. It thus seems clear that no definite relation prevails between age of stem and frequency of horse-shoe sclereids in *A. praelongus*. It is possible that the formation of these horse-shoe sclereids is determined by factors in the environment under which the plants grow and changes in that environment may have brought about this variation in frequency at different internodes. Clearly the presence or absence of horse-shoe sclereids in the cortex of *Aeschynanthus* species cannot be used as a taxonomic character since detection of sclereids depends on what internode is selected for sectioning. *A. parvifolius* (No. 15), for instance, had horse-shoe sclereids in the cortex of the young stem but not in the section taken from the old stem. Al-Talib & Torrey (1961, p.71) concluded from their study of sclereid formation in *Pseudotsuga* that "sclereid initiation and differentiation in the intact plant may well be under the control of hormonal factors in the plant, one of which may be auxin". *Aeschynanthus* might well prove a very suitable subject for experimental work.

Druses occur in the cortex and their distribution is tabulated in Table III, item 5.

The inner cortex in all the stems examined (except the young stem of *A. x splendidus*, No. 33) is bounded on the inside by what Guttenberg (1943) termed the 'Rinden Schichte', the cortical sheath (fig. 2B). This may be continuous or discontinuous and consists of a layer of sclereids with the same horse-shoe thickening which occurs in the cortical cells described in

the last section. These sclereids also have their thickenings only on the radial and inner walls and these thickenings may be moderate in some species and extremely thick with very well-marked pits in others. The layer resembles the strongly developed endodermis found in some monocotyledonous roots (cf. Carlquist 1961 p.98). Examination of a stem of *A. radicans* (No. 21) showed that in the first internode there is no trace of a cortical

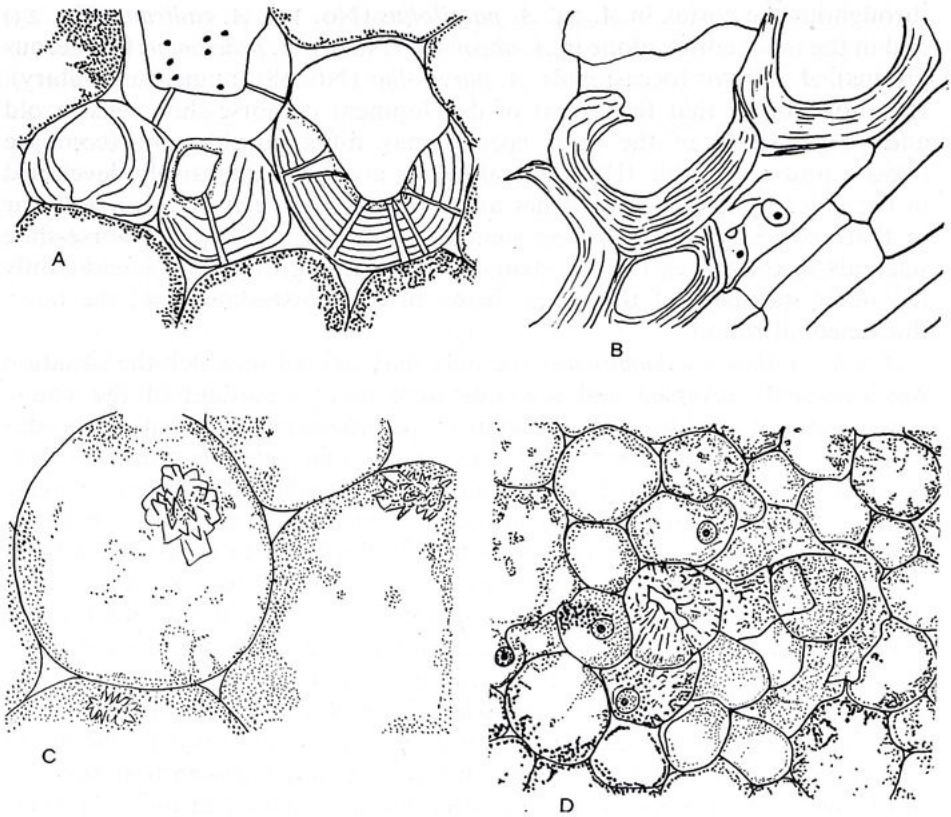

FIG. 2. A. *Aeschynanthus maculatus*, grouped horse-shoe sclereids from cortex, X 300. B. *Aeschynanthus longiflorus*, part of cortical sheath, X 300. C. *Aeschynanthus evrardii*, druses in cells of pith, X 300. D. *Aeschynanthus maculatus*, sclereids in pith, X 300.

