FLORA MALESIANA

SERIES II - PTERIDOPHYTA

Ferns and Fern Allies

Volume 2, part 1: Tectaria Group
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Tectaria Group

by

R.E. Holttum †
**TECTARIA GROUP (R.E. Holtum †, Kew)**


*Caudea* in almost all cases erect or suberect, always with a radially organized dictyostele; scales narrow and rather firm, marginal teeth (if present, except in *Cyclopeltis*) almost always formed at the junction of two cells; i.e., the wall separating the two adjacent cells is elongated at right angles to the margin. Vascular structure of *stipe* consisting of small subequal vascular strands arranged in a U-formation as seen in transverse section (except in *Pleocnemia* where the arrangement is more complex), the two on the adaxial side variously enlarged. *Fronds* amply divided with free veins, or with broader divisions in which veins anastomose variously, in a few species simple, in most (except *Heterogonium*) the *basal pinnae* or lobes longest with elongate basal basiscopic lobes or pinnules; costae or costules of ultimate lamina-elements ± prominent on the upper surface, branching directly from the prominent upper surface of the rachis bearing them, the margins of the lamina decurrent on the sides of the rachis. *Hairs* consisting of several cells, not intergrading with scales, variously present on most parts of the frond, the prominent upper surface of costae of lamina-segments in a majority of cases (at least near the base) covered with short erect hairs of several cells, the outer cell-walls thin and collapsing on drying (in other cases hairs in this position may remain firm on drying); unicellular glands usually ± cylindric, colourless or red to yellow, variously present on surfaces of leaflets, on indusia, and on stalks of sporangia in some genera. *Sori* usually orbicular, covered with reniform or peltate indusia, or exindusiate, in the latter case sometimes spreading along veins. Fertile pinnae or leaflets in some species much contracted, with sporangia borne all along the veins to produce an acrostichoid appearance. *Spores* in most cases with a perispore folded into wings or crests, the wings variously anastomosing, the perispore in other cases spinulose or with obtuse projections. Base chromosome number 40 or 41.

**Distribution** — Pantropic with greatest diversity in the Old World; about 20 genera.

**Taxonomy** — In the 19th century the form of sori and condition of venation (free or anastomosing) were by most authors regarded as the most important bases for classification. Thus the free-veined members of the present group were associated with *Dryopteris* and free-veined *Thelypteridaceae*, and exindusiate species were separated generically. This led to confusions of various kinds.

*) Dr. Holtum submitted the manuscript of his revision of the *Tectaria* Group for publication in Flora Malesiana not long before he passed away in September 1990. Some distributional data were added by the Editor. The illustrations are by P.J. Edwards, Kew.*
The first major work in the 20th century was Christensen's subdivision of the unnatural aggregate of species under Dryopteris in his Index Filicium (1905) which included all free-veined ferns with reniform indusiate sori and their obvious exindusiate relatives. For the first time he distinguished Ctenitis from Dryopteris, pointing out the relationship of the former to Tectaria and also the distinctive characters of thelypteroid ferns (some of which have anastomosing veins). In his last major survey of the classification of all ferns (1938) he retained a major family Polypodiaceae with Dryopteridoideae as one subfamily; this included, in section A, Dryopteris and Tectaria with other genera related to them, with Thelypteridaceae in section B.

In 1940 Ching divided Christensen's Polypodiaceae into several families, one being Aspidiaceae, similar to Christensen's Dryopteridoideae section A of 1938. Ching divided it into two tribes, Aspidieae and Dryopterideae. In 1947 Holttum accepted Ching's two tribes, with minor changes, but placed them as subfamilies in a major family Dennstaedtiaceae, with the idea that Polypodium and its immediate allies form a very different group of ferns. Copeland, writing independently in 1947, recognized a large family Aspidiaceae, including Thelypteris and its allies, also Athyrium/Diplazium and the Lomariopsis group of genera. In his conspectus (1947: 153) the genera here dealt with appear as allies of Ctenitis; to them should be added Cycloptelis which he associated with Polystichum, and Dryopolystichum excluded. Pichi Sermolli (1977) included both dryopteroid and tectarioid genera in his family Aspidiaceae and did not accept a division of it into two groups.

Holttum (1984) discussed the above history in more detail, still retaining separate groups associated with Dryopteris and Tectaria and objecting to the Tryons' arrangement in their book of 1982 in which the two groups are confused. In 1986 Holttum presented a conspectus of all Old World genera of the Tectaria alliance, with comments on those of the New World, pointing out the peculiar characters of Dryopsis Holttum & Edwards [Kew Bull. 41 (1986) 171–204] which perhaps connects the two groups. Most species of Dryopsis are in Mainland Asia but two are Malesian.

The structure of the junction of the bases of leaflets and the rachis that bears them is here presented as the most clear distinction between the genera allied to Dryopteris and those allied to Tectaria. This is seen best in Lastreopsis, Ctenitis and Pteridrys (see fig. 311 in Holttum 1955: 524). In Lastreopsis the relationship is exactly as in Davallia; Ctenitis only differs in the margins of the lamina which are not thickened where they are decurrent on the rachis-wing. In Cycloptelis the relationship of pinna-base to rachis is only evident near the apex of the frond. An arrangement close to Davallia is also shown by Rumohra, a genus included by several authors in Aspidiaceae. But Rumohra differs from all the genera here included in its strongly dorsiventral rhizome-structure, comparable to that of Davallia though not identical with it, and also in its scales. [Pichi Sermolli (1977: 465) cites Chandra's study of the vascular structure in the caudex of Maxonia as evidence of dorsiventrality in a ally of Dryopteris; but the dorsiventrality in Maxonia is only a slight modification of the normal dictyosteole of Dryopteris, very different from that in Rumohra.] Rumohra differs from Davallia in its distribution (widely in South America, also in southern Africa and Australasia) and in its spores. In Malesia, it only occurs in New Guinea. It is perhaps a connecting link between Davallia and the Tectaria group; it needs a comprehensive new morphological study.
Pichi Sermolli (l.c. 1977: 238) has stated that there are four different types of rachis-structure in *Aspidiaceae* but he deals only with the junctions of main rachis with pinnarachises, not with the relationship between lamina-elements and the smaller distal rachises which I believe to be significant. I have expressed disagreement with him in 1984 (l.c.: 314).

**KEY TO THE GENERA**

1a. Teeth present at the bases of sinuses between pinna- or pinnule-lobes, the teeth projecting out of the plane of the lamina ................................. 2  
  b. Teeth of this kind lacking .............................................. 3

2a. Fronds simply pinnate with free veins; no unicellular glands on lamina or in sori  
  Pteridrys (p. 4)  
  b. Fronds mostly bipinnate, their veins forming at least costal areoles; cylindric glands present ................................................................. Pleocnemia (p. 8)

3a. All axes of the frond bearing copious scales, the smaller ones at least partly clathrate with isodiametric cells ........................................... Ctenitis (p. 21)  
  b. Smaller axes of the frond bearing few scales which are not thus clathrate. ........... 4

4a. Veins in sterile fronds anastomosing copiously; free veinlets in areoles (including those along costae) variously directed and in most species forked. ................... 5  
  b. Veins anastomosing to form costal areoles which lack free veinlets, or all veins free ........................................................................................................ 7

5a. Fertile fronds greatly contracted and bearing indusia ............................................. 6  
  b. Fertile fronds not greatly contracted, or if so lacking indusia  
  Tectaria sect. Tectaria (p. 59)

6a. Sterile fronds simple; fertile ones irregularly deeply lobed; indusia reniform  
  Tectaridium (p. 36)  
  b. Sterile fronds pinnate; pinnae of fertile fronds linear, with continuous indusia along each side of the costa ........................................... Chlamydogramme (p. 37)

7a. Some thick multicellular hairs present between veins on the upper surface, at least near sinuses between lobes. ...................................................... 8  
  b. No thick hairs present between veins on upper surface ........................................... 11

8a. Basal basiscopic lobe or pinnule of basal pinnae longer than the other lobes or pinnules .............................................................................................. 9  
  b. Basal basiscopic lobe of basal pinnae much reduced, these pinnae widest at about mid-length ................................................................. Heterogonium (p. 105)

9a. Fronds not greatly longer than wide ................................................................. 10  
  b. Fronds greatly longer than wide, with many pinnae gradually increasing in size downwards ................................................................. Aenigmopteris (p. 102)

10a. Veins anastomosing in some species; fertile fronds, if greatly contracted, not bearing very small pinnules ........................................... Tectaria sect. Sagenia (p. 42)  
  b. Veins all free; fertile fronds bipinnate with very small pinnules, exindusiate  
  Psomiocarpa (p. 100)

11a. Pinnae articulate to the rachis, entire or crenate ................................... Cyclopeltis (p. 116)  
  b. Pinnae not articulate, deeply lobed or pinnate ................................... Lasteropsis (p. 120)
PTERIDDRYS


*Caudex* short, erect or suberect; scales firm, narrow, entire with cordate base, multicellular hairs present with the scales and variously on the fronds; *fronds* simple-pinnate; external form of rachis and its relationship to pinnae as in *Davallia*; *pinnae* deeply lobed, the lobes ± crenate or dentate; *veins* all free, once or twice forked, the basal basiscopic vein in each lobe springing from the base of the costule (rarely from the costa), the basiscopic branch of the basal acroscopic vein (or sometimes both branches) passing to a tooth in the sinus between that lobe and the next, the tooth projecting out of the plane of the lamina; unicellular glands absent on the lamina and from sporangium-stalks; *sori* on the acroscopic branch of each vein terminal or not, indusiate, indusia reniform, sometimes asymmetric. — *Figs. 1, 2.*

Distribution — A genus of 8 known species in SE Asia (including India and Sri Lanka) and *Malesia* (6 species).

Cytology — *n* = 41 (Manton in Holttum 1955).

Note — This genus appears to be most nearly related to *Pleocnemia*, differing from the latter in free veins and in the absence of unicellular glands. But in *Pteridrys cnemidaria* (Christ) C. Chr. (from S China to NE India) there is occasional anastomosis of the basal veins of adjacent pinna-lobes and the relationship between these and the teeth in sinuses between lobes agrees with that in *Pleocnemia*. Apart from sinus-teeth, *Pteridrys* differs from free-veined species of *Tectaria* in the position of the basal basiscopic vein in each lobe which in *Tectaria* springs always from the costa.

KEY TO THE SPECIES

1a. Basal basiscopic lobes of basal pinnae shorter than those next to them .............. 2
b. Basal basiscopic lobes of basal pinnae elongate, longer than those next to them ... 4

2a. Stalks of basal pinnae c. 10 mm long ........................................... 1. *P. syrmatia*

b. Stalks of basal pinnae much shorter, other pinnae mostly sessile ...................... 3

3a. Pinna-lobes broad and obtuse; costae bearing stiff short hairs at least near their bases  

b. Pinna-lobes acute, costae quite glabrous ....................................... 3. *P. acutissima*

4a. Pinnae mostly short-stalked, their basal acroscopic lobes not or little overlapping the rachis; sinuses between pinna-lobes 2–3 mm wide ........................................ 5

b. Pinnae (except the basal ones) quite sessile, their basal acroscopic lobes overlapping the rachis; sinuses between pinna-lobes very narrow ........................................ 6. *P. confertiloba*

5a. Basal basiscopic lobes of basal pinnae distinctly longer than the next lobes; pinna-lobes slightly toothed distally; basal acroscopic veins in larger pinnae twice forked  

4. *P. microthecia*
b. Basal basiscopic lobes of basal pinnæ little longer than the next lobes; the pinna-lobes strongly crenate-serrate almost throughout; basal acroscopic veins in larger ones once forked ........................................... 5. P. olivacea

Fig. 1. Pteridrys syrmatica (Willd) C.Chr. & Ching. a & b. Upper surface of rachis and bases of a) two lower pinnæ, and b) two upper pinnæ, showing structure of the junction, × 8; c. basal basiscopic lobes (one with sori removed), × 2; d. detail of c showing sinus tooth, × 9 (a–c: van Beusekom & Santisuk 2809).

Fig. 2. *Pteridrys acutissima* Ching. a. Base of basal pinna, showing the almost free pinnule, × 1. — *P. microthecia* (Fée) C. Chr. & Ching. b. Base of a basal pinna, × 0.6. — *P. olivacea* (Rosenst.) Copel. c. Base of a basal pinna, × 0.85. — *P. confertiloba* Holttum. d. Base of a middle pinna showing basal lobes overlapping rachis, × 0.85 (a: Ridley 14742; b: Parris 6851; c: Bamler 103; d: Ledermann 7826).

*Stipe* to 50 cm long; basal scales to 15 × 1.5 mm; *lamina* dark olivaceous when dried, to 60 cm long; pinnae to 20 pairs, basal ones a little shorter than those next above them, narrowed at the base on the basiscopic side, middle basiscopic lobes ± elongate, stalks to 2 mm long; suprabasal pinnae sessile or nearly so, to 20 × 3.5 cm, lobed to 5 mm from costae, costules to 8 mm apart, lobes obtuse, slightly crenate distally, apices of pinnae short- to long-caudate; *veins* mostly once forked (twice forked on largest pinnae); a dense tuft of short hairs present on the lower surface of the base of each costa (sometimes also on the upper surface) and a few at bases of costules, slender hairs to 1 mm long ± abundant on lower surface of rachis, costae and rarely on the veins; *sori* terminal on acrosopic branches of veins; *indusia* persistent, reniform, entire, on Malesian specimens usually hairless (hairs present on those of the type).

Distribution — S China and Burma southwards; in *Malesia*: Peninsular Malaysia (Selangor).

Habitat — On stream banks in forest, sometimes near waterfalls, at altitudes to 900 m.


Differing from *P. australis* as follows: suprabasal pinnae to 4.5 cm wide, lobed to 3 mm from costae, lobes ± falcate, narrowed to an acute tip, rather strongly crenate throughout; basal pinnae of large fronds bearing a pair of pinnules, their largest basiscopic pinna-lobes 5 cm long; hairs lacking or very short and sparse at bases of costae. — Fig. 2a.

Distribution — *Malesia*: Malay Peninsula (Perak), Borneo (Sarawak) (one collection from each).

Note — The type was collected by Haniff on a journey to Gunung Korbu in 1909. The collector’s label was not preserved. Ridley assigned numbers in his own series to all Haniff’s specimens and wrote the locality cited for 14142, indicating a source near the summit of the mountain. The evidence that the type was not from a high altitude is as follows. The second collection, reported by Holttum in 1986, was from ‘slope of bat guano in cave mouth’ in a limestone area in Gunung Mulu National Park, Sarawak. There is also a specimen from a low altitude in Perak, consisting of basal pinnae and the pair next above them; these are about intermediate between *P. australis* and the type of *P. acutissima*. The lobes of basal pinnae are little different from those of *P. acutissima*; one of the pair has one almost free basal lobe; hairs at the bases of costae are like those of *P. australis*; the upper pinnae of the frond have not been preserved. More information is needed.


*Stipe* to 60 cm long, lightly rufous and glabrous apart from sparse very short hairs near the base on the abaxial side, basal scales rather thin.
and to more than 2 mm wide; lamina to more than 100 cm long; basal pinnae longest, their bases very asymmetric, the stalk 2–5 mm long below the basal acrosopic lobe (which is up to 3.5 cm long) and more than 20 mm below the basal basiscopic lobe which is commonly 8–12 cm long (to 16 cm) and more than 2 cm wide, deeply lobed; second basiscopic lobe much shorter than the basal one; suprabasal pinnae to c. 30 cm long and 5–6 cm wide, lobed to 5 mm from costae, sinuses between lobes 2–3 mm wide, the lobes slightly falcate, distinctly but shallowly crenate-serrate near their acute tips only; veins in most pinnae once forked (twice forked only in the largest lobes), basal basiscopic veins often arising from the costa below the bases of their costules; all surfaces glabrous apart from sparse very short hairs near the bases of costae (seen only on young fronds); sori at the apices of acrosopic vein-branches; indusia little over 0.5 mm in diameter. — Fig. 2b.

Distribution – S Vietnam; in Malesia: Philippines (widely), Borneo, Celebes, New Guinea.

Habitat – In forest, to 1200 m, reported several times from steep rocky slopes above streams.


Allied to P. microthecia, differing as follows: basal basiscopic lobes of basal pinnae to c. 6 cm long, little longer than the next lobes; suprabasal pinnae lobed to 2–3 mm from their costae, their lobes strongly crenate-serrate throughout. — Fig. 2e.


Habitat – On steep rocky river banks at altitudes to 900 m.

Note – Several collections, from widely separated localities, agree in the specified differences from P. microthecia. The two species are certainly closely allied, agreeing in almost wholly glabrous fronds and the position of basal basiscopic veins on some pinnae.


Allied to P. microthecia, differing as follows: all pinnae sessile; sinuses between pinna-lobes very narrow; basal acrosopic lobes of basal pinnae almost free; basal acrosopic lobes of suprabasal pinnae overlapping the rachis on its abaxial side, all lobes distinctly though shallowly crenate throughout, their apices mostly obtuse. — Fig. 2d.

Distribution – Malesia: New Guinea (known only from the type and one collection from the Markham valley, Wakefield 1417).

Habitat – The type from open rocky forest in a gorge.

PLEOCNEMIA


Caudex usually erect, sometimes to 30 cm or more tall but with little sclerotic tissue; fronds commonly 150–300 cm long; bases of stipes covered with thin narrow dull brown scales, their edges entire or with short teeth formed by the projecting wall between adjacent cells; vascular strands in stipe more numerous than in Tectaria, with additional small accessory strands outside the ring which is present in Tectaria, and additional large strands on the adaxial side also; lamina bipinnatifid to bipinnate-tripinnatifid (or at base tripininate), basal pinnae with greatly enlarged basiscopic lobes or pinnules; rachises with very short sepalate hairs on their raised upper surfaces; pinnae and pinnules ± deeply lobed, with a tooth projecting out of the plane of the lamina in each sinus between two lobes; veins always forming a narrow costal areole, lacking free veinlets within it, between the bases of costules (whether of pinna- or pinnule-lobes) and often similar areoles along costules (the outer veins of costal areoles never joining the costa at their distal ends as normally in Tectaria), with additional anastomosis of veins forming ± isodiamic areoles below the sinuses and external to costular areoles where space allows, rarely with short free veinlets in them; sori variously placed on free or anastomosing veins, round, indusiate or not (indusia reniform where present); thick glandular hairs, spherical, clavate or cylindrical, yellow or red, present at the ends of hairs on the stalks of sporangia, often also on the lower surface of costules and veins. — Figs. 3, 4.

Distribution — Mainly Malesian, extending to NE India and SE China, eastwards to Samoa; about 20 species.

Habitat — Forest ferns, but generally not in the deepest shade; several are reported from rocky places, at least one from limestone.

Cytology — n = 41 [Manton in Holttum (1955); M.G. Price in Holttum (1974)].

Taxonomy — There are two groups of species, for the types of which Presl in 1836 established the genera Pleocnemia and Dictyopteris (later renamed Arctopteris Underw.). I retained both genera in a monographic treatment in 1951 but remarked on their close alliance, and united them in 1974. A probable hybrid having one parent from each group is known (P. × intermedia). The only differences between the two groups are a more complex venation and less distinct sinus-teeth in Arctopteris.

Confusion as regards generic assignment of these ferns in the 19th century resulted from emphasis on two kinds of characters: pattern of venation, which these ferns share with Tectaria sect. Sagenia (and less clearly with some thelypteroid ferns), and the presence or absence of indusia. Until Diels (1899) it was not fully understood that species lacking indusia could be closely allied to others which have them and thus be congeneric.

Furthermore, the distinctive combination in Pleocnemia of some other characters was ignored. To anyone seeing a living plant, as did Gaudichaud when he collected specimens of P. leuzeana, the presence of sinus-teeth which project out of the plane of a pinnule, described and figured by him, is striking. The sinus-teeth were noticed by Gaudichaud, John Smith (who had living plants in his care) and for one species by Van Alderwerelt; Presl, Fée and Hooker ignored them and omitted them from their illustrations. Unicellular yellow or orange glands were noticed by various authors but not thought to be of generic significance. The peculiar vascular anatomy of stipes was observed only by Fée [Gen. Fil. (1852) t. 21A] for P. macrodonta and shown in a distorted form from a dried specimen.
The species here placed as nos 1–4 are closely allied; two of them have been ranked as varieties of *P. irregularis*. They agree in exindusiate sori, for which reason earlier authors placed them in *Polypodium*, or in *Dictyopteris* which Presl placed with polypodioid ferns. The original species of *Pleocnemia* is also exindusiate and was earlier named *Polypodium leuzeanum* by Gaudichaud; in 1836 Presl placed it with polypodioid ferns. But among Cuming’s Philippine collections were four numbers, all resembling *P. leuzeana* in frond-form and venation, two of them clearly indusiate. John Smith, who made the first survey of Cuming’s collections (1841) regarded all four as forms of *P. leuzeana*, which he placed with aspidioid ferns, remarking that indusia in these ferns were often small and soon shed. Hooker [Gen. Fil. (1842) t. 97] accepted John Smith’s judgement and illustrated a fertile pinnule of *P. cunningiana* and a sterile one of *P. conjugata* under the name *P. leuzeana*. Later Beddome (1866) published as *P. leuzeana* a drawing of the sterile apex of a frond (probably *P. conjugata*) from Moulmein in Burma along with an enlarged drawing of a fertile pinnule-lobe of *P. cunningiana*, not stating that the latter was from a non-Burmese specimen (he cited *P. conjugata* and *P. cunningiana* as synonyms).

In 1857 Thomas Moore accepted the genus *Pleocnemia*, defining it by frond-form, venation and indusiate sori, and added one species of *Heterogonium* and one thelypteroid species. In 1864 Hooker, ranking *Pleocnemia* as a section of *Nephrodium*, added two more thelypteroid species, but John Smith (1875) rejected these additions. Beddome (1883) added species here included in *Tectaria* sect. *Sagenia* and he placed all exindusiate species of *Tectaria* in *Dictyopteris*. In general, Van Alderwerelt followed Beddome. Copeland, in all his later works, included the type species of both *Pleocnemia* and *Dictyopteris* Presl in *Tectaria*.

Though Copeland lived for several years at Los Baños, at the foot of Mt Makiling in Luzon, he never discovered distinctions among the plants of *Pleocnemia* s.s. growing in the forest on that mountain and in 1960 included all in *P. leuzeana*. He did recognize as distinct an exindusiate species in Sumatra (*P. olivacea*) in 1914 and Van Alderwerelt another in Java (*P. hemiteliiformis*). From my field and herbarium studies based on Singapore I recognized that *Pleocnemia* is a genus distinct from *Tectaria* and that (apart from *P. irregularis*) three distinct species exist in the Malay Peninsula. After a further study of specimens in the Bogor herbarium I identified the peninsular species as *P. olivacea, P. hemiteliiformis* and *P. conjugata* (Blume) Presl, the last-named based on *Aspidium conjugatum* Blume (type from Java), a name ignored by Backer and Posthumus in their fern-flora of Java. I also saw duplicates of all the Cuming Philippine collections and realized that they do not all belong to one species. I attempted to account for all this new information in a paper published in 1951. In more recent years M.G. Price has made detailed field studies of Philippine species and has confirmed the distinctions between species which I had based on Cuming’s specimens; this further information is included in a second paper, published in the Kew Bulletin in 1974.

The species of *Pleocnemia* s.s. (nos 6–18) are all similar in frond-form and venation. The fronds of mature plants of all are very large and cannot be mounted whole on herbarium sheets. The basal pinnae are of distinctive form on the basiscopic side near the base, but distally are much like those next above them; more distal pinnae decrease gradually. Some herbarium specimens are from immature plants; few are annotated to indicate which
part of a frond they represent. Thus it is sometimes difficult to make comparisons between one specimen and another. For purposes of identification one must rely mainly on the form of pinnules of larger suprabasal pinnae and on the sori they bear. The scales at the bases of stipes are also sometimes important but are lacking from most specimens. The abundance of appressed glands on the lower surface of veins appears to be variable in fronds of the same species, also their thickness; their shape and colour may be distinctive. More evidence from living plants is needed.

In 1912, dealing with specimens from New Guinea, Rosenstock remarked on the differences in spore-form from specimens which he regarded as different varieties of *P. leuzeana*. I examined spores of all species and confirmed that they are of three kinds, basing my key of 1951 on them. They offer important evidence for the distinctions between *P. cumingiana* and *P. presliana* which otherwise are not easy to distinguish except that the former is indusiate, the latter not. Field study has shown that plants of *P. presliana* are smaller and have different scales. Cytological examination might provide further evidence and experimental hybridization might give further understanding.

**Key to the species** — The distinctness of some species (e.g. *P. cumingiana* and *P. conjugata*) is very evident, but for others more difficult to state clearly, and more evidence from field studies is needed. The present key doubtless needs improvement.