sheath, in the second, third and fourth the thickenings on the sclereid walls are only moderate and in the fifth internode they are extremely thick and fully developed. So in comparing the development of the cortical sheaths in different species it was obviously important to ensure that mature stems were examined.

Some species, have a discontinuous sheath, interrupted by ordinary parenchymatous cells, while others have a continuous cortical sheath (Table III, item 6). It has been noted that in a number of species having strong development of horse-shoe sclereids the cortical sheath is several cells thick in places; these are, *Aeschynanthus parvifolius* (No. 15, 18), *A. obconicus* (No. 10), *A.* 30. The extremely thick-walled sheath cells were also found in young stems of *A. obconicus* (No. 9, 11), *A. radicans* (No. 21), *A. parvifolius* (No. 20).

In a number of species in which the cortical sheath in the young stem was found to be only moderately thickened the sheath in the old stem was strongly thickened. These species are *A. nummularius*, *A. praelongus*, *A. pulcher*, *A. kermesinus*, *A. perakensis*, *A. parvifolius* (No. 17 & 18), *A. obconicus*, *A. tricolor*, *A. aff. nummularius*. In others even in the old stems the cortical sheath is still only moderately thickened, as in *A. maculatus*, *A. parvifolius* (No. 15, 16, 20), *A. evrardii*, *A.* 30, *A.* 5 and *A. pachyanthus*.

In *A. evrardii* the young cortical sheath shows prismatic and acicular crystals, and druses were observed in the cortical sheath of the old stem.

An endodermis was found in every one of the *Aeschynanthus* species examined. Sometimes it lies immediately within the cortical sheath and sometimes it is separated from it by a layer of parenchymatous cells. The endodermal cells were in the secondary condition described by Guttenberg (1943), that is they were uniformly thickened all round and suberized. A lignified Casparian strip was also observed when sections of stem of *A. pachyanthus* were treated with phloroglucinol. Passage cells were observed in the endodermis in *A. evrardii* and a few passage cells in *A. hosseusii*, *A. marmoratus*, *A.* 24 and *A. parvifolius* (No. 20) but in the remaining material no passage cells were seen, the endodermis appearing to be continuous. This agrees with Guttenberg's statement (1943, p.43) that "true passage cells can appear also high up in leafy axes as I found in Melastomaceae, in *Pandanus graminifolius* and in Gesneriaceae (*Aeschynanthus* and *Cyrtandra*)". Later, (p.55) he states that the passage cells in these axes occur in an exceptionally short zone which probably explains why they were not seen in more *Aeschynanthus* species by the present author.

In *A.* 5 the endodermis was found to consist of a double layer in places but in none of the species examined has the completely double endodermis illustrated by Guttenberg for *A. pulcher* (1943, fig. 51) been seen. In *A. pulcher* a single endodermis was observed immediately within the cortical sheath. In *A. kermesinus* the endodermis is separated from the cortical sheath by one row of parenchyma and similarly in *A. parvifolius* (No. 17), *A. obconicus* (No. 10) and *A. perakensis*.

STELE.

In all *Aeschynanthus* species the stele forms a continuous hollow cylinder. The phloem in all cases is continuous, with small sieve tubes and companion cells. The only distinction between species lies in the distribution of phloem fibres. *A. evrardii* is distinguished by the occurrence of occasional unlignified fibres, the only species examined in which these have been found. *A. maculatus*, *A. marmoratus*, *A. praelongus*, *A.* 24, *A. parvifolius* (No. 15, 18, 20) all have occasional lignified phloem fibres in the young stem. *A. obconicus* (No. 10) has occasional lignified fibres or groups of two or three lignified phloem fibres. Only in old stems of *A. pulcher*, of the species examined, was the development of phloem fibres extensive; in that species there are numerous lignified fibres forming an almost continuous layer around the outer margin of the phloem. In *A. lamponga* and *A. tricolor* lignified fibres are found in old stems only. *A.* 30, *A. evrardii*, *A. ellipticus*, *A. parvifolius* (Nos. 15, 16, 17, 20), *A. radicans* (No. 21), *A. marmoratus*, *A.* 5, *A. nummularius*, *A. pachyanthus*, *A. aff. nummularius* and *A. perakensis* all lack lignified fibres in young and old stems.

Like the phloem the xylem is continuous in all species, with a few scattered large vessels. These vessels are embedded in a matrix consisting of elements which show either spiral or scalariform thickening in longitudinal section. In some stems a few fibres with living contents have been observed. Such fibres have previously been observed in the Gesneriaceae by Kwiton Jong (private communication).

In the youngest stems the xylem consists of the spirally thickened protoxylem and metaxylem vessels and a few prosenchymatous elements. In older stems secondary thickening develops from a well-defined cambium. In the species examined, however, only *A. evrardii* showed a wide woody cylinder with vessels singly or in groups of two scattered throughout, and no trace of annual rings.

Within the protoxylem in all the species examined lies a medullary sheath consisting of lignified pith elements. In longitudinal section these are rectangular and little longer than the unlignified pith cells and have strongly pitted end walls. Islets of parenchyma lie between the medullary sheath and the xylem and surround the protoxylem elements. The medullary sheath of *A. obconicus* (No. 10) was particularly noted since it contains numerous druses.

In all species the bulk of the pith consists of large thin-walled parenchyma cells which in a number of species contain druses (fig. 2C) or starch grains or both. The occurrence of these cell inclusions may vary according to the age of the stem examined. Available information is tabulated (Table III, items 7 & 8); in *A. obconicus* (No. 9) druses were restricted to the cells nearest the xylem. In addition it may be noted that prismatic crystals were seen in the young stems of *A. longiflorus* and in old stems of *A. ellipticus*.

Nests of sclereids with thick lignified and pitted walls occur in the pith of young stems of *A. evrardii*, *A. maculatus* (fig. 2D), *A. marmoratus*. In *A. maculatus* it was noted that the lumen was very small indeed and that the outer cells of the nests have thickenings of horse-shoe form instead of the uniform all-round thickenings shown by the inner cells. *A. perakensis*, *A.* 5, *A. tricolor* also have nests of sclereids in the pith but in these species the walls though strongly lignified and pitted are very much thinner, sometimes not much thicker than the ordinary parenchyma cells. In the old stems of *A. perakensis* and *A. maculatus* occasional slightly lignified cells were found in place of the nests of sclereids. Sectioning of successive internodes of stems of *A. perakensis* and *A. maculatus* showed that cortical sclereids, sheath and pith sclereids are absent in the youngest internodes of all. Lignified thick-walled pith cells were found only in some of the older internodes, especially those adjoining nodes bearing scale leaves, reduced leaves or only leaf scars. They appear to arise mainly during phases when fully developed leaves are not produced, or have been shed. Thus like the horse-shoe sclereids in the cortex these lignified pith cells are of no systematic value though casual sectioning might give the impression that they were. The old pith of *A. evrardii* contains groups of lignified and thickened cells containing clusters of prismatic crystals whereas in the young stem similar cells contain druses. *A. parvifolius* (No. 18) has no sclereids in pith of the young stem but in the old stem there are large masses of sclereids in the pith.

Cork was only seen in young stems of a few species, where it arises in the

subepidermal layer of the cortex. *A. perakensis* shows a curious epidermal feature which may have some connection with cork production. The epidermis contains groups or strands of cells with suberized cuticular wedges between them. It seems possible that in the older stem the patches might coalesce but such an occurrence has not yet been observed. Similar cuticular wedges have been seen in the epidermis of *A. x splendidus* but they are by no means as extensive in this hybrid as in *A. perakensis*.

In the young stem of *A. ellipticus* the first few layers of cork were observed and in the old stem this had developed into a definite outer zone of cork cells. Cork was also observed in old stems of *A. nummularius*, though not in the young stem, in both young and old stems of *A. kermesinus*, in old but not young stems of *A. aff. nummularius* and *A. pachyanthus* and in young and old stems of *A.* 31.