**KEY TO THE SPECIES**

1a. Fronds usually bipinnatifid apart from basal pinnae; pinnules, if present, mostly adnate to pinna-rachis; many additional areoles always present below sinuses between lobes; sinus-teeth only evident in larger sinuses .......................... 2

b. Fronds amply bipinnate on mature plants, most pinnules not adnate; areoles few below sinuses; sinus-teeth always evident ........................................ 5

2a. Fronds normally bipinnatifid, the largest sometimes bipinnate near the base; sori scattered irregularly, very abundant ........................................................... 1. *P. irregularis*

b. Fronds, at least in basal parts, bipinnate with lobed pinnules; sori all, or almost all, arranged in one row on each side of costules of pinnule-lobes ........................................ 3

3a. Sori midway between costules and margins of pinnule-lobes and also some on basal veins ................................................................. 2. *P. macrodonta*

b. Sori close to margins of pinnule-lobes, lacking on basal veins ........................................ 4

4a. Pinnules of suprabasal pinnae acuminate, to 12 cm long and 2 cm wide at their broadly cuneate bases, not adnate to pinna-rachis ........................................ 3. *P. brongniartii*

b. Pinnules of suprabasal pinnae to 4 × 0.8 cm with blunt apices, adnate to pinna-rachis 4. *P. andaiensis*

5a. Sori present on all vein-branches, in more than 1 row on each side of costules, several sori irregularly arranged on veins below sinuses ........................................ 5. *P. × intermedia*

b. Sori almost always in a single row on each side of the costules (sometimes on both branches of a vein), additional ones below sinuses few ........................................ 6

6a. Sori indusiate .................................................................................. 7

b. Sori exindusiate .............................................................................. 12
7a. Pinnules of middle pinnae lobed c. 2/5 towards costules, lobes distinctly falcate; sinus-teeth narrow. 
8a. Pinnules short-acuminate, lobes obtuse. 
9a. Pinnule-lobes subentire (small teeth distally) 
10a. Stipe dark, glossy; pinnules to 25 × 5 cm, pinnate for half their length

b. Pinnules more deeply lobed; sinus-teeth triangular
b. Stipe not dark and glossy; largest pinnules not thus pinnate
b. Pinnules commonly 8 × 1.8 cm, their lobes crenate, drying greenish
b. Pinnules lobed about 2/3 towards costa; lobes entire or at most minutely crenate-dentate
b. Pinnules lobed more deeply or not; lobes distinctly crenate
b. Pinnules to 6 mm apart; few costular areoles present; basal scales shorter and narrower
b. Sinus-teeth narrow, short, in base of sinus
b. Pinnules of suprabasal pinnae to 4.5 cm wide, their lobes acute
b. Pinnules of suprabasal pinnae to 2.5 cm wide, their lobes obtuse
b. Pinnules all lobed to c. 1 mm from costa, to 2.5 cm wide, spores not spinulose

Polypodium Polypodium 

Fiji.  

Confluent; cm sely and narrow a 6 deep; the long, of lobed, ‘tolerating sinuses; short hairs few hairs, just along the costa, it is harder on the costa, the rest glabrous, lower surface of rachis and costae bearing short hairs on the upper surface, the rest glabrous, lower surface of rachis and costae bearing some hairs 1 mm long, surfaces of costules and veins bearing red glands like those in the sori; veins forming single narrow areoles along costae between one costule and the next and shorter areoles along costules, rest of the lamina below sinuses filled with 4-6-sided areoles, rarely with included free veins; sorus small, close, scattered irregularly, exindusiate, round or often extending along the veins and sometimes confluent; sporangia often bearing red spherical glands on the hairs attached to their stalks. – Fig. 3a. 

Distribution – Southern Burma, Thailand, Vietnam; throughout Malesia; Carolines, Solomons, Fiji. 

Habitat – In lowland forest; in western Malesia ‘tolerating drier conditions than many other terrestrial forest species’ (Holttum 1955); ‘especially on steep valley slopes’ (Backer & Posthumus 1939).

Note – In Thailand and Vietnam very large plants which have more fully bipinnate fronds than those in Malesia. These are named Tectaria cumingiana by Tard. & C. Chr., Fl. Indo-Chine 7 (1941) 412 [= Pleocnemia macrodon (Fée) Holttum] but are much less fully bipinnate than in that species and have sori arranged as in P. irregularris.


Differing from P. irregularris as follows: scales to 2 cm long and more than 1 mm wide; pinnae conspicuously pinnate, the pinnules sessile and mostly ± adnate, unequally cuneate at the base (broader on the acroscopic side), their margins lobed to one third or more towards the costa; sorus in two close rows on either side of each costule, often somewhat confluent, with additional sori near the sinuses in the broader pinnules. – Fig. 3b, c.
Fig. 3. Pleocnemia irregularis (Presl) Holtum. a. A single lobe, showing position of sori, × 2.2. — P. macrodonta (Fée) Holtum. b. A basal basiscopic pinnule, × 0.45; c. detail of lobes showing venation and sinus teeth, × 3.3. — P. andaiensis (Baker) Holtum. d. Two lobes from near the apex of a pinna, × 4; e. one segment from near the base of the same pinna, showing venation, sori and sinus teeth between lobes (sori removed from the right side), × 2.2 (a: cult. Singapore, as in Reinwardtia 1 (1951) 192; b, c: Holtum s.n., Sarawak, cult. Kew 335-58; d, e: Beccari s.n., Andai).


Similar to P. macrodonta in the size and branching of its fronds and in the shape of pinnules, differing in the arrangement of sori which are all near the margins of the lobes of pinnules or of pinnae near the frond-apex.


Differs from P. brongniartii as follows: suprabasal pinnae to 30 cm long, near their bases bearing a few pairs of separately adnate pinnules, the largest 4.5 x 0.9 cm, lobed to almost halfway to the costa, lobes broadly rounded, basal acroscopic ones not enlarged, costules 3.5–4 mm apart connected by 1 row of costal areoles; rather sparse small scales and short hairs present on upper surface of rachis and costa, very slender hairs on the lower surface; unicellular ± elongate reddish glands present on lower surface, mostly on veins, some also on the upper surface; sori in a row near (but not touching) the margin of each pinnule-lobe, the distal ones on free veins; glands not seen in sori. — Fig. 3d, e.

Distribution — Malesia: W New Guinea (known from two collections, the second being van Royen 3144, Sorong District).

Note — The name Nephrodium giganteum, published by Cesati in 1877, was a misidentification of Beccari's specimen later named Polypodium andaiense by Baker.


Basal scales c. 2.5 cm long, very narrow, distally filiform and tangled; basal pinnae to 80 cm long, their basal basiscopic branches 45 cm long, both with separate pinnules almost to the apex; middle pinnules of suprabasal pinnae mostly 8 x 2 cm with winged stalks 2 mm long, lobed 3/4 towards costa, basal lobes deeply crenate, distal ones shallowly; sinus-teeth broad and very short in lower sinuses, narrow and short in distal ones; costules 5 mm apart; veins forming costal areoles with a few additional ones below sinuses, veins in pinnule-lobes twice forked to paucipinnate, the lower veinlets anastomosing irregularly, distal ones
(in crenatures) free; lower surface glabrous apart from thick glandular hairs on costules and veins; *sori* small, exindusiate, on almost all vein-branches both in pinnule-lobes and below sinuses; spores few and shrivelled.

Distribution – Known only from the type.

Habitat – Lower slopes of a ridge in low Dip
terocarp forest.

Note – This is evidently a hybrid between *P. irregularis* and one of the amply bipinnate species, perhaps *P. olivacea*. No other specimens of such possible hybrids are known.


Pleocnemia conjugata var. elatior Holttum, Reinwardtia 1 (1951) 179. – Type: C.G. Matthew 512, Sumatra, G. Singgalang, 150 m (BO).


Basal scales long-attenuate, conspicuously den
tate distally; lamina to 120 cm long; suprabasal
pinnae to 70 cm long, their pinnules sessile, 8–13
cm long, 1.8–2.3 cm wide, lobed a little more
than halfway to costa, very firm, almost glaucous
beneath when living, brown-olivaceous when dried;
costules 5–6(–7) mm apart; lobes distinctly fal-
cate and minutely dentate distally, sinuses between
them very narrow; sinus-teeth small, narrow and
curved; veins forming costal areoles with a few ad-
ditional ones below sinuses, costular areoles usu-
ally near bases of lobes only; glands present on
lower surface of costules and veins; *sori* in a single
row midway between costa and margin of a pinn-
lobe, rather large, indusiate; spores with a narrow
± continuous wing and a few cross-wings. – Fig.
4a, b.

Distribution – Hong Kong, Burma; throughout
Malesia.

Habitat – Apparently in areas with a short regu-
lar dry season (in the Peninsula only in the north)
and in rather open forest.

7. Pleocnemia acuminata Holttum, Rein-
wardtia 1 (1951) 182; Kew Bull. 29 (1974)
351. – Type: Lörzing 5644, Sumatra, Sibo-
langit (BO).

Differs from *P. conjugata* as follows: lamina
more rigid; pinnae and pinnules narrowly acu-
minate; pinna-lobes more widely spaced and acute;
spores as in *P. leuweana*.

Distribution – Malesia: Sumatra (Sibolangit) (2
collections).

Note – This is very near *P. conjugata* and speci-
mens of the latter have also been collected at Sibo-
langit. A local survey is needed.

8. Pleocnemia pleiotricha Holttum, Rein-
wardtia 1 (1951) 182, f. 12, 13; Kew Bull. 29
(1974) 351. – Type: Eimer 21421, Sabah, Ta-
wau (SING; iso BO, K).

Basal scales to 3 cm long and 1.5 mm wide,
rather firm, attenuate but the tips not filiform nor
dentate; pinnules of suprabasal pinnae to 11 × 2.2
cm, with stalks 2 mm long, rather abruptly acu-
minate, lobed 3/4 towards costa, lobes well spaced,
minutely dentate distally (about as in *P. conjuga-
ta*); sinus-teeth broadly triangular; veins forming
costal areoles with no additional ones below si-
nuses, costular areoles usually 1 pair only; red
glands on costules and veins abundant; *sori* indus-
iate, indusia thin. – Fig. 4d, e.

Distribution – Malesia: S Sumatra, N Borneo.

Reinwardtia 1 (1951) 188. – Type: Béguin
1123, Ternate (BO; iso L).
Stipe very dark, glossy; largest suprabasal pinnae 135 cm long; pinnules to 25 cm long, 5 cm wide at the base, pinnate for half their length; third-order leaflets to 3 x 0.8 cm, lobed halfway to their costa, a row of areoles present along each side of costa, 2 or 3 indusiate sori in each lobe; largest pinnatifid pinnules with falcate dentate lobes 3 mm wide separated by more than their own width; spores as in *P. cunningiana*.

Distribution — *Malesia*: Moluccas (known from the type only).

Note — So far as present information goes, the smaller pinnules of the type are not distinguishable from those of *P. cunningiana*, but the very dark glossy stipes are distinctive, and the largest pinnules are far larger and far more fully pinnate than those on the largest known specimen of *P. cunningiana* which has the basal pinnule-lobes just free as tertiary leaflets.


*Caudoxy* 50 cm tall, falling and then resuming upright growth from its apex; stipes not very dark nor glossy, for some distance above the base densely covered with distally very narrow and conspicuously dentate scales to 3 cm long, base of scales 2 mm wide, pinnules of suprabasal pinnae to more than 15 cm long, to 3 cm wide, very deeply lobed; costules 5–7 mm apart; lobes usually narrower, more widely spaced and more deeply crenate-lobulate in fertile than in sterile pinnules (but these characters are very variable); veins forming narrow costal areoles with no additional ones below sori, costular areoles variably developed, veins in crenatures once or twice forked; glands on costules and veins yellow, usually abundant; sori indusiate; spores densely spinulose. — Fig. 4b.

Distribution — Taiwan; in *Malesia*: Moluccas, Philippines, New Guinea; Solomons, Fiji, Samoa.

Note — Rechinger reported that the trunks of this species attained a length of 10 m and were used for house-building in Samoa; this was certainly an error; trunks so used would be from species of *Cyatheaceae*.


Differs from *P. cunningiana* as follows: Pinnules of suprabasal pinnae commonly 8 x 1.8 cm (largest seen 12 x 2 cm), thinner, drying greenish (not brown-olivaceous), their lobes at most crenate.


Note — The distinction between this species and *P. cunningiana* needs to be established through field study.

Fig. 4. Pleocnemia conjugata (Blume) Presl. a. Transverse section of stipe near base, × 2; b. one pinnule lobe of a middle pinna, × 2, with detail of sinus-tooth. — P. olivacea (Copel.) Holttum. c. A pinnule lobe of a middle pinna, × 3.3. — P. pleiotricha Holttum. d. A pinnule lobe of a middle pinna, × 3.3; e. detail of glands, × 23. — P. dahlii (Hieron.) Holttum. f. Pinnule lobes of a middle pinna, × 3.3; g. pinnule lobes of an adjacent middle pinna for comparison; this shows the condition attributed to P. dimidiolobata; × 3.3. — P. cumingiana Presl. h. Lobe of a middle pinna, × 3.3 (a, b: from Reinwardtia 1 (1951) 174; c: van Balgooy 4789; d, e: Elmer 21421; f, g: Croft 240; h: Cuming 107).


Lower 30 cm of stipe ± persistently covered with scales, the longest 5 cm long, gradually narrowed from a base 3 mm wide; pinnules of supra-basal pinnae commonly 8 × 1.7 cm, lobed 2/3 towards their costae, lobes well-spaced, obtuse, their margins at most sinuous and bearing ± abundant short hairs; costules 4–5 mm apart; veins usually dark on lower surface when dried, forming one series of areoles between costal areoles and sinuses, costular areoles many; sinus-teeth short, broadly triangular and slightly oblique; sori exindusiate, sometimes on both branches of a forked vein, also on Anastomosing veins below sinuses; spores with a continuous wing and some cross-wings.

Distribution — Peninsular Thailand; Malesia.

Habitat — Open places in forest at 800–1400 m.

Note — The type of Dictyopteris compitalis shows no indication of the reduced auriculiform pinnae described by the author.


Related to P. hemiteliiformis but fronds smaller, basal scales narrow, to 2.5 cm long, pinnules thinner with costules to 6 mm apart, lobes more close to each other, usually with minute marginal teeth distally, lacking hairs; veins forming basal costular areoles only; sinus-teeth short and narrow, in bases of sinuses; sori exindusiate, sometimes on both branches of a vein; spores as those of P. hemiteliiformis. — Fig. 4c.

Distribution — Western Malesia.

Habitat — In rocky places in lowland forest.


Near P. olivacea in form of pinnules; basal scales not recorded; sinus-teeth broadly triangular, on basiscopic side of sinus; spores with many small obtuse protuberances all over them.

Distribution — Eastern Malesia; Fiji, Samoa.

Habitat — Recorded from ‘rocky bank’ (R.F. Ellen 72, Ceram).


Stipe 100 cm or more long; basal scales 2.5 cm long, pallid and 5 mm wide at their bases, abruptly narrowed to 1.5 mm 5 mm above the base, thin, filiform and dentate distally; lamina 120 cm long; rachises dark castaneous and minutely hairy on abaxial surface; basal pinnæ 85 cm long with three diminishing pinnate basiscopical pinnules, the largest 45 cm long with many deeply lobed tertiary leaflets to 10 × 2.3 cm, largest acrosopic pinnules 17 cm long; pinnules on first supra-basal pinnæ to 16 × 4.5 cm, narrowly acuminate, lobed to less than 2 mm from the costa, firm and opaque when dried, costules to 8 mm apart, lobes crenate to lobulate, narrowed to an acute hardly falcate apex; sinus teeth short and broadly triangular, oblique, on basiscopic side of sinuses, sometimes present also between lobules of pinna-lobes; veins forming very narrow costal areoles, also an almost
complete set of costular ones, free veins passing from the latter to the margin, paucipinnate in lobules; sori exindusiate, in one row on either side of costules of lobes, nearer to costules than to margin, on outer veins of areoles; spores minutely spinulose; elongate unicellular glands present on stalks of sporangia.

Distribution — Malesia: New Guinea (known with certainty from the type only).

Note — Incomplete specimens from Mt Suckling (Milne Bay Prov.) and Sudest Island may belong to this species.


Related to P. cumingiana, differing as follows: fronds of mature plants much smaller; stipe minutely muricate throughout from bases of fallen scales; basal scales narrower, filiform and much tangled; pinnules of suprabasal pinnae to c. 10 × 2.2 cm, abruptly acuminate; cylindrical glands on lower surface of veins red; sori exindusiate; spores with many small peg-like outgrowths.

Distribution — Malesia: Philippines (Luzon, Palawan, Leyte, Mindanao).

Habitat — In forest, mainly at lower altitudes than P. cumingiana.

Notes — Presl cited both Cuming 107 and 33 under P. cumingiana; 33 is P. presliana.

M.G. Price, who made intensive studies of ferns on Mt Makiling, found both P. cumingiana and P. presliana growing in the forest there, and tells me that he regards them as quite distinct.

The illustration in Gard. Chron. (1874) shows sinus-teeth clearly and also a characteristic spore; the plant had been imported from the Philippines.


Pleocnemia tripinnata Holttum, Reinwardtia 1 (1951) 185. — Type: Lauterbach 560, New Guinea (SING; iso BO).


Base of stipe very dark, castaneous distally, scales (near base only) to 2.5 cm long, 1 mm wide at base, distally tiliiform; pinnules of larger suprabasal pinnae to 9 × 2 cm with short winged stalks, lobed 2/3–3/4 towards costae, lobes distinctly crenate, obtuse; sinus-teeth broadly triangular, oblique; veins forming costal areoles and a few additional ones below sinuses, costular areoles present only at bases of pinnule-lobes; sori exindusiate, usually about midway between costules and margin, mostly on acroscopic branches of forked veins (none seen on both branches); spores spinulose. — Fig. 4f, g.


Habitat — In lowland forest.

Note — At Kew is a later collection of P. leuzeana var. echinocarpa named by Rosenstock. The above description is based largely on a plant cultivated at Kew. On other specimens the position of sori is very variable; the condition shown by the type of P. dimidiolobata represents an extreme condition.

DOUBTFUL SPECIES


The type is a frond from a young plant of a species allied to Pleocnemia irregularis. It might represent P. macrodonata, but cannot be identified specifically with certainty.
CTÉNITIS


_Caudex_ short, erect or suberect or rarely prostrate, its apex and the bases of stipes densely covered with thin flat scales which are not more than 1 mm wide at their bases, _stipes_ scaly throughout, with a ± abrupt change from the long basal scales to shorter ones of two different types, distinctive for each species; _lamina_ always bipinnate at the base, the basiscopic pinnules of basal pinnae always longer than the acrosopic ones, the basal ones usually longest and very deeply lobed, in some species pinnate to bipinnate near their bases; _distal pinnae_ or pinnules ± adnate to the rachis and ± decurrent at their bases but their basal basiscopic veins almost always arising from the pinna- or pinnule-midrib; texture of lamina mostly thin with veins distinct on both sides but in some species opaque with the smaller veins indistinct; _veins_ all free, those in each pinna-lobe all arising from the costule of the lobe (not from the costa of the pinna); lower surface of pinna-rachis or pinna-midrib always bearing scales which are progressively smaller distally, similar scales also present on costae of pinnules, some ctenitoid hairs also present and often appressed cylindric unicellular glands, such glands also often present between veins, sometimes with the addition of short hairs of various kinds; upper surface of pinna-rachis or pinna-midrib and of costae of pinnules prominent, always covered with ctenitoid hairs which are thicker than those on the lower surface, similar hairs scattered on veins but not between veins where appressed cylindric glands or short non-ctenitoid hairs may occur; _sori_ usually medial on the veins, not terminal; _indusia_ usually present, sometimes very small and hidden by the mature sporangia, always unpigmented, thin and fragile, usually bearing marginal cylindric glands when young; _spores_ of two distinct kinds. — Figs. 5–8.

Distribution — Pantropic; c. 100 species (Holttum 1986).

Taxonomy — Christensen’s original study was confined to the species of tropical America. The first surveys of allied species in Asia were made independently by Ching (1938) and Ito (1939), both of whom failed to notice the significance of scale-structure and glands which separate _Ctenitis_ (as here defined) from _Tectaria_ and other genera. Copeland (1947) added other species which are here included in _Tectaria_. Holttum (1985) prepared a list of 47 Old World species included in _Ctenitis_ by previous authors but not conforming to the present generic concept.

_Subdivision of the genus_ — Christensen (1920) proposed a subdivision of the American species; I have transferred to other genera two of his groups which both extend to Africa (Holttum 1986). The group which includes the type extends to Africa and Madagascar but not to Asia; its fronds are bipinnatifid. The 43 species of Asia, Malesia and the Western Pacific (Holttum 1985) are divisible into two groups; as shown in the key, 26
of the 28 Malesian species belong to one group, only 2 (one of them uncertainly) to the other. No new infrageneric names are here proposed; to establish them effectively a new conspectus of the whole genus should be made.

KEY TO THE SPECIES

1a. Scales on pinna-rachis narrow with inflexed edges or flat, their bases sometimes widened but not cordate nor point-attached; isodiametric cells few, near base ........... 2
   b. Scales on pinna-rachis flat or nearly so, point-attached at a deeply cordate base; many isodiametric cells in their basal part ...................................... 27

2a. Basal basiscopic pinnules of basal pinnae not longest, less than twice as long as the basal acroscopic pinnules ................................................................. 3
   b. Basal basiscopic pinnules of basal pinnae distinctly longer than the rest, usually twice as long as acroscopic ones ......................................................... 9

3a. Veins thick and prominent on lower surface ................................................. 1. C. kjellbergii
   b. Veins not prominent on lower surface, the smaller ones in many cases indistinct 4

4a. Tertiary leaflets 3 × 3 mm, almost entire, their upper surface densely covered with short hairs .......................................................... 2. C. muluensis
   b. Tertiary leaflets, if present, differently shaped and not thus covered ........... 5

5a. Pinnules or lobes of middle pinnae not lobed nearly to their costae; spreading bristle-like scales present throughout the main rachis ............. 3. C. aciculata
   b. Pinnules or lobes of middle pinnae lobed nearly to their costae; such scales not present ............................................................. 6

6a. Scales on pinna-rachis flat or nearly so .......................................................... 7
   b. Scales on pinna-rachis with inflexed edges, at least near their bases .......... 8

7a. Scales on pinna-rachis not widened at their bases; isodiametric cells at base few; costal scales very narrow ......................................................... 4. C. kinabaluensis
   b. Scales on pinna-rachis widened at their bases, the widened part consisting entirely of isodiametric cells; costal scales with broad base ............. 5. C. pallens

8a. Stipe densely scaly throughout, scales at top of stipe 10 mm long .......... 6. C. tabacifera
   b. Stipe densely scaly near base only; distal scales 3 mm long ...................... 7. C. subconnexa

9a. Lamina opaque; smaller veins not distinct on lower surface .................. 8. C. propinqua
   b. Lamina not opaque; veins distinct ........................................................... 10

10a. Scales on pinna-rachis very thin, few cells wide, lacking conspicuous isodiametric cells ................................................................. 9. C. boholensis
   b. Scales on pinna-rachis wider with reflexed margins, widened at their bases with some isodiametric cells .............................................. 11

11a. Indusium very small, hidden by sporangia at maturity, bearing long slender flexuous glands ................................................................. 12
   b. Indusium distinct but fragile, not long-fringed .......................................... 15

12a. Basal basiscopic tertiary divisions of basal pinnae lobed ......................... 13
   b. Basal basiscopic tertiary divisions of basal pinnae entire ....................... 14
13a. Pinnae narrowly acuminate; appressed glands present on upper surface

10. C. seramensis

b. Pinnae not narrowly acuminate; short erect capitate hairs present between veins on upper surface ........................................ 11. C. bulusanica

14a. Free pinnae to 8 pairs; basal pinnae of mature plants shorter than suprabasal ones

12. C. vilis

b. Free pinnae to c. 4 pairs; basal pinnae longer than suprabasal ones 13. C. silvatica

15a. Lobes of middle pinnae mostly subentire with rounded apices ................. 16

b. Lobes of middle pinnae mostly lobulate, their apices not rounded ............ 17

16a. Lamina to 13 cm long, bearing many suberect hairs between veins on upper surface

14. C. humilis

b. Lamina much longer; hairs on upper surface appressed ........ 15. C. subobscure

17a. Tertiary leaflets of basal pinnae quite free, lobed to their costules, their basal lobes lobulate ........................................ 18

b. Tertiary leaflets of basal pinnae adnate and less deeply lobed, their lobes entire . 20

18a. Lobes of tertiary leaflets of basal pinnae deeply lobulate; thick cylindric glands copious on upper surface ...................... 16. C. minutiloba

b. Lobes of tertiary leaflets of basal pinnae not deeply lobulate; appressed glands on upper surface neither thick nor copious ............ 19

19a. Basal pinnae to 60 cm long .................. 17. C. elata

b. Basal pinnae to 25 cm long .......................... 18. C. koordersii

20a. Lobules or lobes of middle pinnae acute ................. 19. C. sumbawensis

b. Lobules or lobes of middle pinnae not acute .......................... 21

21a. Basal tertiary leaflets lobed almost to their costules, lobes to 6 pairs . 20. C.croftii

b. Basal tertiary leaflets lobed less deeply with fewer lobes .................. 22

22a. Lamina to 60 cm long; basal pinnae more than 20 cm .................. 23

b. Lamina rarely more than 35 cm long; basal pinna to 15 cm ................ 24

23a. Costules of basal basiscopic lobes of upper pinnae arising from the main rachis

21. C. decurrentipinnata

b. Costules of basal basiscopic lobes of upper pinnae arising from costae of pinnae

22. C. alterooblumei

24a. Basal basiscopic pinnules of basal pinnae about twice as long as acrosopic ones . 25

b. Basal basiscopic pinnules of basal pinnae much less than twice as long as acrosopic ones ........................................ 26. C. angusta

25a. Tertiary leaflets of basal pinnae deeply lobed at their bases .................. 26

b. Tertiary leaflets of basal pinnae lobed less than halfway to their costules

25. C. erythradenia

26a. Tertiary leaflets to 18 × 10 mm; scales on rachis very narrow, not stiffly spreading

23. C. setosa

b. Tertiary leaflets to 8 × 4 mm; scales on rachis stiffly spreading 24. C. atrorubens

27a. Tertiary leaflets of basal pinnae and lobes of distal pinnae widely spaced, narrow, falcate ........................................ 27. C. paleolata

b. Tertiary leaflets of basal pinnae and lobes of distal pinnae almost contiguous

28. C. subglandulosa
Fig. 5. *Ctenitis aciculata* (Baker) Ching. a. Base of a basal pinna, × 0.6; b. third acroscopic pinnule of a basal pinna, × 2.2; c. detail of b, × 23; d. upper surface of pinna rachis showing ctenitoid hairs, × 20. — *C. vilis* (Kunze) Ching. e. A basal pinna, × 0.85; f. lower surface of pinna rachis, × 23; g. a middle pinna, basal acroscopic pinnule, × 4; h. sorus, the indusium bearing long flexuous glands, × 46; i. subentire distal lobes of a middle pinnule, × 4 (a–d: *Parris & Croxall 8941*; e–i: *Kunstler 3038*).

Caudex short, erect, covered with thin castaneous scales 8 × 0.5 mm; stipe to 17 cm long, densely scaly, scales above base 3–4 mm long; lamina to 26 × 12 cm; pinnae to 8 pairs; basal pinnae to 7 × 3.5 cm with 2 pairs of free pinnules, subequal on the two sides of the pinna-rachis, largest pinnule c. 17 × 7 mm, deeply lobed, the lobes crenate with rounded apices; distal pinnae little decurrent at their bases; veins distinctly prominent on the lower surface; rachis densely scaly on lower surface, scales to 2.5 × 0.3 mm, flat, gradually attenuate, with a few isodiametric cells near the base, rest of cells oblong, all with rather thick walls, margins of scales minutely denticate; lower surface of costae of pinnules and pinna-lobes similarly scaly near their bases, distally bearing red glands; red cylindrical glands also present on veins, between veins slender pale glands sometimes present; sori inframedial on the veins; indusia reniform, thin, bearing superficial red glands.

Distribution — Malesia: Central Celebes, W New Guinea (Japen Is.).

Ecology — Type from forest at 1200 m; Japen Island specimen 'on the face of limestone rocks', at 1100 m.


Stipe to 15 cm long, slender, dark brown, minutely hairy throughout; basal scales 7 mm long, 0.5 mm wide at their bases, filiform distally, medium brown, thin; scales above base gradually shorter and darker, very narrow with widened bases; lamina to 23 cm long, to 10 cm wide at the base, texture firm and opaque; pinnae to 10 pairs; basal pinnae to 7 cm long (including stalk of 5 mm) bearing several pairs of pinnules, basal pinnules on the two sides about equal, to 16 × 7 mm with obtuse apex, bearing 1 or 2 pairs of tertiary leaflets which are 3 mm long, not quite 3 mm wide, with truncate base and broadly rounded slightly crenate apex, other pinnules gradually smaller, the middle ones deeply lobed near their bases only; lower surface of pinna-rachis and costae of pinnules bearing very short hairs and copious scales, the largest 3 mm long, 0.2–0.3 mm wide at their bases, flat, very narrow distally, cells near base isodiametric; lower surface of leaflets, on and between veins, bearing many appressed pallid cylindrical glands 0.1 mm long; upper surface of pinna-rachis bearing scales as lower, also abundant thicker short hairs; upper surface of leaflets densely covered with very short erect hairs and pale appressed glands; sori about medial on veins; indusia very small, fugacious, bearing minute hairs.

Distribution — Malesia: Borneo (G. Mulu National Park).

Ecology — In montane limestone forest at 1000–1700 m.


Caudex erect, to 50 cm tall; stipe to more than 60 cm long, basal scales to 25 mm long and 1 mm wide, dull brown, thin, decrescent upwards, scales on upper part and on rachis 5–7 mm long, copious, very narrow, stiffly spreading with edges inrolled; lamina to 75 cm long, firm, opaque; free pinnae to 5 pairs and 5 pairs adnate; basal pinnae to 28 cm long, basal pinnules free, then a few pairs increasingly adnate, basal basiscopic pinnule to 9.5 × 2 cm, not or little longer than the next one, deeply lobed, the lobes entire, basal acrosopic pinnule to 4 × 1.2 cm, pinnules and lobes of middle pinnae not deeply lobed; lower surface of pinna-rachis bearing very narrow spreading scales 3–4 mm long; some cylindrical glands present on lower surface of pinna-lobes; smaller veins not evident on either surface; sori mostly on both branches of a forked vein; indusia very small, bearing when young elongate glands. — Fig. 5a-d.

Distribution — Malesia: Sumatra, Java, Borneo (widely), Philippines (Mindanao), SE New Guinea.

Ecology — In forest at altitudes up to 1000 m, sometimes on rocks or tree-trunks.

**KEY TO THE VARIETIES**

1a. Scales on pinna-rachis thin and narrow; upper surface of lamina not glandular
   a. var. **kinabaluensis**

1b. Scales on pinna-rachis very firm; upper surface densely glandular
   b. var. **crassiquama**

a. var. **kinabaluensis**

Stipe to 70 cm long, basal scales light brown, 15–25 mm long, hardly 1 mm wide, upper scales 5–6 × 0.3 mm; lamina to 70 cm long, subcoriaceous, opaque; basal pinnae to 30 cm long, bearing 6 pairs of pinnules, basal basiscopic pinnule 10 × 3 cm with a single lobed adnate tertiary leaflet; pinnules of suprabasal pinnae deeply lobed; veins hardly distinct on either surface; lower surface of pinna-rachises bearing sparse very narrow flat scales, upper surface densely covered with ctenioid hairs; lower surface of pinnules between veins bearing slender appressed glands, upper surface glabrous; sori medial on veins; indusia minute, thin, when young bearing slender glands.

Distribution – Malesia: NE Borneo.

Ecology – In forest at 1000–1500 m, once reported on rocks.


Lamina thinner and veins more distinct; scales of rachises wider and thicker; upper surface of pinnae between veins bearing many appressed glands.

Distribution – Malesia: Borneo (known only from the type).


Stipe to more than 50 cm long; basal scales 20 mm long, narrow, thin, scales for 15 cm above base gradually shorter, those on distal part and on rachis 4–5 mm long, not stiffly spreading, flat, very narrow with widened bases; lamina to 75 cm long, firm and opaque; pinnae to 10 pairs; basal pinnae to 30 cm long (stalk 2 cm) with 4 pairs of free and 3 or 4 pairs of adnate pinnules, basal basiscopic pinnule to 13 cm long with 1 pair free and 2 or 3 pairs adnate tertiary leaflets, basal tertiary leaflet 3.5 × 1.4 cm, obtuse, lobed nearly to its costa at the base, second basiscopic pinnule not longer than the first, basal acroscopic pinnule to 8.5 cm long with a pair of tertiary leaflets; larger pinnules on second pair of pinnae to 7.5 × 1.9 cm, deeply lobed, costules of lobes to 7 mm apart; costules of pinnae-lobes distinct on the lower surface but not the veins; lower surface of pinna-rachis bearing copious scales like those of the main rachis but smaller, clathrate at their bases; on both surfaces between veins some appressed pale glands; sori about medial on each side of costules of pinnule-lobes; indusia very small, fringed with many pale cylindrical glands. – Fig. 6a.

Distribution – Malesia: Philippines (Luzon, Samar, Negros, Mindanao), New Ireland.

Ecology – In forest at altitudes up to 600 m.

Note — The type of *Dryopteris rizalensis* Christ 1906 (Loher s.n., Rizal Prov., Luzon) has not been located; it might represent another species.


Stipe to 63 cm long, very densely scaly throughout; basal scales to 15 × 1 mm, thin, medium brown, those above base gradually shorter but without change of colour, largest on upper part of stipe 8–9 mm long, very narrow, rather weakly spreading, almost flat, their bases a little widened with a few isodiametric cells; rachis-scales similar, on distal part 3–4 mm long; lamina to 70 cm long, texture very firm, opaque; free pinnae c. 12 pairs; basal pinnae to 28 cm long with 7 pairs of
Fig. 6. Spores (SEM), all except f, x c. 860. — a. Ctenitis pallens (Brackenr.) M.G. Price; b. C. propinqua (Presl) Copel.; c. C. boholensis Holtum; d. C. alteroblumei Holtum; e. C. subglandulosa (Hance) Ching; f. ibid., x c. 3260 (a: Jermy 7900, New Ireland; b: Cuming 255, Luzon; c: Ramos BS 42983, Bohol; e, f: Griffith s.n., Assam).

d except near the base, to 8 cells wide, cells all elongate except a few near the base, many short hairs also present, no glands on surface between veins; upper surface of pinna-rachis densely covered with short thick hairs and some scales; surface of pinnales between veins bearing a variable number of appressed glands; sori at forks of veins in pinnales-lobes; indusia small and very thin, bearing many slender glands.

KEY TO THE VARIETIES

1a. Scales on pinna-rachis 3 mm long, very narrow with few isodiametric cells at base
   a. var. subconnexa
   b. Scales on pinna-rachis 1–1.5 mm long, basal 1/3–1/2 formed by isodiametric cells
      b. var. alstonii

a. var. subconnexa

Stipe to 52 cm long; basal scales in a tuft, thin and crinkled, to 20 mm long, 1 mm wide at the base, apex filiform; scales above base gradually shorter for 10 cm, on distal part of stipe and on rachis 2–3 mm long, very narrow, flat with ± widened base; lamina to 70 cm long, texture firm; pinnae widely spaced, 6 pairs free and 3 or 4 pairs increasingly adnate; basal pinnae c. 27 cm long bearing 4 pairs of free pinnaules; basic biocyster pinnaule 8.5 × 3 cm with 1 pair of almost free tertiary leaflets 20 × 7 mm, deeply lobed at their bases, costules of the lobes 3 mm apart; basal acroscopic pinnaule 7 × 3 cm, also with tertiary leaflets; lower surface of pinna-rachis bearing scales 3 mm long, very narrow with widened base, also copious short hairs; lower surface of pinnales between veins (which are not distinct) bearing appressed glands and short erect hairs, glands also present on upper surface; sori medial on veins; indusia thin and very small, bearing slender flexuous marginal glands, similar glands on stalks of sporangia.

Distribution – Malesia: Moluccas (Ceram and Ambon).

Ecology – In forest at 600 m.

b. var. alstonii Holtum, Blumea 31 (1985) 17 — Type: Alston 16937. Batjan, Mt Sibella, 1200 m (BM).

Scales at base of stipe 10 mm long; scales of rachises 1–1.5 mm long with dilated bases.

Distribution – Malesia: Philippines (known from the type only).


Stipe incomplete on all specimens seen, basal scales not known; scales on distal part and on rachis to 3 mm long, narrow, their margins inrolled above the widened base of isodiametric cells; lamina to 28 cm long, texture firm; pinnae well spaced, 3 or 4 pairs free and 2 or 3 pairs adnate; basal pinnae to 8.7 cm long bearing 1 pair of free and 1 pair of adnate pinnaules; basal acroscopic pinnaule 3.5 × 1.7 cm, distinctly longer than the next one, very deeply lobed at its base, the lobes entire, basal acroscopic pinnaule 2.2 × 1.4 cm; second pair of pinnales 8 cm long with 2 pairs of adnate pinnaules; veins in pinnaules mostly simple, their distal parts not distinct on the lower surface; appressed red cylindrical glands present on lower surface of costules of lobes and on veins; sori medial or immedial on pinnaule-lobes; indusia persistent, bearing red glands. — Fig. 6b.

Distribution – Malesia: Philippines (except for the type, known from one other collection from Ilocos Norte).

Note – In 1851 Presl, copying John Smith, cited four Cuming numbers: 80, 151, 252, 255. When publishing the new name Nephrodium preslii, Baker cited only Cuming 255. The other Cuming numbers are now assigned to the species Ctenitis erythradenia, silvatia and decurrentipinnata.

Sipe to 53 cm long, light castaneous, near base covered with scales 12 × 0.5 mm, scales on distal part 4 mm long, very narrow, not spreading; lamina 36 cm long, thin; free pinnae 3 pairs and 6 pairs adnate; basal pinnae 7 cm below the next pair, 14 cm long, basal basiscopic pinnules 6.2 × 2.6 cm, lobed almost to the costa, largest lobes 14 × 6 mm, lobed halfway to their costules; basal acroscopic pinnules 3.7 × 1.4 cm, with crenate lobes; suprabasal pinnae 12.5 cm long, bearing adnate deeply lobed pinnules, the pinnule-lobes mostly entire; veins slender, slightly prominent on the lower surface; lower surface of pinna-rachises bearing almost flat narrow scales 1–2 mm long and slender appressed hairs; sori inframedial in pinnule-lobes; indusia thin but persistent, pilose. — Fig. 6c.

Distribution — Malesia: Philippines (except for the type, known only from one other collection from Bohol).


Basal stipe-scales light brown, narrow, hairpointed; upper ones 4–5 mm long with inflexed margins and basal isodiametric cells; lamina to 45 cm long; free pinnae to 9 pairs, narrowly acuminate; basal pinnae to 16 cm long, bearing 4 pairs of pinnules, the lowest stipitulate; basal basiscopic pinnule 7 × 2.8 cm, acuminate, deeply lobed, basal lobe almost free, 19 × 7 mm, deeply lobulate, basal acroscopic pinnule 2.5 × 0.9 cm, obtuse; pinnules of suprabasal pinnae obtuse, deeply lobed, costules of lobes 3.5 mm apart; sori about medial in lobes of pinnules; indusia very small, bearing slender glands, glands also present on stalks of sporangia. — Fig. 7.

Distribution — Malesia: Moluccas (Ceram and Ambon).

Note — Robinson 1956 from Ambon (BO) was named Dryopteris intermedia by Alderwerelt.


Stipe to 28 cm long; basal scales 8 × 0.5 mm, distal scales dark brown, to 5 mm long; lamina to

23 cm long, firm, brown-olivaceous when dried; free pinnae 2 or 3 pairs; basal pinnae to 10 cm long including a stalk of 7 mm long, basal basiscopic pinnules sessile, to 5 cm long, 2.5 cm wide at their bases, their basal lobes almost free, 18 × 7 mm, lobed 2/3 towards their costules, lobules 4 pairs; suprabasal pinnae sessile with 1 pair of adnate pinnules; lower surface of pinna-rachises bearing narrow scales 2–3 mm long, their margins
inflexed near the base; upper surface of pinnules bearing short capitate hairs between veins; sori inframedial on veins; indusia very small, bearing slender glands.

Distribution — *Malesia*: Philippines (known only from the type collection).


*Polyodium asplenoides* Bory in Bélanger, Voy. Indes Or. 2 (1833) 33, non Sw. 1801. — Type: *Bory s.n.*, Java (P).


*Nephrodium sarawakense* Baker, J. Linn. Soc. Bot. 22 (1886) 225. — Type: Hose 95, Sarawak (K).

*Lastrea padangensis* Bedd., Handb. Ferns Brit. India Suppl. (1892) 60. — Type: *Kunstler 3038*, Perak (K; iso BM, L, P).

*Dryopteris milletii* C. Chr., Index Filic. (1905) 278 [not D. setosa (Blume) Kuntze]. — *Nephrodium setosum* Baker, Syn. Fil. (1867) 274. — Type: Millett s.n., Java (K).

*Stipe* to 20 cm long; basal scales 10 mm long, light brown, scales above base darker, 3–5 mm long, very narrow with inflexed margins; *lamina* commonly 20 cm long (to 35 cm); to 8 pairs of free pinnules and 5 or 6 pairs adnate; *basal pinnules* of mature plants a little shorter than the next pair, commonly 7 cm long with basal basiscopic pinnule 3.5 × 1.4 cm, deeply lobed; middle pinnules with one pair of free deeply lobed pinnules, distal part of these pinnules lobed almost to the costa, lobes oblique, acute, middle ones entire; lower surface of costae of pinnules bearing very narrow scales which are widened with some isodiametric cells at their bases; sori medial on pinna-lobes; indusia very small, often hidden by sporangia, bearing many very slender flexuous pale glands. — *Fig. 5e–i.*

Distribution — *Malesia*: Sumatra, Malay Peninsula and Peninsular Thailand, Java, Borneo (Sarawak), Moluccas (Ambon).

Habitat — Among rocks by streams, often in the flood-zone, less common in rocky crevices away from streams, at low to medium altitudes; the type doubtfully from a mountain summit.

Taxonomy — Under *Aspidium intermedium* Blume cited only one collection, from Burangrang. The only specimen in the Leiden Rijksherbarium with this name and locality written by Blume was collected by Reinwardt, and is evidently the type. It is an unusually large specimen with lamina 39 cm long but only 11 cm wide (the pinnae are much upcurved). It is closely similar to the type of *Nephrodium setosum* Baker. However, in the herbarium Blume also identified other specimens as *Aspidium intermedium*, and sent a pinna of one of them to Hooker; that specimen is the type of *C. alteroblaberi*.

The fern described under the name *Aspidium vilis* by Raciborski in Pteridop. Buicenzorg (1898) is *Macrothelypteris setigera* (Blume) Ching; apparently this is also true of Alderw., Malayan Ferns (1908) 199.


Closely related to *C. vilis* (Kunze) Ching but with broader and shorter fronds; pinnules to 4 pairs, basal ones commonly 9 cm long, longer than the next pair.

Distribution — *Malesia*: Philippines (many localities), New Guinea.

Habitat — In lowland forest, not confined to rocks nor to the flood-zone beside streams.

Allied to C. boholensis Holttum, differing as follows: fronds much smaller; scales on upper part of stipe 3 mm long, stiffly spreading, with inrolled edges; lower surface of pinna-rachises bearing erect hairs; upper surface of pinnae, between veins, bearing many suberect hairs. Stipe c. 5 cm long; lamina to 11 cm long; basal pinnae 2.8 cm long with 1 pair of pinnules; basal basiscopic pinnule 13 x 4 mm, deeply lobed near its base; middle pinnae obtuse, lobed almost to their costae, the lobes falcate, obtuse and mostly entire; sori as in C. boholensis.

Distribution — Malesia: Philippines (Bohol, Mindoro, one collection from each).
Habitat — Bohol: 'at 600 m on rocks in damp forest'; Mindoro: 'on a steep cliff'.
Note — This may be a very dwarf habitat-form of C. boholensis; further collections are needed.


Stipe to 40 cm long, bearing throughout very narrow dark spreading scales, basal ones 12 mm long, gradually shorter distally; lamina to 55 cm long; pinnae closely placed, to 15 or more pairs, almost at right angles to the rachis; basal pinnae to 16 cm long, those on the largest fronds with a few pairs of free pinnules; basal basiscopic pinnule to c. 6 x 1.6 cm, lobed almost to its costa, costules to 5 mm apart, lobes entire; basal acroscopic pinnule 2 cm long, lobed near its base only; suprabasal pinnae sessile, acuminate, very deeply lobed, lobes mostly subentire and obtuse, of firm texture; lower surface of rachis and costae bearing scales like those of the stipe but more sparse, those on costae with many isodiametric cells in their inflexed basal part; upper surface of costae densely short-hairy, a few similar hairs also between veins; veins in pinna-lobes simple; sori medial on veins; indusia very small, bearing short slender glands.

Distribution — Malesia: widely in Western Malesia, also Philippines (Mindanao).
Habitat — In rocky places in forest, often on stream banks.


Stipes closely tufted, at the base only bearing flat brown scales, scales above base darker, setiform, the lower ones 10 mm long, shorter upwards; lamina c. 35 cm long; basal pinnae to 23 cm long bearing 10 pairs of pinnules, the basal basiscopic one 12 x 5 cm bearing 7 pairs of deeply lobed tertiary leaflets, 20 x 8 mm, their lobes 4 x 1.5 mm and lobulate; basal acroscopic pinnule 5 x 1.8 cm, bearing lobed tertiary leaflets to 10 x 6 mm; middle pinnae bearing several pairs of well-spaced lobed pinnules, the lobes to 5 x 3 mm, deeply lobulate; lower surface of pinna-rachises bearing scattered narrow scales 2 cm long with inflexed margins and isodiametric cells at the base; upper surface of all leaflets copiously glandular, the glands pale, thick, appressed, c. 0.1 mm long; sori at apices of veins; indusia firm, reniform, sometimes bearing glands.

Distribution — Malesia: Borneo (Sabah, 2 collections).
Habitat — In forest at 600–1000 m.


Stipe to more than 60 cm long, its basal scales flat, 12 x 1 mm, scales above base 5 mm long, the basal part clathrate with inflexed margins; lamina to c. 100 cm long; suprabasal pinnae to 60 cm long bearing 12 pairs of well-spaced pinnules, mostly stalked, the largest, 15 x 5.5 cm bearing 5 pairs of deeply lobed tertiary leaflets, the largest 3.2 x 1 cm, its basal lobes crenate, their costules 4 mm apart; lower surface of rachises bearing scales 2 mm long, dilated and clathrate at their bases,
margins above base inflexed, also many short hairs; _sori_ near the costules of lobes of pinnules; _indusia_ small, glandular.

Distribution - _Malesia_: Sumatra (Korinchki Peak, 2 collections).

Note - The above description is made from Matthew's own specimen, which he gave to Kew; it is much larger than the one he sent to Alderwerelt but does not include a basal pinnae. The second collection (by Holttum, at SING) is about the same size as Matthew's at BO.


*Dryopteris zeylanica* Alderw., Malayan Ferns (1908) 203, nomen nov. superfl. for _D. obtusiloba_ (Baker) Kuntze, for plants of Celebes only.

Base of stipe not preserved; scales on distal part 3 mm long, very narrow, convex and clathrate at their bases; _lamina_ to at least 50 cm long, thin; _basal pinnae_ 18–20 cm long with 2 or 3 pairs of free and 2 or 3 pairs of adnate pinnules, the pinnules contiguous or imbricate; basal basiscopic pinnule 9 × 3.5 cm, bearing several pairs of mostly adnate tertiary leaflets, the largest ones 20 × 7 mm, deeply lobed, the lobes 6 pairs, lowest ones crenate, their costules 3 mm apart; basal acrosopic pinnule 5.4 × 2 cm bearing 4 pairs of adnate tertiary leaflets; pinnules of upper pinnae all deeply lobed; pinna-rachises covered on the lower surface by many short scales; upper surface of pinnules between veins bearing variable slender appressed glands; _sori_ medial in pinnule-lobes; _indusia_ small, thin, glanduliferous.

Distribution - _Malesia_: Celebes (Minahassa, 2 collections).

Note - _Nephrodium obtusilobum_ Baker occurs only in Ceylon; it belongs to the genus *Dryoptis* Holttum & Edwards, the scales of which are very different from those of _Ctenitis_.


_Stipe_ 40 cm long, slender, at its base bearing light brown scales 12 mm long with filiform apices, above the base dark brown spreading scales with inflexed margins; _lamina_ 40 cm long, thin; pinnae many pairs, stalked, close to each other; _basal pinnae_ 17 cm long, its free pinnules 6 pairs, basal basiscopic pinnule 8–9 cm long with 5 pairs of deeply lobed tertiary leaflets, the lobes entire and slightly falcate; basal acrosopic pinnule 3.5 × 1.2 cm, bearing a single tertiary leaflet; pinnules or lobes of upper pinnae all deeply lobed, the lobes acute; _veins_ in pinnule-lobes pinnate, the veinlets simple; lower surface of pinna-rachises bearing narrow scales 2–3 mm long, clathrate at their bases, upper surface bearing many hairs to 0.5 mm long; upper surface of pinnules between veins bearing slender appressed hairs; _sori_ inframedial on veins; _indusia_ small, persistent.

Distribution - _Malesia_: Lesser Sunda Islands (Sumbawa, Lombok).


_Stipe_ 50 cm long, basal scales narrow, flat, thin, red-brown, 20 mm long, scales above base gradually shorter, upper ones 3–4 mm long, spreading, with inflexed margins; _lamina_ to 50 cm long, firm; pinnae 12 pairs; _basal pinnae_ to 23 cm long, bearing 3 or 4 pairs of free and several pairs of adnate pinnules; basal basiscopic pinnules to 8.7 × 2.4 cm, bearing 1 pair of tertiary leaflets which measure 14 × 6 mm, deeply lobed, the lobes obtuse; basal acrosopic pinnules 4 cm long; lower surface of pinna-rachises bearing narrow scales with dilated clathrate bases and short hairs, upper surface bearing dense thick hairs more than 1 mm long; _sori_ near costules of lobes of pinnules; _indusia_ minute, thin, bearing red cylindric glands.

Distribution - _Malesia_: Papua New Guinea (Morobe Prov., several collections).

Habitat - At 1000–1600 m, on steep slopes or stream banks in forest.

Taxonomy - This species is closely allied to _C. fijiensis_ (Hook.) Copel. but has less deeply divided pinnules, much smaller indusia, elongate basal basiscopic pinnules, and stipe-scales gradually decrescent upwards.