In *A. maculatus* cork was observed just above nodes from which the leaves had been shed, even when the remainder of the internodes was free from cork.

Conclusion.

As has been shown above there may be quite striking variation in the structure of the stem along its length, other than that simply due to age. So in *A. praelongus* there may be many, few or no hippocrepiform cells in the cortex and in *A. maculatus* massively thickened sclereids, slightly thickened sclereids or no sclereids in the pith. Thus random sections are liable to give a misleading impression. There is also a certain amount of variation in species where several stocks have been studied.

None of the features observed is constantly associated with any of the taxonomic sections though the thin-walled rectangular epidermal cells are only found in certain species of the Section *Microtrichium*.

A generic description of the *Aeschynanthus* stem may be given as follows:—

Epidermis with thick cuticle, cells slightly arched. Cells generally of tesselated type but sometimes in Section *Microtrichium* rectangular and orientated parallel with stem axis. Stomata few, anisocytic, often grouped on white patches on stem. Clothing hairs of uniseriate type present on nearly all stems. Glandular hairs with two-celled heads and one-celled stalk embedded in pits in the surface in most species; in a few species longer-stalked superficial glandular hairs occur. Glandular hairs are altogether absent from a few species.

Cortex generally closely packed outside, more loosely packed inside and sometimes containing isolated or grouped hippocrepiform cells. Generally with druses.

Cortical sheath of strongly or moderately thickened hippocrepiform cells present in all old stems. This may be continuous or discontinuous.

Endodermis present in all stems, uniformly thickened and suberized all round, with Casparian strips.

Phloem a continuous cylinder with companion cells. Phloem fibres in some species and an almost continuous pericyclic layer in old stems of *A. pulcher*. Xylem continuous with a few scattered large vessels.

Medullary sheath between xylem and pith consisting of slightly elongated, lignified, pitted pith cells.

Pith cells large thin-walled, generally containing druses and sometimes with starch grains. A few species contain prismatic crystals.

Cork production is superficial.

2. Genera other than Aeschynanthus

The table of materials (Table IV) shows that very much less was available for study in *Agalmyla*, *Lysionotus* and *Loxostigma* than in *Aeschynanthus*. Specimens which do not have a 'C' number are herbarium specimens and examination of these was virtually restricted to ascertaining the presence or absence of cortical and medullary vascular bundles, both of which were known to occur in the stem of the type species of *Agalmyla*, *A. parasitica*.

Agalmyla Bl.		
1. A. parasitica (Lam.) O. Kuntze	C 2854	Malay Peninsula
2. A. tuberculata Hook. fil.	RSNB 865	Sabah
3. ,, ,,	RSNB 1127	,,
4. A. borneensis (Schlechter) B. L. Burtt	C 4045	Sarawak
5. A. (aff. borneensis)	RSNB 1336	Sabah
6. ,, ,,	RSNB 2520	,,
7. ,, ,,	RSNB 2575	,,
8. ,, ,,	RSNB 4315	,,
9. ,, ,,	RSNB 4344	,,
10. ,, ,,	RSNB 4020	,,
11. A. (aff. Dichrotrichum filarskyi K. Schum.)	vR 16104	New Guinea
12. A. (Dichrotrichum villosum Schlechter)	vR 3651	,, ,,
Lysionotus D. Don		
1. L. serratus D. Don	C 4211	Thailand
2. ,, ,,	C 5941	,,
3. ,, pauciflorus Maxim.	C 4519	"Japan"
Loxostigma C.B.Cl.		
1. L. griffithii (Wight) C.B.Cl.	J.D.H. s.n.	Sikkim
2. ,, ,, ,,	P 4062	Assam

Table IV. Materials of *Agalmyla*, *Lysionotus* and *Loxostigma*. Abbreviations in reference numbers: C — cultivated at Edinburgh; RSNB — Royal Society North Borneo expedition; vR — van Royen; J.D.H. — J. D. Hooker; P — Panigrahi. All material other than C was herbarium material.

A. The leaf.

Only the living material of *Agalmyla parasitica* and the three stocks of *Lysionotus* were examined.

The upper epidermis: as usual the upper epidermis in all four consists of small polygonal cells rectangular in cross section covered by a thin cuticle. In *Lysionotus serratus* superficial glandular hairs were observed having two-celled spherical heads and one-celled stalks. The glandular hairs of *Agalmyla parasitica* have a similar form but are half-immersed in shallow pits on the surface. Glandular hairs were not observed in the upper epidermis of *Lysionotus pauciflorus*. These spherical glandular hairs may be contrasted with the conical hairs immersed in deep pits which were described in *Aeschynanthus*. No clothing hairs were observed on the upper surfaces of these leaves, though very often present in the genus *Agalmyla*.

A hypodermis was present in all four species. In *Agalmyla parasitica* it consists of water storage tissue two cells thick composed of cells which are broader than long. In *Lysionotus pauciflorus* and *Lysionotus serratus* (No. 2), the water storage tissue is also two layers thick and in *Lysionotus serratus* (No. 1) three layers thick; in all three the cells are broader than long as in *Agalmyla*.

In all three stocks of *Lysionotus* and in *Agalmyla* a transition zone was observed between the palisade and the spongy mesophyll. In *Lysionotus serratus* and *Agalmyla parasitica* the palisade consists of the more common single layered type but in *Lysionotus pauciflorus* it is two to three layered. In *Agamlyla parasitica* each cell of the palisade layer contains, in addition to the numerous chloroplasts found in the other species, a single druse.

The spongy mesophyll in *Agalmyla* and in *Lysionotus* consists of rounded cells connecting with each other by tubular outgrowths as in *Aeschynanthus*.

The lower epidermis is of small cells, rectangular in cross section in both *Agalmyla* and *Lysionotus*. In *Agalmyla parasitica* there are numerous glandular hairs with two-celled spherical heads half-immersed in pits in the surface. In *Lysionotus pauciflorus* superficial glandular hairs with two-celled spherical heads and a single-celled stalk were observed in the mid-rib region. Similar hairs with glandular heads were observed occasionally on the leaves of *Lysionotus serratus*. In both genera the stomata are anisocytic.

The mid-rib in *Agalmyla* and *Lysionotus* has the bundles enclosed in a matrix of parenchyma; in *Agalmyla* this contains numerous druses, which are absent from *Lysionotus*. All three species have the main bundle enclosed in an endodermis with Casparian strips. In *Agalmyla*, *Lysionotus pauciflorus*, and *L. serratus* (No. 2) the main bundle consists of a simple arc of xylem with an arc of phloem below. In *L. serratus* (No. 1) the arcs of xylem and phloem are surrounded by a further arc of sclerenchyma. Above the main bundles in *Agalmyla* are small bundles with the xylem directed upwards. In *Lysionotus pauciflorus* these small bundles are absent and in *L. serratus* small bundles are scattered above with the xylem directed downwards.

B. The stem.

The type species of *Agalmyla*, *A. parasitica*, is described separately, followed by other material now referred to the genus; then come *Lysionotus* and *Loxostigma*.

Agalmyla parasitica.

Epidermis: cells slightly arched, cuticle thin. Clothing hairs are three to seven celled with acute tips. The glandular hairs are superficial with two celled heads and one celled stalks.

Cork is superficial.

Cortex: the outer cortex is collenchymatous and within lies an inner cortex of thin walled loosely packed cells with druses. In this inner cortex was seen a single vascular bundle. When material consisting of a node and part of an internode was cut in half lengthways, cleared with methyl benzoate and stained with phloroglucinol—HCl by the method of Galavazi (1965), it was found that this cortical bundle was actually a leaf trace which runs

vertically for a considerable distance through the cortex before joining the other leaf trace bundles in the petiole. There is no cortical sheath.

Endodermis was not distinguishable.

Stele: the phloem forms a continuous ring, without phloem fibres, and the xylem a continuous ring with groups of large vessels at intervals.

The pith consists of large thin walled parenchyma cells containing druses. In this pith are four or five or more medullary bundles.

Agalmyla spp.

Ten herbarium specimens which may now be referred to *Agalmyla* (see Burtt, 1968) were examined; of these *A. tuberculata* had been referred to a separate genus, *Tetradema*, by Schlechter and other specimens were previously separated as *Dichrotrichum*.