Caudex massive, suberect; stipe to 75 cm long, stramineous except at base; basal scales 15 × 1 mm, medium to dark brown, firm, flat; scales above base 5–6 mm long, stiffly spreading with inrolled edges and widened clathrate base; lamina to 50 cm or more long, thin; pinnae at least 10 pairs, basal ones 22–30 cm long bearing 5 pairs of free or adinate pinnules; basal basiscopic pinnules 10 cm long with 1 pair of free deeply crenate tertiary leaflets; basal acrosopic pinnules 4 cm long; second pair of pinnae 22 cm long, their largest pinnules 6 × 1.7 cm with basal lobes crenate, costules of the lobes 4 mm apart, several middle pinnules with much-decurrent basal lobes; upper pinnae with decurrent basal lobes the costules of which arise from the rachis; scales of lower surface of pinna-rachis 2–4 mm long, their edges inrolled, many cells near their bases clathrate; hairs on upper surface of pinna-rachis 0.5 mm long; sori on the middle of veins in pinnule-lobes; indusia small, thin, gland-bearing.

Distribution — Malesia: S Sumatra, Java, Bali. Habitat — In mountain forest.

Note — For discussion on Aspidium intermedium Blume see Ctenitis vilis above. Blume sent to Hooker one pinna of the type of the present species with the name Aspidium intermedium; Hooker (1862) merely copied Blume’s description and cited specimens of other species also.


Basal scales of stipe not seen; lamina to 30 cm long, firm but veins distinct on lower surface; free pinnae 4 pairs and several pairs adnate, the costules of basal lobes of distal pinnae arising from junction of pinna-midrib with rachis; basal pinnae to 15 cm long, bearing 2 pairs of free pinnules, distal parts of pinnae shaped like the frond-apex; basal basiscopic pinnules of basal pinnae to 6.5 × 3 cm with acute apex, bearing 1 pair of almost free tertiary leaflets, the largest 18 × 10 mm lobed to its costa near its base, the lobes entire (or the basal ones with sinuous margin) with broadly rounded apices; basal acrosopic pinnules of basal pinnae 3.7 × 2 cm; pinnules or lobes of second, third and fourth pairs of pinnae all deeply lobed and with broadly obtuse apices; lower surface of main rachis and...
Fig. 8. Rachis scales (SEM). — a. Ctenitis alteroblumei Holtum, × c. 40; b. ibid., × c. 80. — c. C. subglandulosa (Hance) Ching, × c. 40; d. ibid., × c. 140 (a, b: Sapiin 2793, Java; c, d: Elmer 22162, Luzon).

pinna-rachises bearing minute hairs and many very narrow scales 2–3 mm long which are not stiffly spreading, their margins inflexed and their widened bases formed by isodiametric cells; lower surface of costae of pinnules bearing sparse very short hairs of 2 or 3 cells and apparently short slender appressed red glands (not clearly seen); hairs on upper surface of costae 0.5 mm long, thick; no hairs nor glands seen between veins on upper surface; sori about medial on simple veinlets in pinnule-lobes or near the bases of one or both branches of forked veinlets; indusia very small, bearing a few slender glands which may be red.

Distribution – Malesia: Philippines (apart from the type, one specimen from North Luzon).


Stipe 20 cm long, dark red, its base covered by tufted narrow red-brown scales 15 mm long, rest of stipe bearing dark brown rigidly spreading scales; rachis-scales like those of the stipe but gradually shorter; lamina to 34 cm long, thin; pinnae imbricate, c. 12 pairs free and several pairs adnate; basal pinnae 11.5 cm long, short-stalked, their basal basiscopic pinnules 5.2 × 1.6 cm bearing 1 pair of deeply lobed tertiary leaflets, basal acroscopic pinnules 20 × 8 mm, their basal lobes lobulate; pinnules of middle pinnae all deeply lobed, the lobes slightly oblique, their costules 3 mm apart; lower surface of pinna-rachises bearing scales 2–3 mm long, their margins inflexed and bases clathrate, upper surface bearing hairs 1 mm long; sori supramedial on veins; indusia thin, covering young sori.

Distribution – Malesia: Philippines (known only from the type).

Habitat – In forest at 820 m.


Stipe to 37 cm long, pale when dry, basal scales flat, light brown, 10 mm or more long, scales above base very narrow, dark brown, to 8 mm long with inflexed margins; lamina to 32 cm long, thin; basal pinnule 15 cm long bearing 1 pair free pinnules and 2 or 3 pairs adnate, basal basiscopic pinnules 6.5 × 2 cm, bearing 1 pair of tertiary leaflets 12 × 5 mm, lobed halfway to their costules; basal acroscopic pinnule 2.5 cm × 1 cm, deeply lobed, lobes subentire; lower surface of pinna-rachises bearing very narrow scales 2–3 mm long with inflexed margins and clathrate base; appressed red glands present on and between veins on lower surface of pinnules; hairs on upper surfaces of pinna-rachises short; sori medial; indusia small, thin, bearing red glands.

Distribution — Malesia: Philippines (Luzon, Mindanao).

Habitat — In ridge forest at 500 m altitude.

Note — This species is allied to C. eatonii (Baker) Ching of Taiwan, differing in rachis-scales, indusia and red glands.


Stipe to 45 cm long, light castaneous, basal scales thin, flat, narrow, 15 mm long, scales above base spreading, dark brown, with inflexed margins, gradually shorter upwards; lamina to 37 cm long, 20 cm wide, thin, with 9 or 10 pairs of free and 3 or 4 pairs of adnate pinnules; basal pinnule 11.5 cm long, bearing 2 or 3 pairs of pinnules, the lowest ones 4 × 1 cm, lobed almost to their costae with 1 almost free slightly crenate tertiary leaflet 7 × 3 mm; pinnules of middle pinnule all deeply lobed; lower surface of pinna-rachises bearing narrow scales 2–3 mm long which have inflexed margins and clathrate bases, also many short hairs, upper surface covered with thick short hairs; sori a little inframedial; indusia thin, small, reniform, bearing pale red glands.

Distribution — Malesia: Papua New Guinea (known only from the type).

Habitat — In moist valley in oak forest at 1550 m altitude.


Stipe nearly 50 cm long, its basal scales 15 mm long, narrow, in a close tuft, above base an abrupt transition to narrow flat scales 2–3 mm long, their cells all somewhat elongate but with dark walls and clear lamina; lamina to at least 50 cm long, texture thin, wholly crenate; basal pinnule 20 cm long with stalks 3.5 cm and 6 pairs of widely spaced pinnules; basal acroscopic pinnule 9 cm long, bearing 1 pair of free and several pairs of adnate tertiary leaflets, all widely spaced; largest tertiary leaflet 2 cm long, lobed almost to its costa, the lobes well spaced, very oblique and falcate, the largest 4.5–5.5 × 1.5 mm; basal acroscopic pinnule 6.5 cm long; pinnules of suprabasal pinnule all widely spaced with widely spaced narrow falcate lobes; scales on lower surface of pinna-rachis narrow, evenly attenuate from base to apex, clathrate but few basal cells isodiametric; sori small, medial or supramedial; indusia small, distinct, bearing cylindrical glands; spores not seen.

Distribution — Malesia: Philippines (known only from the type).

Note — The scales do not indicate clearly whether this species belongs to the same group as C. subglandulosa; the form of spores would decide this question.


Polypodium oldhamii Baker, Syn. Fil. (1867) 311. — Type: Oldham s.n., 1864, Taiwan, Tamsuy (K).


Caudex massive; stipe to at least 120 cm long (Hance), its base covered with light brown thin scales 20–40 mm long, the scales gradually shorter upwards for 5–10 cm, then a subabrupt change to copious appressed overlapping clathrate scales; lamina as long as stipe; basal pinnules of lectotype of Nephrodium rhodolepis 45 cm long, their largest pinnules bearing 4 or 5 pairs of tertiary leaflets, the largest very deeply lobed; scales on smaller axes of frond to 1 mm wide, consisting almost entirely of isodiametric cells or at least of cells not much longer than wide; indusia thin, rather irregular in shape, bearing cylindrical glands and sometimes also hairs of several cells. – Figs. 6e, f, 8c, d.

Distribution – NE India, S China, Taiwan, Ryukyu Is., S Japan, Guam; in Malesia: E Java, Bali, Philippines (Luzon, Panay, Mindoro), E New Guinea; Fiji.

Habitat – In Malesia on mountains in forest at 400–1400 m, in one case on a stream bank.

Taxonomy – Copeland (1960) distinguished C. rhodolepis from C. subglandulosa in the Philippines, but all specimens seen by me from the Philippines appear to belong to one species.

TECTARIDIUM


Caudex short, erect; scales narrow, entire; fronds dimorphous; sterile fronds simple, elongate, entire, with venation as in Tectaria sect. Tectaria; fertile fronds lobed almost or quite to the costa, the lobes well separated each including one main vein with a very narrow lamina on each side of it, the lamina widenend at short intervals, each widened part bearing a sorus, terminal on a short vein; sori indusiate; spores not distinct from those of Tectaria and Heterogonium; fronds intermediate in form between sterile and fully fertile often present. — Fig. 9.

Distribution — A genus of one species, in Malesia native in the Philippines (southern Luzon, Leyte, Samar, Panay).

Notes — In 1926 Copeland distinguished two species, which are here united.

Sterile fronds in this genus have a venation like that of Tectaria singaporeana, but the extreme form of sterile fronds, as seen in the type of Tectaridium macleanii is so peculiar that a generic distinction appears warranted. Pichi Sermolli [Webbia 31 (1977) 467] considered Tectaridium and Luerssena to be closely allied, but the type of the latter (from Sumatra) has sori not significantly different from those of Tectaria pleiosora and the type species is here transferred to Tectaria, as T. kehdingiana. In my opinion Tectaridium represents a quite separate offshoot from Tectaria. Fronds intermediate between sterile and fully developed fertile offer significant evidence.


*Stipe* dark castaneous, of sterile fronds 10–17 cm long, of fertile fronds to 36 cm, minutely hairy near base; scales to 5 mm long, very narrow, hair-pointed; *lamina* of sterile fronds commonly to 20 × 3.5 cm, largest seen 39 × 5.5 cm, opaque, entire, apex short-pointed, base variously cordate to broadly cuneate; veins not distinct on either surface when dried, glabrous apart from dense short hairs on at least the basal part of the upper surface of costa; lobes of extreme form of fertile fronds to 4 cm long, 8–10 mm apart on each side of the costa, the base of each lobe widened to join a ± continuous very narrow wing on each side of the costa (the wing occasionally widened to bear a single sorus); *sori* borne on small ± semicircular lobules of the fertile lobes, opposite each other or alternate, on very short simple veins, indusiate; *indusia* firm, persistent, circular or a little asymmetric, attached along a line from the base to the middle of the sorus. — Fig. 9.

Distribution — *Malesia*: Philippines (Southern Luzon, Leyte, Samar, Panay).

Habitat — Common forest floor fern in primary forest at 450–500 m (Panay); primary forest on limestone and limestone-derived soils (Samar); lowland forest slope, heavy clay soil (Luzon).

Note — A collection in which fertile fronds have a quite distinct wing joining the bases of successive lobes was made type of a separate species *T. primitivum* by Copeland. Deeply lobed sterile fronds, lobes subentire, 4 mm wide, may occur and bear an occasional sorus on an outer vein of a single row of areoles. A plant from Panay cultivated at Kew produced fronds showing a range of forms between sterile and fertile. One frond 5 cm wide, shallowly lobed throughout, produced irregularly arranged sori near the margin, some terminal on short free veins and some on veins surrounding areoles.

**CHLAMYDOGRAMME**


Fronds simply pinnate; pinnae entire, basal ones bilobed or not; venation as in *Tectaria* sect. *Tectaria*; pinnae of sterile fronds 2–3 cm or more wide, pinnae of fertile fronds 2–3 mm wide; sori linear, submarginal, protected when young by the thin pinna-margin and by a continuous inner indusium. — Fig. 10.
Distribution — *Malesia*: NE New Guinea, 2 known species.

Taxonomy — The type species was described as exindusiate; indusia were first reported by Holttum in 1986. Copeland placed the species in the genus *Hemigramma*, in which the sori run along the veins of variably contracted fronds or pinnae. *Hemigramma* is here included in *Tectaria*, with the comment that, as arranged by Copeland, it was not a natural group.

**KEY TO THE SPECIES**

1a. Terminal lamina pinna-like; pinnae 2 or 3 pairs, basal ones forked  . 1. *C. hollrungii*

b. Terminal lamina 5-lobed; pinnae to 7 pairs, basal ones not forked .... 2. *C. elata*


*Caudex* short, erect, covered with very narrow entire scales c. 8 mm long. *Sterile frond*: stipe to 40 cm or more long, mid-castaneous, distally short-hairy, scales above base caducous; *lamina* to more than 30 cm long consisting of 2 or 3 pairs of pinnae with conform terminal lamina, the upper pinnae (if 3 pairs) adnate-decurrent, basal pinnae bilobed; terminal lamina to 25 × 3.5 cm, acuminate; *basal pinnae* to 25 × 3.5 cm with stalks 5–7 mm, their basiscopic lobes to 20 × 3 cm; sparse short hairs present on lower surface of costae and veins with a few between veins; more dense short hairs present on upper surface of costae. *Fertile frond*: stipe to 60 cm long; pinnae c. 2 mm wide. — Fig. 10.

Distribution — *Malesia*: NE New Guinea, 3 collections.

Habitat — On hill slopes in lowland forest.

Note — In one specimen there are rounded additional lobes 5–6 mm long on the acroscopic side at the base of basal pinnae.

Fig. 10. *Chlamydomgramme hollrungii* (Kuhn) Holttum. a. Sterile and fertile fronds, × 0.22; b. transverse section of a fertile pinna, × 18 (a: Hoogland & Craven 10516; b: Hoogland & Craven 10187).
Holttum — Tectaria Group


Sterile frond: stipe to 60 cm or more long, dark castaneous, sparsely short-hairy; largest basal scales 20 mm long, 3 mm wide at their bases, firm, dark with thinner margins; lamina to 70 cm long; free pinnae to 5 pairs and above them 2 or 3 pairs with recurrent bases grading into a 3–5-lobed apex; largest pinnae to 22 × 2.5 cm, their sides almost parallel for much of their length, bases unequally cuneate; basal pinnae simple, with stalks 3 mm long, narrowed to a very narrow wing 10 mm long on the basiscopic side, cuneate at c. 45° on acroscopic side; main veins sinuous, smaller veins distinct but not prominent; lower surface bearing sparse short hairs on all parts, upper surface glabrous. Fertile frond: lamina to more than 60 cm long; pinnae c. 12 pairs, basal ones c. 15 × 0.3 cm, distal ones with soriferous recurrent bases; spores similar to those of C. hollrungii.

Distribution — Malesia: New Guinea (known from type collection only).

Habitat — In narrow gorge in limestone, 1–2 m above flood level, 300 m.

Note — One sterile frond has only 2 pairs of pinnae which are 4 cm wide, below a frond-apex with lobes of similar width. A frond intermediate between sterile and fertile has most pinnae 5–8 mm wide towards their bases, distally like pinnae of a fully fertile frond.

TECTARIA


Sagenia & Stenoemia Presl 1836: see Tectaria sect. Sagenia.

Microbrochis Presl 1851: see Tectaria sect. Sagenia.


Quercifilix Copel., Philipp. J. Sci. 37 (1928) 408; Sledge, Kew Bull. 27 (1972) 422. — Type species: Quercifilix zeilanica (Houtt.) Copel. = Tectaria zeilanica (Houtt.) Sledge.

Ctenitopsis Ching 1938: see Tectaria sect. Sagenia.

Caudex erect or ± prostrate, its vascular structure radially arranged; scales narrow, formed of narrow elongate cells, usually rigid and opaque, in some species with thinner
or fringed margins, in a few small species wholly thin and translucent but the cells not clathrate-isodiametric as in *Ctenitis*; fronds in most species at least pinnately divided, the basal pinnae with elongate basal basiscopic lobes or pinnules, entire or with unlobed basal pinnae only in a few species which have elaborate anastomosis of veins; veins free with basal basiscopic one in each pinna-lobe arising from the costa (except in *T. manilensis*), or anastomosing to form narrow areoles along costa or costules, or more elaborately anastomosing with ± isodiametric areoles having included free branched veinlets variously directed; costae of pinnae and costules of pinnules in most species slightly ridged on the upper surface and covered with ctenitoid hairs, in some species of sect. *Tectaria* slightly grooved and glabrous; upper surface of lamina between veins usually bearing scattered thick ctenitoid hairs at least near the margin, slender hairs variously present on and between veins on the lower surface; sori usually round with reniform or peltate indusia, in a few species ± elongate or asymmetric or spreading along all veins in contractile fertile pinnae; spores usually cristate, the crests forming a more or less definite reticulum, in some species bearing slender spines. — *Figs. 11–16.*

Distribution — Pantropic; c. 210 species, of which c. 40 are neotropic.

Habitat — Almost all species are terrestrial forest plants; a few grow only on rocks, some species only on limestone; a few are rheophytes.

Cytology — Chromosome number 40.

Taxonomy — In describing the new genus *Tectaria*, Cavanilles cited only one species which is therefore the type, but he later included in the same genus other species which are now placed in *Dryopteris*, *Polystichum*, *Nephrolepis*, *Thelypteris* and other genera, their common character being sori covered with reniform or peltate indusia. In 1801 Swartz established the genus *Aspidium* with a similar wide-ranging content, including the original species cited by Cavanilles.

Later authors adopted Swartz's name and treated it variously. Presl, Fée and others attempted to segregate genera on the basis of characters of indusia (whether peltate or reniform) and of venation; they are listed by Christensen (1905). But these 19th century authors did not observe indusia critically and failed to notice other characters now seen to be important, especially of hairs, scales and glands, and most of their generic names are no longer recognized, or if recognized are defined mainly by characters not mentioned by their original authors. Hooker (1862) and Baker (1867), attempting to establish genera of wider scope, confused together unrelated species. It was not until the classification of Diels (1899) that it was clearly recognized that species belonging to the same genus could have, or lack, indusia; he transferred some exindusiates species to *Aspidium*. But Diels included also some extraneous elements and his subdivision of *Aspidium* is valueless. Christensen (1905) cited many generic synonyms but his main subdivision of *Aspidium* is little better than that of Diels; he did however recognize that, of the synonyms cited, *Tectaria* has priority and printed against it 'nom. opt.' Soon afterwards Copeland (1907), actively studying Philippine species, revived the name *Tectaria* for them, but Van Alderwerelt (1908) attempted to revert to the form of indusia to characterize infrageneric groups, misusing the name *Sagenia* Presl. Christensen accepted the generic name *Tectaria* in the third Supplement to his Index (1934), Ching having already (1931) made the first good study of the species of mainland Asia.
Ching and Copeland accepted in Tectaria only species with anastomosing veins. Copeland (1907: 409) however wrote 'Dryopteris dissecta' (Forst.) Kuntze represents, most nearly of known species, the probable origin of Tectaria.' But at that time Christensen had not yet discovered a natural subdivision of the comprehensive Dryopteris of his Index. When he did so (in his monograph of 1913 and 1920), working entirely with tropical American species, he distinguished Ctenitis from Dryopteris s.str. (and from thelypteroid ferns) by the character of its hairs, and pointed out that in its hairs Tectaria agrees with Ctenitis. Ching dealt with the species of Dryopteris and Ctenitis of mainland Asia in 1938 and in so doing came across a few species which have free veins but in other respects resemble Tectaria. He proposed a new genus Ctenitopsis for these species (one was Forster's dissecta) and also species with free veins later transferred by Holttum to Heterogonium; Copeland (1947) transferred all these to Ctenitis and wrote (p. 124) 'Tectaria is probably of ctenitid origin' and (p. 130) 'Ctenitis is more primitive than Tectaria, therefore it is the probable parent genus.' By the latter comment he meant that anastomosing veins are a specialized character as compared with free veins and that therefore the primitive species of Tectaria had free veins. But Copeland overlooked the fact that the type species of Ctenitis, and most other American species included in that genus by Christensen, differ from Tectaria in their scales and also in bearing cylindric glands which are lacking in Tectaria; Manton (1954) also showed that they differ in chromosome number. Forster's species which was the subject of Copeland's comment in 1907 differs only from acknowledged species of Tectaria in its free veins, and the species T. fusiceps (Bedd.) C. Chr. bridges the gap by having veins anastomosing to form costal areoles in its sterile fronds but all free in fertile ones. The free-veined species here accepted in Tectaria are most abundant in mainland Asia (NE India and China) and in the Philippines. There are a few others in Malesia and the Pacific but no related species in tropical America or in Africa [T. brauniana (Karst.) C. Chr. of Colombia, which also has free veins, is certainly not closely related to the species of Asia and needs further study]. Thus SE Asia is here regarded as the centre of origin of the genus. Tectaria ingens (Atk.) Holttum in NE India has fronds up to 3 m tall (including the stipe) and is perhaps the nearest existing species to a prototype for the genus.

In considering a subdivision of Tectaria, vein-pattern appears to be our only guide, and the clearest division [Holtum, Kew Bull. 38 (1983) 108, f. 1] is between species which have veins free or anastomosing in the pattern indicated for Sagenia by Presl, and those which have copious anastomosis with branched veinlets in the areoles as in the type species of Tectaria. There are, however, in Peninsular Thailand and Peninsular Malaysia, especially on limestone, intermediates between the two. Apart from these species, a distinct line can be drawn between species which have narrow costal areoles lacking included free veinlets and those in which costal areoles do contain free veinlets. The division is here accepted, with sectional rank for the two divisions. As sect. Sagenia is clearly the primitive group, it is dealt with first.

Description of species — A common feature of all species except a few which have entire fronds or unlobed basal pinnae is that the basal pinnae are larger than those next above them and have elongate basal basiscopic lobes or pinnules. In the development of a young plant, each successive frond has basal pinnae gradually larger and more complex in
structure, and in many species fronds of less than mature size and form may bear sori. The shape and size of the basal pinnae of fronds of mature plants provide some of the most distinctive characters for distinguishing between species. The result is that fronds of immature plants are sometimes difficult to identify with certainty. The arrangement of sori is independent of size of fronds, also (in some cases) pubescence, but scales, which in Ctenitis provide good distinguishing characters, are not greatly varied in Tectaria. The reader is therefore warned that fronds of immature size may be difficult to identify from the keys. It is thus important for field botanists and collectors to choose fronds from mature plants for preservation; it is helpful also to include specimens of immature plants with notes on their status, which few collectors have done. It is also important to collect complete basal pinnae; the type specimen of T. setulosa (Baker) Holtttm consists of a pair of suprabasal pinnae and these have been misinterpreted as basal ones.

KEY TO THE SECTIONS OF TECTARIA

1a. Veins free, or anastomosing to form narrow costal or costular areoles lacking free included veinlets, such veinlets in other areoles few, short, unbranched and directed towards the margin ........................................ Sector Sagenia (p. 42)
b. Veins freely anastomosing; branched free veinlets variously directed present in many areoles ........................................ Sector Tectaria (p. 59)

Section Sagenia


Microbrochis Presl, Epim. Bot. (1851) 51. — Type species: Microbrochis apiifolia (Schk.) Presl = Tectaria apiifolia (Schk.) Copeland.


Distinctive characters as in the above key.

Distribution — Throughout the distribution of the genus; c. 65 species of which c. 10 are neotropic; in Malesia 26 species.

Taxonomy — The type species of Sagenia and Microbrochis are identical in venation and both are West Indian. Presl distinguished them by the form of their indusia only, peltate in Sagenia and reniform in Microbrochis; but in fact the indusia of the type species of Sagenia are not truly peltate nor are they clearly distinct from those of the type of Micro-


**Heterogoniwn**

**brochis. Tectaria coadunata** (J. Sm.) C. Chr. in Asia is closely related to them both and all three were regarded as conspecific by Hooker. There are allied species in Africa. Thus the *Sagenia* form of venation is pantropic and must have had an early origin from the free-veined form which, as above noted, is regarded as primitive for the genus *Tectaria*.

Presl's name *Sagenia* was variously misused by later authors. Baker used it (1867: 296–300) as an infrageneric name in *Nephrodium*, a genus defined solely by the reniform indusia of sori and comprising mainly species now placed in the family *Thelypteridaceae*; thus Baker's *Nephrodium* § *Sagenia* differs from Presl's definition of *Sagenia* both in indusia and venation, and is most unnaturally associated with a very different group of ferns. In 1908 Van Alderwerelt revived the use of *Sagenia* as an infrageneric group in *Aspidium*, again defining it in a sense contrary to that of Presl.

*Stenosemia* Presl was established for one widely distributed species which has exactly *Sagenia* venation in sterile fronds, but much-contracted fertile fronds with a simpler venation along which the sporangia are so crowded that they appear to be acrostichoid. There is an allied species in Madagascar. *Stenosemia pinnata* Copeland has the frond-form of *Heterogoniwn* and is here placed in that genus.

**KEY TO THE SPECIES OF SECTION SAGENIA**

1a. All veins free in fertile fronds ............................................. 2
b. At least costal areoles present in fertile fronds .......................... 14

2a. Fronds very thin, appearing only in the rainy season; caudex creeping, succulent

1. T. manilensis

b. Fronds not very thin, persistent; caudex not succulent ........................ 3

3a. All pinnae very deeply lobed; free tertiary leaflets present on basal pinnae .... 4
b. Pinnae much less deeply lobed; tertiary leaflets rare ........................... 9

4a. Bases of upper pinnae and pinnules narrowly decurrent, their basal lobes sometimes separately attached to rachis ........................................ 5
b. Bases of upper pinnae not narrowly decurrent, their basal lobes never separately attached to the rachis ....................................... 6

5a. Basal pinnae to 22 cm long; axes glabrous on lower surface .......... 2. T. mesodon
b. Basal pinnae to 45 cm long; axes short-hairy on lower surface ........... 3. T. laxa

6a. Hairs 1 mm long present between veins on upper surface .................. 7
b. Hairs on upper surface between veins few and short, mostly near sinuses

5. T. trichotoma

7a. Basal pinnae to 12 cm long ................................................. 8
b. Basal pinnae to 27 cm long; fronds not or little dimorphous .......... 4. T. ramosii

8a. Fronds strongly dimorphous; distinct indusia present

4a. T. ramosii × Psomiocarpa apiifolia

b. Fronds not dimorphous; indusia small or lacking ........................... 4b. T. ramosii × T. aurita

9a. Basal pinnae to at least 40 cm long; suprabasal pinnae bearing 3 or 4 pairs of sessile or adnate pinnules .................................................. 6. T. setulosia
b. Basal pinnae not over 25 cm long; suprabasal pinnae bearing at least one pair of free pinnules ....................................................... 10
10a. Sporangia bearing short capitate hairs .................................. 7. T. moussetii
b. Sporangia lacking such hairs .......................................................... 11
11a. Fronds dimorphous; irregular slight anastomosis of veins in sterile fronds; scales on stipe black, 10 × 1 mm ......................................................... 8. T. fuscipes
b. Fronds not or little dimorphous; no anastomosis, scales otherwise ................ 12
12a. Pinnae very firm, their longest lobes, if sterile, sharply dentate; no hairs near sinuses on upper surface ....................................................... 9. T. rigida
b. Pinnae thinner, their largest lobes not sharply dentate; some hairs present on upper surface at least near sinuses ........................................ 13
13a. Basal pinnae 7 cm long on fronds with lamina 25 cm long; very narrow black scales present on rachis ......................................................... 10. T. andersonii
b. Basal pinnae proportionately longer, with free pinnules even on smaller fronds; scales on rachis few and not black .................................................. 11. T. dissecta
14a. Pinnae of fertile fronds much contracted as compared with those of sterile fronds 15
b. Pinnae of fertile fronds not or little contracted ........................................ 17
15a. Sporangia covering the lobes of fertile pinnae ...................................... 12. T. aurita
b. Sporangia forming separate sori ................................................................ 16
16a. Veins distinct on lower surface; rachis not dark and glossy ..................... 13. T. impressa
b. Veins not distinct on lower surface; rachis dark and glossy .. 15. T. bamleriana
17a. Middle pinnae entire or shallowly lobed ................................................. 14. T. barberi
b. Middle pinnae deeply lobed or pinnate ...................................................... 18
18a. Hairs between veins on upper surface present only near sinuses ............... 19
b. Hairs scattered generally between veins on upper surface ....................... 24
19a. Free pinnules on basal pinnae at most 1 pair .......................................... 20
b. Free pinnules on basal pinnae at least 3 pairs ........................................... 22
20a. Fronds opaque; smaller veins not distinct on lower surface ................. 15. T. bamleriana
b. Fronds not opaque, or smaller veins distinct on lower surface ................ 21
21a. Pinna-rachis very dark; basal pinnae not over 30 cm long; New Guinea
b. Pinna-rachis not dark; basal pinnae to 45 cm long; W Malesia ......... 17. T. griffithii
22a. Rachis and pinna-rachis densely short-hairy with very narrow dark scales on lower surface ........................ 17. T. griffithii var. amplissima
b. Rachis and pinna-rachis neither densely short-hairy nor scaly on lower surface 23
23a. Suprabasal pinnae almost sessile with sessile basal pinnules ................. 18. T. nesiotica
b. Suprabasal pinnae stalked with several stalked basal pinnules ............. 19. T. kingii
24a. Sori indusiata ...................................................................................... 25
b. Sori exindusiata ..................................................................................... 29
25a. No free pinnules on basal pinnae ......................................................... 22. T. christii
b. At least 1 pair of free pinnules on basal pinnae ...................................... 26
26a. Anastomosis confined (or nearly so) to costal and costular areoles ........ 27
b. Anastomosis comprising more than one series of small areoles below sinuses between pinna-lobes ........................................................ 28
27a. Free tertiary leaflets rarely present on basal pinnae ......................... 23. T. devexa
b. Free tertiary leaflets present on fronds of mature plants .................. 19. T. kingii
Holttum — Tectaria Group

28a. Hairs on lower surface of costae and costules to 0.3 mm long; veins not prominent

b. Hairs on lower surface of costae and costules to 1 mm long; veins prominent on both surfaces of dried specimens ........................................ 26. T. pubescens

29a. Very short hairs abundant between veins on both surfaces ........................................ 21. T. adenophora

b. Hairs between veins on upper surface thick, to 0.5 mm or more long, none or few on lower surface .......................................................... 30

30a. Basal pinnae of mature plants bearing several pairs of free or adnate pinnules, one tertiary leaflet usually present ........................................ 24. T. ferruginea

b. Basal pinnae of mature plants bearing one pair of pinnules; tertiary leaflets lacking 20. T. squamipes


a. var. manilensis

Caudex short-creeping, succulent, bearing short narrow thin scales; stipe to 18 cm long, its distal part ± densely hairy; lamina very thin, shrivelling in the dry season, to 18 cm long and wide, deltoid-pentagonal with 3 or 4 pairs of free or adnate pinnae; basal pinnae to 13 cm long, lobed to a very narrow wing along the rachis; basal basiscopic lobe to 8 cm long and 3 cm wide, lobed to a very narrow wing, its larger lobes deeply lobulate; basal acrosopic lobe of basal pinna 2.5 cm long; basal veins in pinna-lobes rarely arising from the costa; rachis and costae of pinnae bearing hairs 0.5–1 mm long on the upper surface, shorter rather thick hairs also present on the lamina between veins, hairs on lower surface fewer and more slender; sori on short acrosopic branches of veins in pinnule-lobes; indusia reniform or asymmetric, sometimes with short hairs. — Fig. 12a–c.

Distribution — Southern Burma, Thailand; in Malesia: Malaysia (Langkawi Is. and Perlis), Philippines (Luzon, Palawan), SW Celebes.

Habitat — Usually on limestone; in Luzon reported on a clay bank, streamside. Fronds of plants in cultivation in Singapore withered periodically though not subjected to drought; new ones developed after a period of rest.


Stipe to 7 cm, lamina to 10 × 9 cm with only the basal pinnae free.

Note — Known only from the type locality whence plants cultivated in Singapore alongside plants of the typical variety maintained their distinctive characters over three years. C.G. Mathew reported that plants grew in a dense mat at the entrance to a limestone cave.


Caudex short, subectate, bearing firm dark scales 12 × 1 mm; stipe c. 30 cm long, dark, glossy, short-
hairy in the groove only; lamina 30 cm long, very firm, drying dark, free pinnae 3 or 4 pairs and 2 or 3 pairs adnate; apical lamina very obliquely lobed almost to its axis, the lobes with narrowly decurrent bases, upper pinnae similarly lobed, their basal lobes sometimes separately attached to the rachis, all their lobes lobulate, the lobules falcate; basal pinnae to 25 cm long, bearing 2 pairs of stalked pinnales and an apical lamina like that of the frond, basal basiscopic pinnae to 14 cm long with 1 pair of free tertiary leaflets; largest tertiary leaflet 4 cm long, very deeply lobed, the lobes crenate, basal acrosopic pinnae 8 cm long; short hairs present on upper surface of rachises and costae, also near sinuses between lobes of pinnae, lacking elsewhere; veins concorlous at both sides, more prominent on upper surface than on lower; sori at the ends of acroscopic branches of forked veins near margin; indusia small, dark, firm, glabrous.

Distribution – Malesia: Philippines (Mindanao).


Closely allied to T. mesodon and similar in texture and frond-form, differing in its much larger fronds with all parts more widely spaced; stipe to 75 cm long, lamina to 60 cm or more; basal pinnae to 45 cm long (including stalks 6 cm long), their basal basiscopic pinnales 24 cm long and largest tertiary leaflets 8 cm long, basal acrosopic pinnales 16 cm long; veins distinct on both surfaces; very short hairs scattered on all minor axes on their lower surface, also some between veins. – Fig. 12d.

Distribution – Malesia: Philippines (Northern Luzon, several collections).

Habitat – In dry forest at 500–1000 m.


Caudex short, suberect; stipe to 65 cm long, dark, glossy, bearing rather thin dark scales 10 × 1 mm near the base only; lamina to 55 cm long with 5 pairs of free and 2 pairs of adnate pinnae below a short apical lamina; basal pinnae to 27 cm long with stalks 2 cm long, bearing 3 pairs of well-spaced free and 1 or 2 pairs adnate pinnales; basal basiscopic pinnae 13 × 5.5 cm bearing 2 pairs free and 1 or 2 pairs adnate tertiary leaflets, its apical lamina very deeply lobed, the lobes obliquely lobulate; largest tertiary leaflet 2.5 × 1.6 cm, very deeply lobed; basal acrosopic pinna 5 × 2.3 cm; basal basiscopic lobes of distal pinnales on all pinnae shortly decurrent, their veins arising from the pinna-rachis; veins all free; hairs on upper surface of costae dense and thick, scattered ones more than 1 mm long, similar long hairs also present on and between veins; hairs on lower surface sparse and shorter; sori supramedial at ends of veins in lobules of pinna-lobes; indusia thin, persistent, more than 1 mm diameter when young.

Distribution – Malesia: Philippines (Samar and Bohol).

Habitat – On limestone-derived soils.

Probable hybrids:

4a. Tectaria ramosii × Psomiocharpa api- folia Presl. – Collection: Western Samar, Price & Hernaez 398, also a sterile frond of Price & Hernaez 74 (K); habitat as T. ramosii.

Fronds strongly dimorphous; sterile fronds similar to those of Psomiocharpa but with larger segments, lamina to 16 × 16 cm; fertile fronds more elongate (lamina 18 cm long, basal pinnae 7 cm), their pinnae and pinnales much contracted; sori indusiate, indusia firm, reniform.

4b. Tectaria ramosii × Tectaria aurita (Sw.) Chandra. – Collection: Western Samar, Price & Hernaez 20 & 74 (K).

Fronds very dimorphous; sterile fronds similar in form to those of T. aurita but with slight and irregular anastomosis of veins and lack of buds at bases of pinnae; fertile fronds less contracted than those of T. aurita with distinct separate small sori; indusia very small or lacking.

& C. Chr., Fl. Indo-Chine 7 (1941) 351. —


Caudex short, suberect; stipe 30 cm long, castaneous, hairy in the groove only, basal scales 12 × 1 mm, firm, dark; lamina to 50 cm long, firm; free and adnate pinnules to 6 pairs; apical lamina 13 cm long, acuminate, lobed almost to its axis, its basal lobes 6 × 1.3 cm, upcurved, deeply crenate; upper pinnules similar with crenate lobes; basal pinnules to 25 cm long (stalk to 5 cm), oblique-ascending, bearing several pairs of pinnules; basal basiscopic pinnule 12.5 × 5.5 cm with 1 or 2 pairs of free tertiary leaflets; basal acroscopic pinnule 7 × 3.5 cm; veins in pinna-lobes mostly forked, concolorous; lower surface glabrous, upper surface densely short-hairy on rachises, short hairs also present near sinuses between pinna-lobes. Sori about medial between costules of pinna-lobes and margin, terminal on acroscopic branch veinlets; indusia dark, very firm, to 1.5 mm wide, with irregular small papillae on the upper surface.

Distribution — Vietnam; Malesia: Philippines (S Luzon, Panay, Sibuyan, Palawan, Balabac), Borneo (Sabah).

Habitat — One specimen from Tonkin was found on limestone; one from Sabah on ‘ultrabasic steep cliffs and banks.’

Note — The largest specimens from Vietnam are considerably larger than any from Malesia (one has a basal pinna 55 cm long) but otherwise show no difference.

6. Tectaria setulosa (Baker) Holttum, comb. nov. — Nephroidium setulosum Baker, J. Bot. 28 (1890) 265. — Ctenitopsis setulosa (Baker) C. Chr., Notul. Syst. (Paris) 7 (1938) 87; Tard. & C. Chr., Fl. Indo-Chine 7 (1941) 352. — Type: Balansa 1836, Tonkin (P; iso K).


KEY TO THE VARIETIES

1a. Larger pinnule-lobes obuse, fertile ones crenate; sori mostly in one row on each side of costae; no anastomosis .

b. Larger pinnule-lobes acute, fertile ones deeply lobulate; sori 2 or 3 pairs in each lobule; some anastomosis of veins

a. var. setulosa

Caudex short, erect; stipe to 55 cm long, short-hairy throughout, basal scales 12 × 1 mm, scattered narrower ones also above base; lamina to 70 cm long, rather thin; basal pinnules to 40 cm long, their basal basiscopic pinnules to 16 × 6 cm deeply lobed with crenate lobes, the basal lobes forming free tertiary leaflets; suprabasal pinnules bearing 3 or 4 pairs of free or adnate pinnules; distal adnate pinnules lobed to 3–4 mm from the costa, their basal basiscopic lobes decurrent on the rachis; pinnarachises and costae short-hairy throughout on lower surface with sparse shorter hairs on veins, densely hairy on upper surface, the hairs more than 0.5 mm long, scattered similar hairs present between veins; lateral veins in lobes of pinnae slender and prominent on the lower surface, forked or subpinnate; fertile pinnules as large as sterile ones, their lobes obuse, crenate; sori about medial in the lobes, at the ends of acroscopic vein-branches, or a few additional ones also on basal lobes; indusia large, firm, glabrous.

Distribution — Tonkin, N Burma; in Malesia only known from the Malay Peninsula (Cameron Highlands, Pahang).

Habitat — In wet ground under tall Musa plants, at 1850 m.

Note — The type consists of a pair of suprabasal pinnae; these are wrongly described as basal pinnae in the Fl. Indo-Chine.

b. var. raciborskii (Alderw.) Holttum, stat. nov. — Dryopteris raciborskii Alderw., Malayan Ferns (1908) 197, 816, new name for Aspidium sagenoides auct.; Racib., Pteridop. Buitenzorg (1898) 179, non Mett. — Type: Raciborski s.n., W Java, G. Salak (BO; K, L).

Fronds somewhat larger than those of var. setulosa, larger lobes of pinnae and pinnules acute, sterile pinnae broader and less deeply lobed than fertile; lobes of fertile pinnaules deeply lobed with 3 pairs of sori in each lobule; irregular slight anastomosis of veins in sterile pinnaules especially near bases of lobes.

Distribution — Known only from the original collection.

7. Tectaria moussetii Hoyt, Blumea 35 (1991) 553. — Type: Mousset 130, E Java, Lawang, near Poespno, 700–800 m (K; iso L, UC).

Caudex not seen; stipe to 50 cm long, dark purplish-brown, glabrescent, rachis similar, both bearing narrow dark glossy scales; basal scales to 10 x 1.5 mm; lamina to at least 50 cm long; pinnae 7 pairs or more, well spaced; basal pinnae of type specimen 16 cm long (stalk 10 mm) with 1 pair of separately adnate pinnaules, basal basiscopic pinnaule 7 cm long, deeply lobed, its lobes 7 mm apart; middle pinnae deeply lobed at their bases, lobes crenate, costules 10–12 mm apart; lateral veins in lobes mostly forked; lower surface of pinnae-rachis short-hairy near its base, short scales present throughout; upper surface of pinnae bearing thick hairs between the veins; sori terminal on acroscopic vein-branches; indusia thin, often with short slender hairs; sporangia bearing short capitulate hairs near the annulus.

Distribution — Malesia: East Java, Bali (3 collections).

Note — Zollerling F146 from Bali is larger than the type, having lamina 60 cm long and basal pinnae 23 cm long with 2 pairs of free pinnaules. The capitulate hairs on sporangia are unique in the genus.


Caudex short, erect; fronds dimorphic, the fertile ones with contracted pinnae; stipes commonly 30 cm long, light castaneous, bearing many narrow black scales; lamina to 30 cm long; pinnae 3 or 4 pairs, basal pinnae to 14 cm long, basal basiscopic pinnaules to 6 cm long; middle pinnae of sterile frond lobed about 3/5 towards their costae, the lobes subentire and sinuses between them narrow; middle pinnae of fertile fronds very deeply lobed, the lobes crenate and well-spaced; veins usually forked in lobes of sterile pinnae, the basal ones irregularly anastomosing (rarely in Malesian specimens), often simple in lobes of fertile pinnae; thick hairs present between veins on upper surface, most abundant on sterile pinnae, slender ones less abundant on lower surface; sori on acroscopic branches of veins; indusia variably hairy.

Distribution — Widely in Southeast Asia; in Malesia: E Java and SW Celebes.


Caudex short, erect; stipe to 35 cm long, slightly castaneous, its basal scales 10 mm long, barely 1 mm wide, firm with filiform tips; lamina c. 30 cm long; pinnae 3 pairs stalked, 2 pairs sessile or adnate; basal pinnae 15 cm long with 2 pairs of stalked pinnaules, basal basiscopic ones 7 cm long with basal lobe almost free; lobes of all pinnae falcate, acute, the margins of sterile ones acutely dentate; veins as in T. dissecta; very short hairs present on upper surface of rachis and near bases of pinna-rachises, none between veins on the upper surface; sori terminal on acroscopic branches of veins in pinnae-lubes; indusia firm, dark, glabrous.

Distribution — Malesia: Sumatra (G. Sago; known only from the type collection).

Habitat — Ravine in forest, 900–1000 m.


Caudex short, erect; stipe to 22 cm long, dark-castaneous, bearing short stiff erect hairs and scales throughout; basal scales to 12 mm long, 0.5 mm wide at the base, apex filiform, very dark, scales on stipe and rachis 2–3 mm long, very narrow; lamina to 25 cm long, firm, drying dark brown on
lower surface; pinnae to 5 pairs free and 3 pairs adnate, horizontal, hardly upcurved distally; basal pinnae 7 cm long with 1 pair of free pinnales, basal basiscopic one 2.2 × 0.9 cm, acroscopic 1.5 cm long; other pinnae lobed almost to their costae near the base, costules to 8 mm apart, lobes obtuse and slightly crenate; lower surface of costae bearing erect hairs 0.2–0.4 mm long, fewer and shorter hairs on veins, few between veins; upper surface of costae bearing dense thick hairs 0.4 mm long, between veins hairs only present near the margin; sori on acroscopic branches of veins, nearer to margin than to costule; indusia reniform, firm, with a few short hairs.

Distribution – Malesia: Borneo; Sarawak (Miri Dist.; known only from the type collection).

Habitat – Upper slopes of a limestone hill, limestone rocks outcropping and deep ‘mor’ soil, in shaded place.


Caulix short, erect; stipe to 50 cm long or more, rather dark, minutely hairy; basal scales 10 × 1.2 mm, dark, firm, those above base with pale thinner margins, distal scales and those on rachis thin, mostly caducous; lamina to 60 cm long, always much longer than wide; pinnae to 10 or more pairs, oblique and ± upcurved, apical lamina lobed almost to the rachis; basal pinnae to 20 cm long (stalk to 2 cm) bearing up to 3 pairs of pinnales (at least one pair in small plants); basal basiscopic pinnae to 12 cm long, very deeply lobed but rarely with a free tertiary leaflet; middle pinnae sessile, short-acuminate, very deeply lobed, the lowest lobes at least crenate, lateral veins in the lobes once or twice forked, the basal basiscopic one always arising from the costa; lower surface of costa bearing ± abundant short hairs, hairs between veins usually lacking or few; upper surface of costa bearing dense thicker hairs, between veins some thick hairs (variable); sori on the acroscopic branches of veins, sometimes terminal, usually nearer to the margin than to the costule; indusia well developed, dark when dried, glabrous or variously short-hairy when hairs are present on the lower surface. — Fig. 11a, e.g.


Habitat – This species appears to be adapted to a climate with a regular dry season. The largest plants are reported as terrestrial in forest. In Borneo all plants for which the habitat is recorded were found on limestone or (one from Mt Kinabalu at 1000 m) pendulous from rocks near a stream. In central Java one plant was found on an old wall.

Variability – The largest plants seen are from Luzon, the Lesser Sunda Islands and Christmas Island. Most plants from New Guinea have abundant erect very slender hairs between veins on the lower surface and also copious hairs on the upper surface, the latter thinner than those on plants which have a few thick hairs; some Philippine plants are similar but those on limestone have few hairs on the lower surface. Limestone plants in Sarawak are rather small but typical in subpersistence. A few specimens from limestone in the Philippines are very small, possibly the result of exposure.


...
Fig. 11. *Tectaria*, types of venation; scales. — *T. dissecta* (G. Forster) Lellinger. a. Fertile lobes of a middle pinna with sori removed from the right, × 2.5. — *T. devexa* (Kunze ex Mett.) Copel. b. Fertile lobes of a middle pinna with sori removed from the right, × 2.5. — *T. melanocaula* (Blume) Copel. c. Base of a middle pinna with sori removed on the right, × 2.5. — *T. singaporeana* (Hook. & Grev.) Copel. d. Vein pattern between two lateral veins, × 2.5. — *T. dissecta*. e. A rhizome scale with margin and tip details, × 100. — *T. devexa*. f. Hairs from laminal veins, × 150. — *T. dissecta*. g. Hairs from rachis and midrib, × 150 (a, c, g: Price 1763; b, f: Anderson s.n., Sarawak; c: Mousset s.n., Java; d: Parris 10559).
Holttum — Tectaria Group


Caudex short, erect; stipe of sterile frond to 30 cm long, of fertile to at least 45 cm; basal scales 10 mm long, narrow; sterile frond tripartite, broadly deltoid-pentagonal in outline; terminal lamina deltoid, deeply multi-lobed, the lobes all entire, acute to acuminate, the lower ones slightly reduced or in the largest fronds elongate and deeply lobed; pinnae opposite or nearly so, to 16 cm long, short-stalked, deeply lobed, the basal bispinose lobe to 9 cm long, asymmetric, wider and more deeply lobed on its bispinose side, a bud present at the base of each pinna; veins forming areoles along costa of lobes of apical lamina and of pinnae, sometimes with additional areoles below sinuses between lobes; lower surface of costa variously hairy, hairs on some Sumatran specimens more than 1 mm long, usually shorter or lacking; upper surface always densely short-hairy on costa, between veins scattered thick hairs variously abundant; fertile frond shaped as sterile but all parts narrow; venation of very narrow areoles; sporangia abundant all along veins; spores with very thin translucent wing; n = 40 (Walker). — Fig. 12e.

Distribution — Throughout Malesia except for the Malay Peninsula; Solomon Islands, New Hebrides.

Habitat — In most cases reported as growing on rocky streambanks in forest, in some cases on limestone, also reported terrestrial in forest.

Variability — Some specimens are very small; one such was named var. minor by Christ [Verh. Naturf. Ges. Basel 11 (1895) 252, type from limestone in Celebes] but it is not clear whether the dwarf form is constant; experiment is needed. Polybotrya cicutaria Blume was described from a sterile frond which has very narrow lobes.

Probable hybrids: see 4. Tectaria ramosii.


Aspidium immersum Hook., Sp. Fil. 4 (1862) 58, non Blume 1828. — Type: Wallach s.n. (K).


Aspidium zollingerianum auct.: Bedd., Ferns Brit. India (1867) t. 251 (non Kunze 1846).

Caudex short-creeping or suberect, bearing dimorphic fronds with occasional intermediates; stipe castaneous, longest on fertile fronds, its basal scales to 8 mm long, firm with fragile margins; sterile lamina to c. 30 cm long with 3 or 4 pairs of pinnae and a deeply lobed terminal lamina; basal pinnae to 20 cm long, usually with 1 pair (rarely 2 or 3) of pinnules, the basal bispinose one to 12 × 3 cm, lobed 1/3 towards its costa; middle pinnae lobed to at least halfway to their costa, the lobes oblique, obtuse; veins forming narrow areoles along costa of pinnae and costules of lobes with additional oblique areoles a few of which have an included free veinlet; short hairs present on both surfaces of costae and costules, also some on upper surface near margins; pinnae of fertile fronds ± contracted and more deeply lobed, the venation ± modified with absence of regular costular areoles; sori mostly at the ends of free veins in areoles, variably impressed (most deeply where the lamina is most constricted), indusia large, firm.
Distribution – NE India & S China southwards to Peninsular Thailand; in Malesia known only from 2 collections, one from Langkawi ls. and one from Sumatra (type of Aspidium prominens, probably Pulau Weh).

Habitat – Usually on limestone in forest.

Note – Wallich cited 3 localities for his no 379: Amherst, Tavoy and Penang. The Penang specimen in his herbarium at Kew is T. brachiata (Z. & M.) Morton. Ching’s lectotype is unlocalized. A specimen of Wallich 379 from Tavoy in Herb. Hooker is a syntype of T. barbieri (Hook.) Copel. Matthew collected other specimens on limestone on Pulau Weh in January 1912.


Aspidium kunstleri Bedd., Handb. Ferns Brit. India Suppl. (1892) 44; Alderw., Malayan Ferns (1908) 236. — Type: Kunstler 405, Perak, Gopeng (K).