Epidermis: the cells are thin walled and arched (but they could not always be distinguished in the dried material). *A. borneensis* had large pedestalled clothing hairs of up to eight cells and *A. sp.* (No. 9) clothing hairs which are six-celled, stout at the base and tapering to a point. Glandular hairs were seen only in *A. borneensis* where they are superficial with two-celled heads and one-celled stalks.

Cork, where present, as in *A. spp.* (No. 5, 6, 8 & 10) and *A. sp.* (aff. *Dichrotrichum filarskyi*), is superficial. In the last many tangential walls in the cork are thickened and lignified, and so are some in *A. sp.* (No. 10).

Cortex: in *A. borneensis* the outer cortex consists of four or five layers of collenchyma. The outer cortex is also collenchymatous in *A.* (*D. villosum*), *A. sp.* (No. 10), and *A. tuberculata;* in *A. sp.* (No. 5 & 7) the outer three or four layers are collenchymatous.

In *A. sp.* (*Dichrotrichum* aff. *filarskyi*) the cortex is fairly narrow and consists mainly of thin walled cells with druses but with an occasional thick walled, lignified sclereid. Unlike the hippocrepiform sclereids of *Aeschynanthus* these are uniformly thickened all round. The inner cortex of *A. sp.* (*D. villosum*) also consists of large thin walled cells with an occasional lignified sclereid. In *A. sp.* (No. 9) the entire cortex consists of thin walled cells with very small starch grains and druses and *A. sp.* (No. 6) has a cortex of thin walled cells containing druses and numerous thick walled sclereids some of which also contain druses. *A. sp.* (No. 7) has occasional sclereids in the collenchymatous outer cortex and an inner cortex of large thin walled cells with one druse per cell. The remaining species all have an inner cortex of large thin walled cells with druses *A. sp.* (No. 7) having in addition an inner cortical zone containing numerous starch grains. In *A. sp.* (No. 8) occasional lignified sclereids were visible in the cortex in a few sections only, indicating that they are very sparse. Three cortical bundles were found to be present in *Agalmyla tuberculata* (No. 3); in the other specimens they were absent.

An endodermis consisting of thin walled rectangular cells with Casparian strips on the radial walls was seen in *A. borneensis* but an endodermis was not distinguishable in any of the herbarium material.

No pericyclic fibres were observed in *A. borneensis* but they were present in each of the other nine species. In *A. sp.* (aff. *D. filarskyi*) and *A. sp.* (*D. villosum*) they form a complete ring several cells deep. In *A. sp.* (No. 9) the pericyclic fibres form an almost complete ring with few gaps and with starch grains in the fibres. In *A. tuberculata*, *A. sp.* (No. 6 & 7), the pericycle forms

an almost continuous ring of fibres several rows thick, but in *A. sp.* (No. 5) it consists of a broken ring with large gaps filled by parenchyma. In *A. sp.* (No. 8) the pericycle consists of a broken ring of fibres which is only in places several cells thick.

Stele: the phloem in all the specimens examined forms a continuous narrow ring without fibres. Within this lies a continuous ring of xylem. In *A. borneensis* this contains only a few large vessels but in *A. sp.* (aff. *D. filarskyi*), *A. sp.* (*D. villosum*), *A. sp.* (No. 5, 7 & 9) there are numerous large vessels in radial groups. In *A. sp.* (No. 10) there was a ring of large vessels several cells deep at the outside of the xylem and a considerable quantity of minute starch grains in the fibres of the inner zone.

Pith: in *A. sp.* (aff. *D. filarskyi*), *A. sp.* (*D. villosum*) and *A. tuberculata* the pith consists of large thin walled cells but there are no medullary bundles. The cells of *A. sp.* (aff. *D. filarskyi*) and *A. tuberculata* contain druses, those of *A. sp.* (*D. villosum*) starch grains. The remaining species all have medullary bundles in the pith. In *A. borneensis* there are twelve such bundles but the number generally is smaller; thus there are six centric medullary bundles in *A. sp.* (No. 9 & 10), five in *A. sp.* (No. 5).