Caudex short, erect, its apex covered with stiff brown scales 15 x 1.5 mm; fronds of young plants 3–5–lobed, of older ones with a trilobed apical lamina and a pair of bilobed acuminate pinnae, all lobes entire; fronds of mature plants with stipe to 70 cm long and lamina to 50 cm long, stipe and rachis dark brown and bearing short erect hairs; pinnae to 7 pairs; basal pinnae commonly to 18 cm long, stalked (stalk 2 cm), deeply lobed on the basiscopic side, with basal lobe to 12 cm long, shallowly lobed on acroscopic side; middle pinnae with ± sinusous margins or irregularly lobed on the largest fronds; main veins in pinnae 8–10 mm apart, smaller veins anastomosing between them with many excurrent free veinlets in the areoles; sori small, mostly at the ends of short veinlets in areoles, when very young having (at least in some cases) small reniform indusia but later appearing exindusiate; tetraploid (Manton in Holttum 1955).

Fig. 12h, i.

Distribution – Southern Burma and Thailand; in Malesia: Sumatra, Malay Peninsula, Borneo, Sulu Archipelago.

Habitat – In lowland forest.

Notes – Hooker cited three syntypes for Polypondium barbieri: Wallich 379 from Tavoy, Wallich s.n. from Penang and Barber s.n. from Borneo. The Tavoy specimen was part of the material named Aspidium variolosum by Wallich. The types of A. kunstleri Bedd. and Phegopteris polycarpa Mett. are unusually large specimens. Mettenius noted the resemblance of the latter to A. barbieri Hook.; Christensen saw the type and confirmed to me that it is not distinct.

Manton found a plant from Singapore to be tetraploid. Experiment is desirable to indicate the relationship of this species to others; if it is allotetraploid, one parent is probably T. impressa.


Aspidium beccarianum Baker, Malesia 3 (1886) 43; Alderw., Malayan Ferns (1908) 238. — Aspidium cesatianum C. Chr., Index Filic. (1905) 68, nom. nov. superfl. — Tectaria cesatiana (C. Chr.) Copel., Philipp. J. Sci. 6 (1911) Bot. 76; ibid. 78 (1951) 416, nom. illeg. — Type: Beccari s.n., Andai, W New Guinea (Fl).

Aspidium ledermannii Brause, Bot. Jahrb. Syst. 56 (1920) 114. — Tectaria ledermannii (Brause) C. Chr., Index Filic. Suppl. 3 (1934) 181. — Type: Ledermann 9409, NE New Guinea (B).


Fig. 12. Tectaria manilensis (Presl) Holttum. a. Complete frond, × 0.33; b. venation at base of upper (adnate) pinna, undersurface, × 2.6; c. thick hairs on upper surface of lamina between veins, × 33. — T. laxa (Copel.) Price. d. One tertiary leaflet, × 2.2. — T. aurita (Sw.) S. Chandra. f. Whole frond, × 0.33; e. sterile and fertile fronds, × 0.26. — T. bamleriana (Rosenst.) C. Chr. g. Venation of an acroscopic lobe, × 1.7. — T. barberi (Hook.) Copel. h. Venation of a fertile pinna, × 1.7; i. venation of a sterile pinna, × 1.7 (a–c: Smith 3054; d: Price 3345; e: Croft 1682; f, g: Ratcliffe 188; h, i: Piggott 2968).
*Caudex* erect, its apical scales firm, to 10 × 1 mm, similar scales at base of stipe, those above base very narrow; *stipe* and rachis dark, glossy on abaxial surface; *lamina* to 30 cm long, variably ± dimorphous in fronds of the same collection; *pinnae* to 3 pairs; apical lamina deltoid, very deeply lobed, the larger lobes lobulate; *basal pinnae* short-stalked, to 18 cm long, lacking free pinnules, basal basiscopic lobes to 8 cm long deeply lobed when fertile; middle pinnae sessile, very deeply lobed, the lobes lobulate or crenate, widest on sterile fronds with narrow sinuses between them, narrower with wider sinuses when fertile, a *bud* present on the acroscopic margin near base of a pinna; *veins* not distinct on lower surface, forming narrow costal and costular areoles and other ones about as in *T. impressa*, included veinlets usually few; *lower surface* of pinnae glabrous or with sparse minute hairs on veins; upper surface of costae densely short-hairy, a few thick hairs present between veins near margin; *venation of fertile pinnae* usually less complex, the sori in one row on each side of costules in pinna-lobes; indusia to nearly 1 mm diameter, reniform, dark, firm, sometimes bearing short hairs. – Fig. 12g.


Habitat – In lowland forest, twice reported growing among rocks, in one case on limestone (Manus Is.), once at 1100 m on a steep ridge.

Note – The Ceram specimen is apparently a young plant; the fronds have only one pair of pinnae but the largest is fertile.


*Caudex* and bases of stipes lacking; *stipe* and rachis very dark, glossy, bearing throughout many narrow light brown scales; *lamina* incomplete, probably 50 cm long with c. 4 pairs of pinnae; apical lamina 20 cm long, lobed to a narrow wing, lobes to 10 pairs, lowest 8 × 1.5 cm, deeply obliquely lobulate; *basal pinnae* 28 cm long (stalk 3 cm) with 1 pair free pinnules and 1 pair adnate, basal basiscopic pinnule 17.5 × 7 cm bearing one free tertiary leaflet, the rest lobed to a narrow wing, the lobes close, oblique and deeply lobulate; *veins* distinct on lower surface, forming costal and costular areoles, other areoles below sinuses few; *lower surface* glabrous apart from sparse minute hairs on costae and costules; dense short hairs present on upper surface of costae and a few hairs near sinuses; *sori* on free veins near apices of pinna-lobes, otherwise on anastomosing veins; *indusia* rather large, thin, glabrous.

Distribution – *Malesia*: W New Guinea (known only from the type.


**KEY TO THE VARIETIES**

1a. Basal pinnae with 1 pair of pinnules . . . . 2
1b. Basal pinnae with 5 pairs of pinnules

2a. Veins amply anastomosing in fertile fronds

a. var. *amplissima*

2b. Veins all free in lobes of fertile pinnae

b. var. *singaporeana*

a. var. *griffithii*

*Caudex* erect, its apex covered with scales to 20 mm long, 2 mm wide at the base; *stipe* to 60 cm long, dull dark brown, bearing many very narrow
scales throughout; lamina deltoid-pentagonal, to 60 cm long and wide; free pinnae 2–4 pairs, widely spaced; basal pinnae commonly 30 cm long (to 45 cm) with 1 pair of free pinnules, the rest lobed to 5–10 mm from the costa, the costules 3–4 cm apart, the lobes acuminate; basal basiscopic pinnule to 20 × 6 cm, widest in the middle, deeply lobed with costules 1.5 cm apart, lobes falcate, acute, entire; acroscopic pinnule to 10 × 2.8 cm, shallowly lobed; second pinnae of large fronds sessile with one free pinnule; veins concolorous but distinct on lower surface, forming narrow costal and costular areoles, also other areoles below sinuses (often with short excurrent included veinlets) and an additional outer row in lobes of pinnae, costular areoles not formed in distal parts of lobes of fertile pinnae; lower surface glabrous or sparsely hairy on costae and costules, usually with some narrow scales; upper surface of costae and costules densely covered with short thick hairs, groups of similar hairs present near margins or at sinuses; sori on free veins in areoles near base of pinna-lobes, on acroscopic branches of quite free veins distally; indusia large, firm, persistent.

Distribution – Assam (Khasia Hills), Burma, Vietnam, Thailand; in Malesia: N Sumatra, Malay Peninsula, W Java, Borneo, Celebes, Philippines (Luzon to Mindanao).

Habitat – In lowland forest, sometimes near limestone.


Differs from the type of the species because the veins in the lobes of the fertile pinnae are totally free. Anastomosis in sterile pinnae is also much less than in var. griffithii, the outer row of areoles in lobes being lacking.

Distribution – Malesia: Singapore (known only from Bukit Timah).


Pinnae to 12-jugate, the lowermost 50 cm long provided with 6-jugate pinnules, the lowermost basiscopic pinnules provided with 3-jugate tertiary leaflets; rachis and costae beneath densely short hairy.

Distribution – Malesia: Sumatra (known only from the type collection).


Caudex erect; frond with stipe 200 cm long, the stipe 80 cm (collectors); rachis dark brown, glabrescent and glossy on abaxial surface, hairy adaxially; basal pinnae not seen, suprabasal pinnae subsessile, to 42 cm long, bearing 12 pairs of sessile free pinnae and 3 or 4 pairs adnate; pinnules 2.5 cm apart, to 8.7 × 1.7 cm, lobed to 1 mm from the costa, lobes oblique, little more than 2 mm wide and separated by wider sinuses, their margins crenate, apices obtuse, basal basiscopic and acroscopic lobes subequal and not reduced; veins forming narrow areoles along costae of pinnales, those in the lobes all free, a forked one corresponding to each crenature; upper surface of costae of pinnales densely short-hairy near the base only, lower surface bearing a few narrow scales; sori on acroscopic branches of veins, apparently terminal; indusia dark, firm, glabrous.

Distribution – Malesia: New Guinea (known only from the type collection).

Habitat – In forest, at 950 m.


Caudex erect or ± prostrate; stipe to 45 cm long, castaneous, adaxially glabrous apart from scales; basal scales to 20 mm long and more than 2 mm wide; lamina to 40 cm long; pinnae to 4 pairs free and 3 pairs ± adnate; apical lamina small; basal pinnae to 30 cm long, free pinnales to 4 pairs, basal basiscopic pinnule to 17 cm long with 2 pairs of deeply lobed tertiary leaflets (largest 3.5 × 1.7 cm) and 2 pairs adnate; basal pinnales on second pair of pinnae bearing 1 pair of tertiary leaflets; pinnales on middle pinnae very deeply lobed with ± crenate lobes; veins forming costal and costular areoles, usually no additional areoles below sinuses between pinna-lobes; lower surface almost glabrous; upper surface of rachis and pinna-
rachises densely short-hairy, surface between veins bearing very few hairs except near sinuses; sori mostly at the ends of acroscopic branches of veins in pinnule-lobes, marked by prominences on the upper surface; indusia thin, at first covering sori, shrivelling later and then not conspicuous.


Ecology — In lowland forest, on steeply sloping ground, in one case on limestone.


Caudex erect; stipe at least 40 cm long, dark, glabrescent on abaxial surface, bearing many narrow mid-brown scales throughout, similar scales also present on rachis and on costae of pinnae; lamina to 50 cm long; free pinnae 3 pairs and 2 pairs adnate; basal pinnae to 23 cm long (stalk 7 mm) bearing 1 pair of free or adnate pinnules; basal basiscopic pinnules 12 × 3 cm, lobed to 3 mm from their costae, costules of lobes to 12 mm apart, lobes 8 mm wide, deeply crenate, obtuse, basal acroscopic pinnule 5 cm long, rest of basal pinnae lobed to 2–3 mm on each side of their costae; suprabasal pinnae almost sessile, deeply lobed with oblique obtuse deeply lobulate lobes; veins forming costal and costular areoles with few additional areoles below sinuses; lower surfaces glabrous or nearly so apart from scales; thick hairs present between veins on upper surface; sori mostly on acroscopic branches of free veins in pinna-lobes; indusia small and apparently caducous.

Distribution — Malesia: Papua New Guinea (also known from Milne Bay Prov.).

Habitat — The type from forest on exposed summit ridge at 1100 m; the Milne Bay specimen from forest at 430 m.


Caudex apparently short-creeping with tufted fronds; stipe 20–30 cm long, ferrugineous, short-hairy, scaly near the base only, scales black, rigid, 7 mm long, less than 1 mm wide; lamina to 20 cm long, consisting of 2 pairs of pinnae and a deeply lobed apical section 12 cm long, dark rusty brown when dried; basal pinnae of type 8 cm long (stalk 2 mm), acuminate, lobed to 4–5 mm from its costa, basal basiscopic lobe 6 × 1.5 cm and shallowly lobulate, the other lobes subentire, of Ramos 4710 to 20 cm long; upper pinnae slightly adnate, lobed halfway to costa, lobes oblique, rounded; veins forming narrow areoles along costae and costules, also a second series below sinuses and in broader lobes; many very short erect hairs between veins on both surfaces; sori mostly on the outer veins of costal and costular areoles; indusia small, bearing short hairs, soon caducous.

Distribution — Malesia: Philippines (known from the type and 2 collections from Zambales Province, Luzon).


Caudex short-creeping; stipe to 20 cm long, slender, castaneous, glabrescent on abaxial side; basal scales to 8 × 1 mm, thin, light brown; lamina of type 28 cm long, consisting of apical section and 2 pairs of pinnae; apical section 21 cm long, deltoid, lobed to 5–6 mm from its axis, basal lobes 8 × 2.7 cm, obliquely lobulate halfway to costa, the lobules broadly rounded; upper pinnate adnate, 9 × 3.5 cm, lobed halfway to costae, lobes slightly crenate with rounded apices, apex acute, not acuminate; basal pinnae 13 cm long, lobed to 5 mm from costae, the lobes ± overlapping, basal basiscopic lobe 6.5 × 3.3 cm, deeply lobulate with crenate lobules and a very obtuse apex; acroscopic lobes all about equal, oblique, 3 × 1.5 cm; veins forming costal and costular areoles, also several additional ones below sinuses and an outer row in pinna-lobes; lower surface of costae bearing slender hairs to 1 mm long, short erect hairs present on and between veins; upper surface bearing copious short hairs between veins; sori in one row on each side of main veins in pinna-lobes, on the outer veins of areoles or on short veins within the second row of areoles; indusia large, thin, glabrous.
Distribution – North Thailand; Malesia: Philippines (Luzon), Borneo (Sabah; one collection).

Habitat – In Luzon on limestone at 1500 m (type) and near a waterfall; in Sabah pendulous on rocks by stream at 1000 m.

Note – This is very near T. coadunata but appears to differ constantly in lack of pinnules on basal pinnae and in closely shallowly lobed non-acuminate upper pinnae. The largest Luzon specimen has a lamina 38 cm long, basal pinnae 19 cm.


KEY TO THE VARIETIES

a. var. devexa

Caudex short, suberect; stipe to 30 cm long, slender, light castaneous, glabrescent; basal scales to 10 mm long, less than 1 mm wide; lamina to 35 cm long, thin; pinnae 3–5 pairs; basal pinnules to 18 cm long (stalk 1.5 cm) with 1 pair of free pinnules, basal basiscopic pinnule to 8 × 3.5 cm, very deeply lobed, the lobes lobulate up to halfway to their costules, basal one sometimes almost free; upper pinnae adnate on the basiscopic side, lobed as pinnules of basal ones, costae of lobes to 10 mm apart; veins forming costal and costular areoles, additional ones below sinuses few; lower surface of costae bearing hairs 0.5 mm long, whole lower surface on and between veins bearing many very slender shorter hairs; upper surface similarly hairy with thicker hairs; sori near the margins of lobules of pinna-lobes, mostly on the acrosopic branches of free veins; indusia thin, glabrous or with short hairs; n = 40 (Manton in Holttum 1955). – Fig. 11b, f.

Distribution – Southern Burma and Thailand; Malesia: Western Malesia, Central and SW Celebes, Philippines. Specimens from Taiwan, SW China and Tonkin have sparse longer hairs on the upper surface but are otherwise similar.

Habitat – Always on limestone, usually at the base of rocks.

Taxonomy – The first description of this species (as Aspidium intermedium) was by Mettenius in 1838, with citation of A. devexum as a synonym; the latter name was not validated until 1864, almost simultaneously with the publication of A. membranaceum Hook.


Frond-form and size as var. devexa, differing in almost glabrous lower surface between veins and sparse thick hairs 0.5 mm-long between veins on upper surface.

Distribution – Sri Lanka, Christmas Island (Indian Ocean).

The type plant cultivated at Kew was found by S. K. Roy to be tetraploid [Blumea 13 (1965) 135]. Brass 32188, from a neighbouring locality, has larger fronds with lamina to 40 cm long and regular pluriserrate areoles below sinuses; its highest pinnae have costules of their crenate lobes 12 mm apart; costules of upper pinnae of var. devexa of comparable size are 6 mm apart.


*Tectaria gymnocarpa* Copel., Philipp. J. Sci. 9 (1914) Bot. 4; ibid. 78 (1951) 415. — Type: *G. King 401*, Papua, Loane (MICH).

Frond-form as *T. kingii* but basal pinnae shorter (to c. 25 cm), their basal basiscopic pinnules bearing at most one pair of adnate tertiary leaflets; veins often forming additional areoles below sinuses in sterile fronds, not in fertile ones; hairs always present on lower surface of costae, costules and veins, variable, sometimes to 1 mm long, few or none between veins; hairs on upper surface between veins abundant, at least 1 mm long (to 1.5 mm); sori exindusiata, usually rather large and slightly irregular in shape.

Distribution — Malesia: widely in New Guinea (only the type from the West); Solomon Islands. Habitat — In forest from low altitudes to 2000 m, twice recorded on limestone. Plants found at higher altitudes appear to be more hairy on both surfaces, with longer hairs, than those from low altitudes, and to have smaller fronds.

Note — The types of *Pleocnemia membranacea* var. *novoguineensis* and *Tectaria gymnocarpa* both have fewer and shorter hairs on the abaxial side of rachises than most other specimens and fewer thick hairs between veins on the upper surface; they are thus nearer to *T. kingii*.


Note on the species — In the North of India Clarke distinguished two varieties, one with large fronds glabrous on the lower surfaces and one somewhat smaller with fronds hairy beneath. He wrongly called the latter var. *coadunatum*; it is variable and has not been clearly distinguished. In northern Thailand, on limestone, there is a more densely hairy form which may represent a distinct variety.

KEY TO THE VARIETIES

1a. Basal pinnae of mature plants to 50 cm long, pinnate; those of small plants deeply lobed but not pinnate

b. Var. *coadunata*  

2. Basal pinnae to 15 cm long, pinnate

b. Var. *minor*  

a. Var. *coadunata*  

Fronds large, with basal pinnae to 50 cm long bearing a pair of free pinnules; lobes of pinnae and
pinnules very broad; veins forming costal and costular areoles lacking free included veinlets and many other areoles, some with short included veinlets; lower surfaces glabrous, thick hairs present between veins on upper surface.

Distribution – NE India, SW China, N Thailand.

— Tectaria macrodonta auct.: Holttum, Revis. Fl. Malaya 1, 2 (1955) 505, quoad plantas peninsulares. — Type: Henderson SF 21383, Pulau Langkawi (K; SING).

Caudex short-creeping; stipe to 50 cm long, its base swollen and persistent; basal scales thin, to 5 mm long; lamina of type 26 cm long consisting of 3 pairs of pinnulae and a deeply lobed deltoid apical portion 15 cm long (its lowest lobes 5.5 x 1.5 cm); basal pinnulae 15 cm long (stalk 10 mm), their basal basiscopic pinnules 9 x 2 cm, lobed halfway to the costa, the lobes obtuse, basal acrosopic pinnules 3.5 x 1.4 cm; suprabasal pinnulae sessile, deeply lobed, the lobes falcate, obtuse, the larger ones with sinuous margins; hairs 0.2 – 0.3 mm long present on lower surface of costae and a few very slender ones between veins, many thicker hairs present between veins on upper surface; sori mostly on free veins in outer areoles, marked by depressions on the upper surface when dried; indusia rather large, glabrous.


Habitat – On limestone.


Caudex short, erect; stipe to 50 cm long; basal scales to 15 x 1 mm, those above base gradually shorter, very narrow scales present on abaxial surface of both stipe and rachis, hairs 0.5 mm long also on rachis; lamina to 60 cm long consisting of 3 – 5 pairs of pinnulae and a terminal portion c. 15 cm long; basal pinnulae to 28 cm long (stalk 3 – 5 cm) bearing 3 or 4 pairs of pinnules with a deeply lobed apex like that of the lamina, basal basiscopic pinnule to 12 cm or more long, broadly lobed to 3 – 5 mm from its costa with 1 or 2 tertiary leaflets to 5 x 1.5 cm lobed halfway to the costule; first suprabasal pinnulae with 1 pair of free pinnules; lobes of fertile pinnulae and pinnules narrower than sterile; veins prominent on both surfaces, forming additional areoles below sinuses in less deeply lobed parts of pinnulae: rather sparse hairs up to 1 mm long present on lower surfaces of costae and costules, also scattered on veins, thick hairs more than 0.5 mm long, scattered between veins on upper surface; sori in a row halfway between costules of lobes and margin, the lower ones on short veins in areoles, distal ones on free veins; indusia rather large, glabrous, shrivelling when old.

Distribution – Malesia: NE New Guinea; Solomon Islands (Bougainville).

Habitat – In forest at 500 – 600 m.

Section Tectaria

Taxonomy — The generic names Hemigramma Christ and Quercifilix Copel., cited as synonyms above, call for comment. The sterile and fertile fronds of the types of both genera are strongly dimorphous, the sterile ones having venation as in Tectaria sect. Tectaria, the fertile ones having a greatly contracted lamina with simplified venation and sporangia borne all along the veins, giving an acrostichoid appearance.

Christ established the genus Hemigramma (1907) for a Java fern originally named Hemionitis zollingeri Kurz (Tectaria zollingeri here) with the allied Philippine species (here named Tectaria hilocarpa) as a variety. Copeland (1928) added other species, two of which (from Hong Kong and Tonkin) have broader fertile pinnule in which the venation, though contracted, is normal for Tectaria sect. Tectaria; these two are not nearly related to the type of Hemigramma. All these ferns, including the type of Quercifilix, represent different modifications of fertile fronds which have evidently arisen on different evolutionary
lines. The Philippine *Tectaria hilocarpa* hybridizes naturally with *Tectaria crenata*. Copeland in 1928 also included in *Hemigramma* the very different species here named *Chlamydomgramme hollrungii*, not noticing its peculiar indusia.

The vein-pattern in sect. *Tectaria* is closely similar to that in several genera of *Polypodiaceae*; this appears to be a remarkable example of parallel evolution.

**KEY TO THE SPECIES OF SECTION TECTARIA**

1a. Fronds pinnate or bipinnate, or elongate and lobed to a winged rachis ................................. 2  
   b. Fronds simple, not elongate if deeply lobed ................................................................. 74  
2a. Rachis not wholly winged .................................................. 3  
   b. Rachis wholly winged (also part of stipe) or the wing not quite continuous in mature plants ............................... 61  
3a. Suprabasal pinnae deeply lobed or pinnate in fronds of mature plants ................................. 4  
   b. Suprabasal pinnae, if any, entire or nearly so in fronds of mature plants; pinnules, if any, narrow, entire or nearly so .................................................. 19  
4a. Rachis very dark and at length glossy ............................................................................... 5  
   b. Rachis not very dark nor at length glossy ................................................................. 12  
5a. Sori small, irregularly scattered ..................................................................................... 6  
   b. Sori larger, in one row on each side of main veins or of costules near apices of pinna-lobes ................................. 9  
6a. Indusia small; sori not confluent .................................................................................. 7  
   b. Indusia lacking; sori sometimes confluent .............................................................. 30. *T. simonsii*  
7a. Thick hairs on upper surface confined to sinuses ................................................................ 8  
   b. Thick hairs between veins generally on upper surface ........................................... 29. *T. holltumii*  
8a. Lobes of basal pinnae deeply lobulate ........................................................................ 27. *T. melanocaula*  
   b. Lobes of basal pinnae entire or nearly so ............................................................. 28. *T. nebulosa*  
9a. Suprabasal pinnae shallowly lobed apart from the acute basal lobes ................................. 31. *T. durvillei*  
   b. Suprabasal pinnae deeply lobed with acute to acuminate lobes ................................. 10  
10a. Basal pinnae of largest fronds 30 cm or more long bearing at most 1 pair of pinnules; suprabasal pinnae lacking pinnules ................................................................. 11  
   b. Basal pinnae of largest fronds less than 30 cm long, bearing 2 pairs of pinnules; 2 pairs of suprabasal pinnae each with 1 pair of pinnules .................................. 34. *T. athyriosora*  
11a. Basal pinnae to 30 cm long; lower surface of costae and veins bearing hairs more than 0.5 mm long ................................................................. 32. *T. melanorachis*  
   b. Basal pinnae to 60 cm long bearing a pair of stalked pinnules; all parts of lower surface bearing minute hairs with spherical tips ........................................... 33. *T. danfuensis*  
12a. Fronds strongly dimorphous; sterile pinnae broad and shallowly lobed ................................. 35. *T. brachiata*  
   b. Fronds not strongly dimorphous; pinnae deeply lobed .................................................. 13  
13a. Sori all near margins of pinna-lobes ............................................................................... 36. *T. calcarea*  
   b. Sori mostly not near margin ................................................................................. 14
14a. Some sori on free veinlets in areoles, or on branches of free veins near apices of pinna-lobes .................................................. 15
b. Sori all on connected veins ............................................. 17

15a. Basal pinnae to more than 30 cm long; lobes of upper pinnae acuminate and deeply lobed .................................................. 37. T. curtisi
b. Basal pinnae shorter; lobes of upper pinnae obtuse, at most crenate .......... 16

16a. Basal scales 7 × 1.5 mm, thin, light brown; lamina very firm ..... 38. T. cherasica
b. Basal scales to 15 × 1 mm, firm, dark; lamina thin, translucent

39. T. translucens

17a. Sori indusiate; basal acroscopic lobes of pinnae not longer than the next lobes .. 18
b. Sori exindusiate; basal acroscopic lobes of pinnae much elongate 42. T. macrota

18a. Thick hairs lacking between veins on upper surface; indusia glabrous
b. Thick hairs present between veins on upper surface; indusia fringed with hairs 41. T. villosa

19a. Basal pinnae bearing narrow pinnules ........................................... 20
b. Basal pinnae lacking free pinnules ........................................... 23