In *A. sp.* (aff. *D. filarskyi*) the pith as well as the cortex and pericycle contains simple and compound starch grains.

Loxostigma griffithii.

The epidermal cells are slightly arched. The clothing hairs are up to five-celled with apices blunt or acute.

Cork was of superficial origin and suberized.

The outer cortex consists of a layer about five cells deep of small celled collenchyma with triangular thickenings at the corners of the cells. The inner cortex consists of much larger parenchyma cells with thin walls. Around the stele is a layer having thicker walls with a trace of lignin which appears to constitute a cortical sheath comparable with that observed in so many *Aeschynanthus* species but much less strongly developed. This layer was packed with very large simple starch grains.

Endodermis: within the cortical sheath lies the endodermis, a layer of thin walled rectangular cells with Casparian strips on the radial walls.

Pericycle: within the endodermis lies a continuous ring of pericyclic fibres which are strongly lignified and about three cells wide.

Stele: the phloem consists of a continuous narrow ring without fibres. The xylem is a much wider ring with a few large vessels in radial groups.

The pith consists of large thin walled parenchyma cells which in the Panigrahi material from Assam were packed with starch grains. There were few starch grains in the pith in Hooker's Sikkim specimen.

Lysionotus spp.

The epidermal cells are slightly or scarcely arched. 'Newskin' peels showed a group of three stomata and a patch of ten stomata in *L. serratus.*

Cork: in *L. pauciflorus* and *L. serratus* (No. 2) the stems were covered with a layer of superficial cork, thick in the latter and in *L. pauciflorus* the cork cells contain starch grains.

The cortex in *L. serratus* (No. 1) consists of thin walled parenchymatous cells becoming very large towards the interior where many cells are packed

with large starch grains. There are occasional thick walled lignified cells and an occasional cell contains a monoclinic crystal. In *L. pauciflorus* the outer cortex consists of closely packed thin walled parenchymatous cells with occasional thick walled lignified sclereids with small lumina set in a circle beneath the cork. The inner cortex consists of more loosely packed cells containing numerous small starch grains. In *L. serratus* (No. 2) the cortex consists of rounded, thin walled closely packed parenchyma cells. The outer cortex contains numerous groups of sclereids with uniformly thickened, stratified, lignified walls; these are more numerous than in *L. pauciflorus*. There are numerous starch grains in the cortex.

The endodermis in all three species consists of a layer of rectangular thin walled cells with lignified Casparian strips on the radial walls.

Stele: in both species the phloem forms a continuous cylinder without phloem fibres. The xylem contains large vessels in radial groups and fibres between packed with starch grains.

The pith in *L. serratus* consists of large thin-walled cells with starch-grains and druses, and (in No. 1) with occasional monoclinic crystals. The pith of *L. pauciflorus* contains abundant large starch grains, but no druses.

Part II. The taxonomic implications

The rather extensive survey undertaken in *Aeschynanthus* covered at least one species in each section of the genus. The descriptions and tabulations of characters given above add little to the morphological diagnoses and provide no incentive to undertake the laborious task of extending them to all known species by the use of herbarium material. The work has thus yielded a rather meagre profit from the point of view of classification *within* this genus, and it is clear that the distribution of hair types, sclereids and cell-inclusions is often not reliable even at the species level. What has been achieved, however, is the demonstration of the essential unity of the genus anatomically. The value of this becomes evident directly comparison is undertaken with other groups of the tribe *Trichosporeae*.

Before making any such comparison, however, the genus *Agalmyla* needs brief consideration. The material studied included the type species of *Agalmyla*, *A. parasitica*, *A. tuberculata* (a species placed by Schlechter in his genus *Tetradema*), *A. sp.* (*Dichrotrichum villosum* Schlechter) and *A. sp.* (*Dichrotrichum* aff. *D. filarskyi* K. Schum.), and finally *A. borneensis* (Schlechter) B. L. Burtt (the species on which *Dichrotrichum* sect. *Agalmylopsis* Schlechter) was founded and *A. johannis-winkleri* (Kraenzlin) B. L. Burtt.