20a. Caudex long-creeping; lamina to 80 cm long ................... 43. T. semibipinnata
b. Caudex short, erect; lamina much shorter ......................... 21

21a. Lamina to 25 cm or more long; pinnae 2–4 pairs, pinnules entire or minutely denticulate; rachis hairy on upper surface .................................................. 22
b. Lamina to 10 cm long; pinnae 1 pair, deeply crenate-lobate, each with 1 pinnule; no hairs on rachis .................................................. 46. T. subdigitata

22a. Distal parts of lower pinnae entire; almost all sori in 2 rows between main veins
b. Distal parts of lower pinnae irregularly obliquely lobed; sori small, numerous, irregularly scattered 45. T. jacobsii

23a. Fertile pinnae much contracted, covered beneath with sporangia ..................... 24
b. Fertile pinnae not very narrow, most sori distinct ..................... 25

24a. Pinnae of fertile frond 1 pair, c. 1 cm long ..................... 47. T. zeilanica
b. Pinnae of fertile frond several pairs, much longer ................ 48. T. lombokensis

25a. Fertile pinnae to 1.5 cm wide, sterile to 3.5 cm ................... 49. T. teratocarpa
b. Fertile pinnae much wider where fronds are dimorphous .................. 26

26a. Pinnae (including basal ones) all narrowly decurrent .................. 27
b. Pinnae not all narrowly decurrent ........................................... 28

27a. No buds at bases of pinnae; indusia very small, not distinct on mature sori
50. T. subcaudata
b. Buds present at bases of pinnae; indusia distinct .................. 51. T. fauriei

28a. A large acuminate lobe present on acroscopic base of pinnae, at least on basal ones
42. T. macrota
b. Acroscopic basal lobes lacking ........................................... 29

29a. Sori irregularly arranged, some elongate or coalescent .................. 30
b. Sori not coalescent, or if so in 2 rows between main veins ................ 33
30a. Suprabasal pinnae narrowed at their bases ........................................ 31
   b. Suprabasal pinnae with broadly rounded to cordate bases .................. 32
31a. Sori mostly not confluent, some with small indusia; buds present at bases of upper pinnae ........................................ 52. T. suluensis
   b. Sori mostly confluent, no indusia, no buds ................................. 53. T. semipinnata
32a. Many sori running along veins; no indusia ...................................... 54. T. sumatrana
   b. Sori all on free veinlets in areoles, none linear; small indusia present 69. T. angulata
33a. Sori near margins only; pinnae 1 pair ........................................ 55. T. craspedocarpa
   b. Sori not only near margins; pinnae more than 1 pair ....................... 34
34a. Sori in 1 row on each side of main veins, or with occasional additional ones especially near costae ............................... 35
   b. Sori not only in 1 row on each side of main veins .......................... 51
35a. Sori on free veinlets in areoles .................................................. 36
   b. Sori not all on free veins in areoles ......................................... 46
36a. Sori much elongate ................................................................. 56. T. dolichosora
   b. Sori not or little elongate ...................................................... 37
37a. Areoles in fertile pinnae each with a single veinlet ......................... 38
   b. Areoles in fertile pinnae mostly containing forked veinlets .............. 39
38a. Basal pinnae unlobed; indusia not peltate .................................... 57. T. pleiosora
   b. Basal pinnae lobed; indusia peltate ......................................... 58. T. repanda
39a. Stipe and rachis dark and glossy .............................................. 40
   b. Stipe and rachis not dark and glossy ........................................ 43
40a. Pinnae not auricled on acroscopic side ....................................... 41
   b. Pinnae auricled on the acroscopic side .................................... 31. T. durvillei
41a. Pinnae commonly 25 cm long; basal scales 1.5–3 mm wide .................... 59. T. crenille
   b. Pinnae to 17 cm long; basal scales not over 1 mm wide .................... 42
42a. Basal scales not contorted; middle pinnae to 3 cm wide ...................... 60. T. isomorpha
   b. Basal scales much contorted; pinnae to 5 cm wide .......................... 61. T. exauriculata
43a. Basal pinnae bearing at least 1 large basiscopic lobe ....................... 44
   b. Basal pinnae unlobed ............................................................. 57. T. pleiosora
44a. Bases of pinnae broad, cordate on basiscopic side ........................... 62. T. brevilobata
   b. Bases of pinnae subequally cuneate .......................................... 45
45a. Fertile pinnae 3–5 cm wide; indusia not peltate ................................ 59. T. crenille
   b. Fertile pinnae 2–3.5 cm wide; indusia peltate ................................ 58. T. repanda
46a. Fronds with a simple or trilobed apex and 1 pair of unlobed pinnae ........ 63. T. ternata
   b. Fronds mostly with several pairs of pinnae, basal ones lobed ............ 47
47a. Sori regularly spaced and separate ............................................. 48
   b. Sori irregular, often ± elongate and confluent ................................ 50
48a. Indusia large; bases of pinnae cordate on basiscopic side ................... 49
   b. Indusia very small; bases of pinnae cuneate to rounded both sides .......... 66. T. decastroi
49a. Stipes not very dark; basal pinnae with 2 basiscopic lobes ... 64. T. tabonensis
   b. Stipes nearly black; basal pinnae with one large basiscopic lobe
      65. T. subcordata

50a. Pinnae to 2 cm wide, no buds on rachis; sori often elongate or confluent parallel to main veins ........................................... 67. T. rufescens
   b. Pinnae wider; buds present at bases of pinnae; lower sori elongate at right angles to main veins 68. T. siifolia

51a. Caudex erect or suberect; stipes tufted ................................ 52
   b. Caudex long-creeping, fronds seriate .......................... 60

52a. Pinnae commonly 5 cm or more wide ................................ 53
   b. Pinnae not or little over 2 cm wide ............................ 58

53a. Buds present on upper surface of midrib of apical lamina or at bases of pinnae 54
   b. Buds lacking in either position .................................. 55

54a. Pinnae to 4 pairs; scales not twisted, few persistent above bases of stipes
      69. T. angulata
   b. Pinnae 1 pair; scales twisted, to 20 mm long, many persistent above bases of stipes
      70. T. croftii

55a. Pinnae 1 pair ...................................................... 56
   b. Pinnae to at least 3 pairs ....................................... 57

56a. Rachis very dark and glossy; apical lamina 5-lobed ............. 28. T. nebulosa
   b. Rachis otherwise; apical lamina 3-lobed ........................ 71. T. schmutzii

57a. Bases of pinnae narrowly cuneate ................................ 72. T. fissa
   b. Bases of pinnae rounded to subcordate on basiscopic side ... 73. T. polymorpha

58a. Pinnae to 5 pairs .................................................. 74. T. microlepis
   b. Pinnae 1 or 2 pairs ............................................... 59

59a. Buds present on upper surface of costa of apical lamina; small indusia present
      75. T. trifida
   b. Buds lacking; no indusia ......................................... 76. T. rheophytica

60a. Pinnae commonly to 3 cm wide, their bases narrowly cuneate
      77. T. menyanthidis
   b. Pinnae commonly 6 cm wide, their basiscopic bases rounded
      78. T. herpetocaulos

61a. Pinnae or pinna-like lobes of fertile fronds 3 mm wide, wholly covered beneath by sporangia ........................................ 62
   b. Pinnae or pinna-like lobes of fertile fronds much wider; sori distinctly separate ... 63

62a. Rachis-wing not quite continuous; one pair of pinnae present 79. T. taccifolia
   b. Rachis-wing quite continuous, decurrent below lowest lobes 101. T. hilocarpa

63a. At least the sori remote from costae in 1 row on each side of main veins; indusia conspicuous ........................................ 64
   b. Sori otherwise arranged; indusia in most cases small or lacking ............ 67

64a. All sori in a regular row on each side of main veins ............. 65
   b. Some additional sori, irregularly shaped and arranged, present between the two rows near the costa 58. T. repanda × 101. T. hilocarpa
65a. Unwinged stipe very short, winged part broad; lobes of lamina well-spaced

80. T. decurrens
b. Unwinged stipe longer, upper part of wing not broad; lobes of lamina not widely spaced ............................................. 66

66a. Fertile lobes of lamina to 20 x 2 cm ........... 80. T. decurrens hybrid
b. Fertile lobes of lamina to 30 x 6 cm .................... 81. T. sulitii

67a. Many sori ± confluent ........................................... 50. T. subcaudata
b. Sori not confluent ................................................. 69

68a. Sori indusiate, confluent ones a minority .............. 53. T. semipinnata
b. Sori exindusiate, confluent ones many, irregular .......... 53. T. semipinnata

69a. Indusia large with stiff hairs on them .................. 82. T. tricuspis
b. Indusia not thus hairy, small or lacking .................. 70

70a. Sori very numerous, each consisting of few sporangia; lower surface between veins hairy throughout .............. 83. T. schultzei
b. Sori larger; lower surface not hairy ....................... 71

71a. Sori indusiate; indusia small but conspicuous .......... 72
b. Sori exindusiate or with occasional rudimentary indusia .... 73

72a. Wing continuous throughout rachis and also most of the stipe; no buds

84. T. vasta
b. Wing formed by narrowly decurrent bases of pinnae, not continuous on mature plants; buds present on rachis near pinna-bases .................. 51. T. fauriei

73a. Lobes of frond narrowly acuminate .................. 85. T. grandidentata
b. Lobes of frond abruptly short-acuminate ............... 86. T. beccariana

74a. Fronds simple with a broad, often cordate base, entire or variously lobed ... 75
b. Fronds simple, in most cases unlobed, narrowed towards base .......... 92

75a. Lamina ± deeply lobed ........................................... 76
b. Lamina entire or crenate ........................................ 87

76a. Sori distinctly and persistently indusiate ............ 77
b. Sori exindusiate, or indusia minute ....................... 83

77a. Lamina hairy on all parts of lower surface of fertile fronds .......... 78
b. Lamina of fertile fronds glabrous on lower surface ........ 82

78a. Apices of lobes obtuse ........................................ 87. T. novoguineensis
b. Apices of lobes acuminate ................................... 79

79a. Sori near margin only .................................... 55 T. craspedocarpa
b. Sori generally distributed on fronds of mature plants ........ 80

80a. Stipe to 5 cm long; fronds not dimorphous; indusia bearing hairs

88. T. johannis-winkleri
b. Stipes to 20 cm long; fertile fronds contracted indusia not hairy

91. T. palmata var. dimorpha

81a. Lamina much longer than wide, near base lobed 1/3 way to costa; lobes contiguous and decrescent distally .............. 89. T. nitens
b. Lamina little longer than wide, near base lobed more deeply, the lobes widely divergent .......... 82
82a. Basal lobes narrowly acuminate, upcurved; sori irregular .......... 90. T. stalactica
b. Basal lobes spreading, not narrowly acuminate, sori uniform .... 91. T. palmata
83a. Fronds trilobed, lateral lobes lacking basal lobules ............... 84
b. Fronds 5-lobed, or 3-lobed with basiscopic lobules on lateral lobes 86
84a. Lateral lobes acuminate, similar in shape to apical lamina ........ 85
b. Lateral lobes very short, abruptly acute .......................... 94. T. subtriloba
85a. Lamina to 19 cm long; scales hair-pointed ........................ 92. T. filisquamata
b. Lamina to 28 cm long; scales not hair-pointed .................... 93. T. microchlamys
86a. Sori small, nearly all discrete, rarely coalescent, sometimes with small indusia
  91. T. palmata var. platanifolia
b. Sori often elongate along veins, exindusiata ..................... 95. T. christovalensis
87a. Lamina to 19 cm long; scales hair-pointed ........................ 87. T. novoguineensis
b. Lamina to 28 cm long; scales not hair-pointed .................... 96. T. minuta
88a. Both surfaces covered with short erect hairs ...................... 88. T. novoguineensis
b. Both surfaces glabrous ............................................. 96. T. minuta
89a. Surface between veins densely hairy on both sides ................ 97. T. labrusca
b. Surface between veins glabrous on both sides ..................... 90
90a. Free included veinlets present in areoles; sori mostly punctate 98. T. brooksii
b. Free veinlets rare in costal areoles; sori mostly elongate ...... 99. T. inopinata
91a. Fronds strongly dimorphous, fertile ones very narrow and at maturity almost covered beneath with sporangia .............. 92
b. Fronds, if dimorphous, having distinctly separate sori .......... 93
92a. Fronds, both sterile and fertile, unlobed (margins at most sinuous), sterile fronds glabrous beneath, fertile commonly 8 mm wide .......... 100. T. zollingeri
b. Fronds, both sterile and fertile, sometimes deeply lobed; sterile fronds hairy on veins beneath; simple fertile fronds and the lobes of others commonly 3 mm wide
  101. T. hilocarpa
93a. Sterile lamina to 20 × 1.5 cm (immature plant) ............... 43. T. semibipinnata
b. Sterile lamina proportionately much wider ...................... 94
94a. Fronds dimorphous; sori elliptic, 3–4 mm long, indusiata 102. T. kehdingiana
b. Fronds not or little dimorphous; sori otherwise ................ 95
95a. Unwinged stipe to 4 cm long .................................... 96
b. Unwinged stipe longer, at least on fertile fronds ................ 98
96a. Sori indusiata .................................................... 97
b. Sori exindusiata .................................................. 86. T. beccariana
97a. Sori in 1 row on each side of main veins ........................ 80. T. decurrens
b. Sori more numerous .............................................. 103. T. pandurifolia
98a. Caudex creeping (immature plants) ................................ 63. T. ternata
b. Caudex erect ........................................................ 99
99a. Margins of fronds entire; lamina of fertile fronds commonly 30 × 6 cm
  104. T. singaporeana
b. Margins of fronds sinuate-lobate; lamina of fertile fronds c. 18 × 3 cm
  105. T. rara


*Caudex* short, suberect; *stile* to 60 cm long, nearly black, at first minutely hairy, glabrescent; basal scales firm, to 12 × 2 mm; *lamina* of young plants ovate, cordate, deeply lobed; of mature plants to 60 cm long, consisting of apical lamina and 1–3 pairs of pinnae; apical lamina to 25 cm long, deeply lobed, the lobes acuminate, lowest ones deeply lobulate, base short-decurrent; *upper pinnae* sessile, deeply lobed, lobes acuminate on large fronds; middle pinnae to 25 × 11 cm, their costules 2 cm or more apart, lobes acuminate, crenate; *basal pinnae* to 30 cm or more long, sometimes bearing 1 pair of stalked pinnules, basal basiscopic pinnule or lobe 15 cm long, shaped as upper pinnae; sparse short hairs present on lower surface of costae and veins, a few also between veins; hairs on upper surface of costae dense, short, between veins only near the margin; *sori* small, scattered irregularly, mainly on short free veins in areoles; indusia small, glabrous, subreniform; spores minutely spinulose.

— Fig. 11c.

Distribution — Peninsular Thailand; in *Malesia*: Sumatra, Malay Peninsula, Java, Philippines (Luzon, Negros, Sulu Arch.), Sulawesi, New Guinea.

Habitat — On or among rocks (including limestone) or steeply sloping ground, in forest.

28. *Tectaria nebulosa* (Baker) C. Chr., Index Filic. Suppl. 3 (1934) 182. — *Nephrodium nebulosum* Baker, J. Bot. 18 (1880) 213. — *Aspidium nebulosum* (Baker) C. Chr., Index Filic. (1905) 84; Alderw., Malayan Ferns (1908) 246. — Type: *Beccari 575*, Ajer Mantjoer, W Sumatra, 360 m (Fl; iso K).

Fronds of immature plants similar to those of *T. melanocaula*, their stipes nearly black, lamina 5–7-lobed with entire lobes and cordate base; next stage with 5-lobed terminal lamina and 1 pair of bilobed pinnae, all lobes entire or nearly so; lamina of fronds of mature plants 55 cm long, pinnae 2 pairs, basal pinnae 28 cm long, their basal basiscopic lobes to 14 × 4 cm very shallowly bluntly lobulate, upper pinnae lobed not more than half-way to their costae; lower surface almost glabrous on all parts; sori small and very numerous, much as in *T. angulata* (Willd.) Copel. but not all on free veinlets, indusia distinct, about as in *T. melanocaula*.

Distribution — *Malesia*: Sumatra (known only from 3 collections from the Padang Highlands).

Note — The Kew isotype consists of 2 fertile fronds, each with 5-lobed apical lamina and 1 pair of forked basiscopic pinnae. C.G. Matthew collected specimens with sterile 5-lobed lamina in the Anai Kloof and one frond of mature size (above described) on Bukit Siboga near Padang Panjang. The latter is intermediate between *T. melanocaula* and *T. angulata* in frond form and in sori; it differs from *T. angulata* in its 5-lobed apical lamina lacking buds and in the lobing of its pinnae.


*Stipe* and rachis very dark, at first rather copiously minutely hairy, glabrescent; *lamina* to 32 cm long, shaped as in *T. melanocaula* but the apical part cordate at its base and basiscopic pinnae not pinnate; *basal pinnae* to 20 cm long, their basal basiscopic lobes to 10 × 3 cm, lobulate less than half-way to their costae; lower surface of costae and veins bearing many slender hairs 0.5–1 mm long with shorter ones between veins; hairs on upper surface of veins short, hairs 1 mm long scattered between veins; *sori* similar in arrangement, size and indusia to those of *T. melanocaula*; spores not seen.

Distribution — *Malesia*: Borneo (Sabah), known only from the type collection and *Clemens 27313* (Dallas) and 29516 (Tenompok).
Habitat — The type was found on rocks (not limestone) near the river in a deep gorge; no habitat notes with the Clemens specimens.


Aspidium kwarenkoense Hayata, Icon. Pl. Formos. 8 (1918) 138. — Tectaria kwarenkoensis (Hayata) C.Chr., Index Filic. Suppl. 3 (1934) 181; DeVol, Fl. Taiwan 1 (1975) 344. — Type: Faurie s.n., Kwarenko, Taiwan (TI, not seen).

Caudex short-creeping to suberect; stipe to 50 cm long, very dark, glossy above the base, basal scales narrow, firm, very dark; lamina to 50 cm long, 'dark bluish green' when living, consisting of a deeply triobled apex and 1–3 pairs of pinnae; upper pinnae sessile, subentire, with ± dilated and auricled subcordate base; basal pinnae of large fronds stalked, to 24 cm long, with 1 pair of free pinnules like the upper pinnae or with falcate acute basal auricles, the distal part trilobed; main veins in pinnae upcurved, cross-veins irregular, small veins slender, prominent; hairs 0.1 mm long present on lower surface of costae, sparse and variable elsewhere; hairs on upper surface of costae short and slender, fewer on main veins, a few near margins; sori all on connected veins, small and unevenly arranged, often ± confluent, exindusiata; spores cristate or with many small irregular wings.

Distribution — NE India to SW China, southwards to Burma and Thailand; in Malesia: northern half of Malay Peninsula (3 collections), Borneo (one collection from Sabah).

Habitat — The Peninsula specimens were found on steeply rising ground or on 'ledges of rock-face' in forest at 600–750 m, the Sabah specimen on limestone rock in forest.

Note — The Sabah specimen differs in longer hairs on lower surface of costae and many short slender hairs between veins, also in the presence of small fragile indusia on some sori.

31. Tectaria durvillei (Bory) Holttum, comb. nov. — Aspidium durvillei Bory in Duperrey, Voy. Monde 1 (1828) 266. — Type: d'Urvilie s.n., Waigecou Is. at Offak (P; iso K).

Lastrea barclayi Carr. in Seem., Fl. Vit. (1873) 359.

— Nephroidium barclayi (Carr.) Baker, Syn. Fil. ed. 2 (1874) 504. — Tectaria barclayi (Carr.) C.Chr., Index Filic. Suppl. 3 (1934) 177. — Type: Barclay s.n., New Ireland (BM).


Tectaria papuana Copel., Philipp. J. Sci. 6 (1911) 76. — Aspidium papuanum (Copel.) Alderw., Malayan Ferns Suppl. (1917) 191. — Type: C. King 160, Papua (UC; iso BO).

Caudex suberect or short-creeping with tufted stipes; stipe very dark, to 40 cm long, minutely hairy, basal scales medium brown, not rigid, to 15 × 1.5 mm; lamina of fronds of young plants ovate-acuminate, then 3–5-lobed with cordate base, next stage with 3-lobed apical lamina and 1 pair of entire bilobed pinnae bearing also ± developed basal acrosopic auricles; lamina of fronds of mature plants very firm, to 40 cm long, consisting of a triobled apex and 3 pairs of pinnae; basal pinnae to 25 cm long, broadly crenate-lobate with one or more large basiscopic lobes and a narrower elongate acrosopic one, the basal lobes separately adnate on largest fronds; middle pinnae ± crenate-lobate, usually bearing an obtuse to acute acrosopic auricle; at least the midlobe of the apical lamina of the frond crenate-lobate; costae of pinnae dark at the base on the lower surface, paler distally, minutely hairy; main veins 6–7 mm apart, pale and prominent on the lower surface, variably short-hairy, as also surface between veins; upper surface minutely hairy on costae, hairs between veins few, very short, near margin only; sori in one row on each side of main veins, often with some additional ones near the costa, on free veins in areoles, in some specimens (including the type) distinctly impressed, always marked by prominences on the upper surface; indusia reniform, persistent, sometimes bearing short superficial hairs; spores cristate. — Fig. 18e.

Distribution — Malesia: widely in New Guinea; Solomon Islands.
Fig. 13. Tectaria brachiata (Zoll. & Moritzi) Morton. a. Fertile and sterile fronds, × 0.22. — T. melanorachis (Baker) Copel. b. Sterile frond, × 0.22. — T. durvillei (Bory) Holttum. c. Sterile frond, × 0.22. — T. keckii (Luerssen) C. Chr. d. Base of a fertile lobe (sori removed on right side), × 4. — T. curtisii Holttum. e. Lobe of a basal pinna (sori removed), × 6.6 (a: Matthew s.n., 3-1-1912; b: Hose 233; c: Sambui 9; d: 1962 Unesco Limestone Exp. 551; e: Curtis 3376).
Habitat – In lowland forest, especially near stream banks; small plants also collected in more exposed places on limestone.

Note – The many specimens indicate great variability. The type has rather large sori strongly impressed, and almost glabrous lower surfaces; there appears to be every gradation between this and smaller not-impressed sori. The specimens most hairy on the lower surface are from eastern New Guinea. The type of T. papuana has almost entire pinnae and strongly impressed sori. The type of Aspidium wendlandii consists of trifoliate fronds from immature plants.


Caudex short, erect; stipe very dark, to 50 cm or more long, copiously scaly at the base, scales to 20 mm long, little over 1 mm wide, firm, twisted, smaller narrower scales less abundant distally and on lower surface of rachis and costae of pinnae; lamina very similar in size and shape to that of T. melanocaula, differing as follows: lower surface of all axes of the frond, and veins, bearing hairs up to more than 0.5 mm long, similar shorter hairs ± abundant between veins; upper surface also bearing many short hairs between veins, also very small spherical glands; sori larger, in a row on each side of main veins in pinna-lobes (some additional ones present near costae of pinnae); indusia large, bearing slender hairs like those between veins on the lower surface; spores densely covered with very short spines. — Fig. 13b.

Distribution – Malesia: Borneo.

Habitat – Always on limestone.


Caudex erect; stipe dark, minutely hairy throughout, the basal 20 cm persistently scaly, the scales spreading and not rigid, to 20 × 1 mm; basal pinnae to 64 cm long, bearing one pair of short-stalked pinnules; basiscopic pinnule to 30 cm long and 6 cm wide, near its base lobed more than halfway to the costa, costules of lobes to 2 cm apart, lobes falcate, acute, entire; second pair of pinnules bearing 1 pair of adnate pinnules; apical part of frond and of basal pinnae more than 30 cm long, near its apex lobed to 2 cm from its axis, less deeply towards its base, the lobes almost contiguous and narrowly acuminate, the basal ones 5–6 cm wide, lobulate 1/3 towards their costae; lower surface of all parts bearing copious hairs not more than 0.1 mm long, the smaller ones appearing to be capitulate, the larger ones obuse; upper surface of costae and costules densely covered with hairs 0.2 mm long, no hairs between veins except near margin; sori rather large, in 1 row on each side of main veins in lobes of pinnae and of apical lamina, some additional ones also present near costae of pinnae, mostly on free veins in areoles, not forming prominences of the upper surface; indusia thin, rather irregularly reniform with minute marginal papillae; spores minutely and copiously spinulose.

Distribution – Malesia: New Guinea (New Ireland), known from the type and Jermy 7869 and 8006 (cult. R. B. G. Kew).

Habitat – The type from alluvial silt in water-channels of Danfu Valley, Jermy 8006 from a shady limestone rock-face.


Closely related to T. melanorachis, differing in firmer texture of fronds which are proportionately longer with more deeply lobed pinnae; lamina of largest frond 60 cm long, basal pinnae 25 cm long bearing 1 pair of stalked and 1 pair of adnate pinnales, basal basiscopic pinnule 14 cm long, acroscopic 8–9 cm long; two pairs of suprabasal pinnae each bearing one pair of sessile or slightly adnate pinnules; all veins rather strongly prominent on the lower surface; lower surface of pinna-midrib and main veins sparsely minutely hairy; upper surface of pinna-midrib densely very short-hairy, between veins ± abundant very short more slender hairs; sori rather large with large thin indusia, variable in form, the receptacle variably elongate (to more than 2 mm long); indusia often asymmetric at the base, glabrous with minutely papillose margin.
Distribution – Malesia: Philippines (Samar, probably also Bohol).
Habitat – On limestone.