Agalmyla parasitica has a cortical vascular bundle and several medullary bundles and it was clearly important to see how these two features were distributed in the other material. The combinations of cortical and medullary bundles was found in no other species. One specimen of *Agalmyla tuberculata* and the New Guinea material *A. sp.* (*Dichrotrichum villosum*) and *A. sp.* (*Dichrotrichum* aff. *filarskyi*) had neither type, but the gap between these and *A. parasitica* was bridged by another specimen of *A. tuberculata*, which has 3 cortical bundles but none in the medulla, and the six specimens of *A. borneensis* (or closely allied species) and one of *A. johannis-winkleri* which all have medullary bundles but none in the cortex. Knowledge of the distribution of these bundles in all the other species of *Agalmyla* (sensu lato)

would clearly be valuable, but at the moment the pattern parallels the morphological pattern—that typical *Agalmyla* and typical *Dichrotrichum* are linked by intermediate forms.

The other two genera, *Lysionotus* and *Loxostigma* lack both cortical and medullary vascular bundles. They also lack the cortical sheath of horse-shoe cells characteristic of *Aeschynanthus*, although in *Loxostigma* a weakly lignified sheath is recognizable. (Outside the tribe *Trichosporeae* a sheath of horse-shoe cells has been found in *Chirita asperifolia* (Bl.) B. L. Burtt of the tribe *Didymocarpeae*.)

We return to a comparison of *Aeschynanthus* and *Agalmyla*, two genera which are more obviously distinguished vegetatively than by the differences in flower, fruit or seed. Briefly *Aeschynanthus* has pairs or whorls of equal-sized rather thick and fleshy leaves borne on relatively thin, often rather tough, stems; the leaf margin is entire or obscurely toothed, the teeth being little more than projecting hydathodes; the lateral veins are scarcely visible externally. In *Agalmyla* the leaves of a pair are usually very unequal, one being reduced to a small stipule-like structure which is not exactly opposite the developed leaf; the latter is larger and thinner than the leaves of *Aeschynanthus* and the margin varies from toothed to deeply lobed; the lateral veins are prominent on the lower surface; the stem of *Agalmyla* is relatively thicker, fleshier and more brittle than in *Aeschynanthus*, and old stems are often hollow.

In leaf anatomy it is noteworthy that the thinner leaf of *Agalmyla* is none the less provided with a water-storing hypodermis. The difference in the prominence of the veins is, of course, reflected in the anatomy of the leaf section, but the morphological expression is, for taxonomic purposes, just as adequate. The anatomy can scarcely be said to add a new character.

The sunken glands which are so much a feature of *Aeschynanthus* leaf anatomy are paralleled in *Agalmyla* by a gland which is partially sunken. There is a difference, but not a fundamental one.

The salient anatomical feature of the stem of *Aeschynanthus* is the cortical sheath of horse-shoe cells. This is completely lacking in *Agalmyla*. The range of material examined has been wide enough to justify the view that this is a good constant distinction: it is no doubt the main underlying cause of the observable difference in stem-texture. On the other hand the early view that *Agalmyla* was characterised by cortical and medullary bundles (always absent from *Aeschynanthus*) has not withstood the wider survey: such bundles are not a constant feature of *Agalmyla*.

Points of agreement between the two genera are that both show transitional tissues between the palisade and spongy mesophyll and both have the vascular bundle of the mid-rib surrounded by an endodermis whose cells have Casparian strips. Neither feature is by any means exclusive to these two genera but they are not universal in the family. They do, therefore, constitute significant links.

Because of the wide difference in leaf-form, and because of certain small floral differences, one of us (B.L.B.) had been prepared to contemplate the possibility that *Aeschynanthus* and *Agalmyla* were very much less closely allied than their current positions in the classification suggest. It seemed possible that the adoption of the largely epiphytic or climbing habit in tropical rain forest had brought with it the associated adaptations of bird-

pollination and elongate fruits containing seeds with capillary appendages: all features closely associated with habit and habitat. The anatomical evidence, when reviewed, does not endorse this idea. There are definite anatomical resemblances and only one major and constant difference: the presence of the cortical sheath in *Aeschynanthus*. On leaf form one would have expected *Lysionotus* to share this character, but it does not do so. The conclusion is, therefore, that the juxtaposition of *Aeschynanthus* and *Agalmyla* remains the most natural arrangement.

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