Caudex short, suberect, scales to 5 mm long, medium brown, irregularly fringed with slender hairs when young; fronds strongly dimorphous. Sterile frond: stipe to 20 cm long, light castaneous, scaly near base only, short-hairy distally; lamina to 25 cm long; pinnae to 3 pairs; basal pinnae to 15 cm long, the largest bearing 1 pair of entire pinnules, rest of pinna deeply lobed near its base only; suprabasal pinnae shallowly lobed to subentire with rounded to subcordate base; apical lamina deltoid with few broad entire lobes; both surfaces minutely hairy on costae and main veins, marginal hairs on upper surface very few and short; veins amply anastomosing, with many free veilets, some branched, in areoles. Fertile frond: stipe to 50 cm long; lamina as sterile but all parts much contracted; basal pinnae to 10 cm long; sori all on free veinlets in areoles, impressed, with large thin entire indusia. — Fig. 13a.

Distribution – Peninsular Thailand; in Malesia: Malay Peninsula (north only), Java, Bawean, SE Sulawesi, Tanimbar Is.; N Queensland.
Habitat – The Peninsular specimens were found in rocky places but not on limestone; the type also from rocks (unspecified).


Caudex short, suberect, its scales to 5 mm long, entire; stipe to 30 cm long, medium brown, glabrescent abaxially, not glossy; lamina to 35 cm long, very firm; free pinnae to 8 pairs; basal pinnae to 17 cm long (stalks 2.5 cm) bearing 2 pairs of deeply lobed pinnules, the lobes obtuse, basal basiscopic pinnule 6 cm long, acrosopic 4 cm, apical part of pinna acuminate and deeply lobed like the frond apex; on largest fronds 2 or 3 pairs of suprabasal pinnae bearing a pair of pinnules; distal pinnae stalked and deeply lobed; veins slender and distinct on lower surface but not prominent; costae of pinnae minutely hairy on both surfaces near bases of pinnae only: marginal hairs on upper surface few and very small; sori large, in depressions near edges of pinna-lobes, mostly not on free veinlets; indusia large, persistent, glabrous.

Distribution – Malesia: Philippines (Leyte, Samar, Bohol).
Habitat – In forest on limestone and limestone-derived soils (Price & Hernaez 10, W Samar). Young plants with lamina of frond 6 cm long (pinnae 2 pairs) may be fertile.


KEY TO THE VARIETIES

1a. Upper pinnae lobed to 5 mm from their costae
   a. var. curtisii
   b. Upper pinnae lobed to 10 mm from their costae .................................. b. var. hendersonii

a. var. curtisii

Stipe to 70 cm long, castaneous near base, paler distally, its basal scales to 10 mm long, very narrow, dark and firm; lamina to at least 60 cm long; pinnae 3 pairs stalked, 1 pair sessile and 2 pairs adnate; basal pinnae more than 30 cm long (stalk 4 cm), bearing 1 pair of free pinnules and 1 pair adnate; basal basiscopic pinnule 20 cm long, 7 cm wide above its base, lobed to 5–6 mm from its
costa, the lobes well spaced, to 4 × 1.2 cm, lobulate, acuminate, upper pinnae similarly lobed; veins forming narrow costal and costular areoles in which frequent free veinlets are present, additional areoles also present below sinuses, some with included veinlets; lower surface of pinna-midrib, costae of lobes, and veins bearing rather sparse slender hairs 0.2–0.3 mm long, abundant slender erect hairs 0.2 mm long between veins; upper surface of pinna-midrib and costules of lobes bearing copious short hairs, no hairs between veins except a few short ones near margins; sori mostly on short veins in areoles or on acrosopic branches of free distal veins; indusia rather large, thin, bearing a few short hairs. — Fig. 13b.

Distribution — Malesia: Malay Peninsula (known only from the type collection).

b. var. hendersonii Holtum, Blumea 35 (1991) 549. — Type: Henderson 22325, Pahang, G. Senyum (K; iso BM, SING).

All parts of the frond larger than in var. curtisii; fourth pair of pinnae 22 cm long, lobed to 10 mm from costae, costules 2.5 cm apart, largest lobes 5.5 × 1.8 cm; lower surface glabrous between veins.

Distribution — Malesia: Malay Peninsula (besides the type collection, one young plant from Sungei Keteh, Kelantan, probably belongs to this variety; it has hairs between veins on the lower surface, as in var. curtisii).

Note — These specimens are comparable in size and shape of pinnae with some specimens of T. coadunata from NE India, but the latter differ in the presence of veinlets in costal areoles and in the almost glabrous upper surface.


Caudex short-creeping; stipe 27 cm long, glabrous distally, its base thickened, its basal scales dark, firm, to 15 × 1 mm with filiform apex; lamina to 40 cm long, thin; pinnae to 4 pairs (2 pairs stalked) below a multilobed apex, its lower lobes deeply lobulate; basal pinnae to 19 cm long (stalk 1.5 cm) bearing 1 pair of stalked pinnules and 1 pair adnate; basal basiscopic pinnule 12 cm long, deeply lobed and widest at mid-length; second pair of pinnae bearing 1 pair of pinnules; veins forming costal areoles which have many free included veinlets, rarely forked, free veinlets also present in some costular areoles and (sometimes forked) in additional areoles below sinuses; lower surface rather sparsely and variably short-hairy on pinna-midrib and costae of lobes (hairs 0.2–0.3 mm long), short erect very slender hairs variably present between veins; upper surface densely hairy on costae, many short rather slender hairs usually present between veins with longer ones near sinuses between lobes; sori on outer veins of costal and costular areoles or on free veins near apex of lobes; indusia thin, reniform, variably very short-hairy.

Distribution — Malesia: Malay Peninsula (Pahang, at the type locality and Panching, 20 km west of Kuantan, southern Kelantan).

Habitat — In limestone rock-crevices and in forest at the foot of limestone cliffs.


Caudex short, erect or suberect; stipe light castaneous, sparsely short-hairy, its basal scales dark, firm, to 15 × 1 mm with filiform apex; lamina to 40 cm long, thin; pinnae to 4 pairs (2 pairs stalked) below a multilobed apex, its lower lobes deeply lobulate; basal pinnae to 19 cm long (stalk 1.5 cm) bearing 1 pair of stalked pinnules and 1 pair adnate; basal basiscopic pinnule 12 cm long, deeply lobed and widest at mid-length; second pair of pinnae bearing 1 pair of pinnules; veins forming costal areoles which have many free included veinlets, rarely forked, free veinlets also present in some costular areoles and (sometimes forked) in additional areoles below sinuses; lower surface rather sparsely and variably short-hairy on pinna-midrib and costae of lobes (hairs 0.2–0.3 mm long), short erect very slender hairs variably present between veins; upper surface densely hairy on costae, many short rather slender hairs usually present between veins with longer ones near sinuses between lobes; sori on outer veins of costal and costular areoles or on free veins near apex of lobes; indusia thin, reniform, variably very short-hairy.

Distribution — Malesia: Malay Peninsula (known only from the type collection).
Note – The type was collected in forest at the foot of limestone cliffs. It has very thin fronds and few hairs between veins on the upper surface, but a small plant from the same locality is copiously hairy in that position. The type has also fairly numerous forked veinlets in areoles. Specimens from Panching (an isolated limestone hill free of forest) are firmer in texture, very hairy between veins on the upper surface and have rare forked veinlets in areoles.


Caudex short, suberect; stipe to 50 cm long, light brown when dry, when young short-hairy, glabrescent; basal scales to 10 mm long, less than 1 mm wide, rigid, almost black; lamina to 60 cm long and 50 cm wide, firm, drying dark olivaceous both sides; pinnae 1–3 pairs, apical lamina broadly deltoid and deeply lobed, not or little decurrent, the lowest lobes ± deeply lobulate; upper pinnae of large fronds deeply lobed, lobes broad, entire, obtuse to acute; basal pinnae of largest fronds bearing 1 pair of pinnules, basal basiscopic pinnule or lobe deeply lobed, basal acrosopic one lobed on largest fronds, remaining lobes entire, the lower ones acuminate; lower surface between veins glabrous on fronds of mature plants but rather densely hairy on those of young plants; the hairs between veins on the upper surface near margins only on mature plants but ± abundant on young plants; sori in one row on each side of costules of pinna-lolobes with some additional ones near the costae on large fronds, always on connected veins and large, with large thin persistent glabrous indusia. — Fig. 13d.

Distribution – Peninsular Thailand; Malesia: Peninsular Malaysia.

Habitat – On limestone rocks.

Note – The type may have been destroyed at Kaliningrad. The original description agrees with the common limestone fern above described and with no other at Batu Caves.


In frond-form and venation agreeing with T. keckii, differing in rather densely hairy lower surface of rachis and costae, thick hairs 0.5 mm long between veins on upper surface and indusia fringed with short hairs. The type consists of an apparently creeping short caudex bearing two fronds which are not quite fully expanded, the lamina probably 20 cm long when mature; apical section 9 cm long, deltoid and deeply lobed, pinnae 2 pairs, basal ones 11 cm long (stalks 15 mm), deeply lobed with one pair of adnate pinnules. On the same caudex are bases of much larger stipes which would have borne larger fronds.

Distribution – Malesia: Lesser Sunda Islands (known from the type only). Habitat – In wooded ravine.

42. Tectaria macrota Holttum, Blumea 35 (1991) 552. — Type: Mouset 617, Java, Mt Tengger, Gerbo (P; iso K, L).

Caudex suberect or short-creeping, bearing tufted stipes; stipe to 60 cm long, light castaneous, minutely hairy in the groove only, basal scales to 10 × 1 mm, firm, dark; frond of young plants 3–5-lobed, successive ones with trilobed apex and 1 pair of pinnae lobed on the basiscopic side; lamina of mature plants to 40 cm long, consisting of a (usually) trilobed apex and 2 or 3 pairs of pinnae; lobes of frond-apex short-acuminate with a short obtuse lobe corresponding to each main vein; suprabasal pinnae commonly 20 cm long, 4–5 cm wide above the base, basiscopic base rounded, acrosopic base bearing an acuminate subentire lobe 6–10 × 1.5–2 cm, margins above base of pinna lobed as those of frond-apex; basal pinnae of largest fronds 25 cm long (stalk 3 cm) bearing 1 pair of subequal pinnules to 16 × 3.5 cm, the basiscopic ones sometimes longest; main veins in pinnae to 10 mm or more apart, cross-veins irregular; lower surface bearing sparse hairs (some to 0.4 cm long, ± 4 mm apart between veins, ± 1 mm long between veins on upper surface, and indusia fringed with short hairs. The type consists of an apparently creeping short caudex bearing two fronds which are not quite fully expanded, the lamina probably 20 cm long when mature; apical section 9 cm long, deltoid and deeply lobed, pinnae 2 pairs, basal ones 11 cm long (stalks 15 mm), deeply lobed with one pair of adnate pinnules. On the same caudex are bases of much larger stipes which would have borne larger fronds.

Distribution – Malesia: Lesser Sunda Islands (known from the type only). Habitat – In wooded ravine.

42. Tectaria macrota Holttum, Blumea 35 (1991) 552. — Type: Mouset 617, Java, Mt Tengger, Gerbo (P; iso K, L).

Caudex suberect or short-creeping, bearing tufted stipes; stipe to 60 cm long, light castaneous, minutely hairy in the groove only, basal scales to 10 × 1 mm, firm, dark; frond of young plants 3–5-lobed, successive ones with trilobed apex and 1 pair of pinnae lobed on the basiscopic side; lamina of mature plants to 40 cm long, consisting of a (usually) trilobed apex and 2 or 3 pairs of pinnae; lobes of frond-apex short-acuminate with a short obtuse lobe corresponding to each main vein; suprabasal pinnae commonly 20 cm long, 4–5 cm wide above the base, basiscopic base rounded, acrosopic base bearing an acuminate subentire lobe 6–10 × 1.5–2 cm, margins above base of pinna lobed as those of frond-apex; basal pinnae of largest fronds 25 cm long (stalk 3 cm) bearing 1 pair of subequal pinnules to 16 × 3.5 cm, the basiscopic ones sometimes longest; main veins in pinnae to 10 mm or more apart, cross-veins irregular; lower surface bearing sparse hairs (some to 0.4 cm long, ± 4 mm apart between veins, ± 1 mm long between veins on upper surface, and indusia fringed with short hairs. The type consists of an apparently creeping short caudex bearing two fronds which are not quite fully expanded, the lamina probably 20 cm long when mature; apical section 9 cm long, deltoid and deeply lobed, pinnae 2 pairs, basal ones 11 cm long (stalks 15 mm), deeply lobed with one pair of adnate pinnules. On the same caudex are bases of much larger stipes which would have borne larger fronds.

Distribution – Malesia: Lesser Sunda Islands (known from the type only). Habitat – In wooded ravine.
mm long) on costae and main veins, sparse short hairs present between veins; upper surface closely short-hairy on costae, fewer hairs on veins, none between veins; sori numerous, rather small, irregularly arranged, sometimes ± confluent to form a row parallel to the costa, mostly not on free veinlets in areoles; no indusia seen; spores with a strongly defined cristate network.

Distribution — Malesia: Java (E Java, Tengger Mts; known from 3 collections by Mouset and Backer 36619).

Habitat — Forest, 700–800 m.


Tectaria modesta C. Chr., Dansk Bot. Ark. 9, 3 (1937) 72, t. 6. — Type: Sarawak Mus. Coll. 218, Kuching (BM).

Caudex long-creeping with well-spaced fronds, 8 mm diameter (dried), its scales 2 mm wide, less than 10 mm long; stipe to 90 cm long, pale or lightly reddish, glabrous with a few scales near the base; lamina to 80 cm long, pinnate with pinnate-like apex, basal 1 or 2 pairs of pinnules with stalks 2–3 cm long bearing 1 or 2 pairs of pinnules about the same size as apical lamina; suprabasal pinnae sessile, to 25 × 2.5 cm, narrowed gradually to both ends, entire or with slightly sinuous margins; main veins c. 10 mm apart, uppercurved, with several series of areoles between them; surfaces of pinnae both glabrous; sori small, scattered irregularly, not at the ends of veins in areoles; indusia small, reniform, glabrous; slender paraphyses present.

Distribution — Malesia: Malay Peninsula, Borneo, N Celebes.

Habitat — On muddy river banks within the tidal zone but in fresh water, the pinnae floating at high tides.

Note — The type of T. modesta is a young plant with simple fronds, lamina to 20 × 1.5 cm. No one has reported the conditions under which spores can germinate to produce young plants.


KEY TO THE VARIETIES

1a. Sori not elongate nor confluent ........... 2
b Sori irregularly elongate and sometimes confluent ........... c. var. allosora

2a. Margins of pinnae and pinnules entire
b Margins of pinnae and pinnules minutely denticate ........... b. var. denticulata

a. var. lobbii

Caudex erect or suberect, bearing a tuft of fronds and tough tangled roots; stipe to 25 cm long, light castaneous, glabrous, its basal scales narrow, to 10 mm long, not rigid; lamina very firm, to 25 cm long, consisting of a pinnate-like apex and 2–4 pairs of pinnae; rachis densely short-hairy on the adaxial surface; upper pinnae commonly 12–15 × 1–1.5 cm, entire, narrowed gradually to base and apex, a bud sometimes present at the base of uppermost ones; basal pinnae bearing 1 or 2 (rarely 3) pinnules which are alternate, with decurrent bases, shaped as upper pinnae; main veins oblique, uniting in a series of arcs near the margin with irregular areoles between them containing branched free veinlets; surface glabrous apart from short hairs on upper surface of costae; sori in 2 ± regular rows between main veins, additional ones sometimes present; indusia large, firm, peltate or subreniform.

Distribution — Malesia: Borneo, Philippines (Bohol).

Habitat — On rocky stream banks in the flood zone.
Fig. 14. Tectaria jacobsii Holtum. a. Venation (sori removed on the right), × 2.2; b. minute hairs on adaxial surface of rachis, × 23; c. a basal pinna, × 0.26. — T. suluensis Holtum. d. Apex of frond, × 0.17; e. detail of buds, × 1.3. — T. dolichosora Copel. f. Venation of a middle lobe of apical part (sori removed on the left), × 2.2. — T. fauriei Tagawa. g. Venation of a middle pinna (sori removed on the right), × 2.2; h. bud on rachis near base of a pinna, × 4. — T. pleiosora (Alderw.) C.Chr. i. Fertile frond, × 0.1; j. detail of venation (sori removed on the right), × 2.2 (a–c: Jacobs 5590; d, e: Kondo & Edano PNH 38624; f: Ramos & Edano BS 28960; g, h: Holtum SF 20071; i, j: Rick 22).
b. var. **denticulata** Holttum, Blumea 35 (1991) 552. — Type: *P. S. Ashton S 18175*, Sarawak, Bintulu, Ulu Tubau, on frequently flooded river banks (K).

Distribution — *Malesia*: Borneo (known only from the type collection).


Distribution — *Malesia*: Moluccas (Halmahera, Morotai).

45. **Tectaria jacobsi** Holttum, Blumea 35 (1991) 552. — Type: *M. Jacobs 5590*, Brunei, junction of rivers Temburong and Belalang at 500 m (K; iso L).

Growth-habit of *T. lobbii* but whole plant larger; *stipe* to 35 cm long, its basal scales 2.5 mm wide at their bases; *lamina* to nearly 40 cm long; pinnae to 5 pairs, the uppermost (adnate) one with a bud at its base, the lamina-apex obliquely lobed near its base; *upper pinnae* to 14 × 2.5 cm, narrowly acuminate; *basal pinnae* to 22 cm long (stalk to 2.5 cm) bearing 2 pairs of pinnules, those on the acrosopic side entire (to 10 × 1.4 cm), the basal basiscopic one (14 cm long) irregularly lobate on its basiscopic side, the basal lobe 2.5 × 0.6 cm, almost free with an obtuse apex, apical part of pinna lobed as frond-apex; surfaces glabrous apart from minute hairs on adaxial surface of rachis; *main veins* of pinnae c. 9 mm apart, at 45°, almost reaching the margin with 2 or 3 rows of areoles between them; *sori* small and numerous, irregularly scattered, some on free veinlets in areoles; indusia firm, reniform to almost peltate. — **Fig. 14a, b.**

Distribution — *Malesia*: Borneo (known only from the type collection).

Habitat — In river bed below the regular high-water level, on shaly wet rocks in shade.

Note — The irregular lobing of the frond apex and of distal parts of pinnae may indicate a hybrid origin, in which case *T. lobbii* is indicated as one parent, but there is no clear evidence of the other possible parent. Jacobs collected specimens of typical *T. lobbii* at a neighbouring locality.


Caudex short, erect, bearing many tough roots; *stipe* to 10 cm long, dark brown, glabrous, basal scales narrow, not rigid; *lamina* firm, to 12 cm long, consisting of an apical leaflet and 1 or 2 pairs of pinnae, apical leaflet 8 × 1.4 cm, its base narrowly decurrent, its apex acuminate, its lower middle part obliquely lobulate; *basal pinnae* short-stalked, bearing one free elongate narrow entire pinnule and rarely a second one, apical part of pinna shaped as frond-apex; *main veins* in pinna close together and very oblique, the areoles between them having few included veinlets; *surfaces* glabrous apart from a few minute hairs in the adaxial groove of the rachis; *sori* often in only one row between main veins, additional ones sometimes present; indusia firm, glabrous.

Distribution — *Malesia*: Borneo (known only from the type collection).

Habitat — No information, but evidently a rheophyte, as *T. lobbii*.

Note — The apical parts of the frond and of basal pinnae are lobed in about the same way as those of *T. jacobsi*.


*Acrostichum quercifolium* Retz., Observ. Bot. 6 (1791) 39. — *Gymnoperis quercifolia* (Retz.) Bernh., Neues J. Bot. (Schrader) 1, pt 2 (1806) 20; Hook., Icon. Pl. 10 (1854) t. 905; Bedd., Ferns Brit. India (1863) pl. 47; Handb. Ferns
Brit. India (1883) 432. — Type: *Koenig s.n.*, Sri Lanka.

Caudex slender, creeping; scales thin, narrow, to 4 mm long; fronds dimorphous. Sterile frond: stipe 3–8 cm long bearing copious slender hairs; lamina to 10 cm long, consisting of an apical section and 1 pair of pinnae; apical lamina to 7 × 4 cm, ± ovate in outline, variably lobed to a depth of 10 mm, apex rounded, base broad-cuneate; pinnae short-stalked, to 3 cm long and 2.5 cm wide at base which is widened on the basiscopic side with 2 or 3 small lobes; venation normal for sect. *Tectaria* but areoles few; lower surface of costae bearing many slender hairs more than 1 mm long, sparse minute hairs present on upper surface of costae and between veins near margin. Fertile frond: stipe to 18 cm long, almost glabrous; lamina to 8 cm long, variously divided, at maximum with apical section 5.5 cm long, 2.5 mm wide distally with 2 pairs of narrow lobes to 10 mm long; pinnae to 3 cm long with a narrow basiscopic lobe to 8 mm long; sporangia borne densely along the veins which form a single series of areoles.

Distribution — Sri Lanka, Thailand, N Vietnam; in *Malesia* known only from Peninsular Malaysia (Pulau Tioman) and Borneo (Sabah).

Habitat — On earth banks in shade, or on stream-sides, sometimes on rocks.

Cytology — n = 80 (Manton 1954).


Caudex not known; fronds dimorphous. Sterile frond: stipe 12 cm long, minutely hairy, its basal scales to 5 mm long; lamina 22 cm long, consisting of 3 pairs of pinnae and a pinna-like apex 16 × 3.8 cm; basal pinnae 15 × 3 cm, short-stalked, with a basal basiscopic lobe 12 × 2.3 cm, otherwise entire; suprabasal pinnae somewhat shorter, simple and entire, abruptly narrowed at the base on the basiscopic side; lower surface of costae minutely hairy near bases of pinnae only, upper surface similarly hairy throughout. Fertile frond of type: stipe 43 cm long, stramineous; lamina 28 cm long, consisting of 4 pairs of pinnae and a pinna-like apex, all c. 1.5 mm wide; apex 15 cm long, uppermost pinnae much decurrent on rachis, second pair of pinnae 9 cm long and decurrent 5 mm, third pair slightly decurrent, basal pinnae 18 cm long (including stalk 5 mm), forked 15 mm above their bases, basiscopic lobes 13 cm long (basal pinnae of Elbert 673 13 cm long with 2 lobes 8 cm and 5 cm long on the basiscopic side), all pinnae and lobes c. 2 mm wide, covered beneath with sporangia on each side of the costa except for a narrow margin.

Distribution — *Malesia*: Lesser Sunda Islands (Lombok, known from the type and Elbert 673, Rindjani Mts.).

Note — Sections of fertile pinnae of *Elbert 673* show a series of vascular strands underlying the narrow fertile surface area, indicating a venation as in *T. hilocarpa* but closer. Fertile pinnae of the type have inrolled margins (due to immaturity?) and therefore appear narrower, but do not otherwise differ.


Caudex short, erect; fronds dimorphous. Sterile frond: stipe to 35 cm long, light castaneous, glabrous above base; lamina to 24 cm long, consisting of terminal lamina and 1 or 2 pairs of pinnae; terminal lamina to 19 × 3.5 cm, entire, apex caudate-acuminate, base slightly decurrent; upper pinnae sessile, to 12 × 2.8 cm, narrowed at their bases; basal pinnae short-stalked, with or without a basiscopic lobe; main veins in apical lamina to 10 mm apart along midrib, cross-veins almost straight, 2 or 3 series of areoles between them; sparse short hairs present on lower surface of midrib and veins, upper surface glabrous apart from very short hairs near bases of pinna-midribs. Fertile frond: stipe a little longer than on sterile fronds; apical lamina to 16 × 1.9 cm with short lateral lobes at its base; upper pinnae to 12 × 1.5 cm, their bases decurrent; basal pinnae to 13.5 cm long, to 1.8 cm wide above their basal lobes the largest of which are 5.5 × 0.7 cm (on some specimens the pinnae are narrower); venation much simplified as compared with sterile fronds; sori
irregularly scattered, some of them confluent along veins especially near to and parallel with the margins, and in narrower pinnae; indusia distinct except on some confluent sori.

Distribution - Malesia: New Guinea (known only from the type collection).


Caudex short, erect; stipe to 30 cm long, narrowly winged at least distally, red-brown, glabrescent; basal scales to 7 × 1 mm with thin margins; lamina to 30 cm long with 3 pairs of pinnae, all with narrowly decurrent bases which form an almost continuous wing on each side of the rachis, usually not quite reaching the next lower pinnae; middle pinnae to 17 × 4 cm, narrowly caudate-acuminate, entire, with narrowly cuneate base; basal pinnae sometimes with a narrow basiscopic lobe to 12 × 2 cm; main veins on pinnae 8–9 mm apart along the costa, upcurved, cross-veins prominent on the lower surface with 2 rows of areoles between them; upper surface of midribs bearing very short hairs, rest of frond glabrous; sori small, irregularly scattered, many of them coalescent, mostly not on free veinlets; indusia very small, thin, persistent but ± obscured by developing sporangia.

Distribution - Malesia: Borneo (W Kalimantan and Sarawak).

Habitat - In lowland forest.

Note - The type consists of a young plant bearing small fronds which are trilobed or trifoliate, not fully fertile. The above description is based mainly on P. W. Richards 2245 from Sarawak, near Mt Dulit (K).


Tectaria gymnosora Holtum, Dansk Bot. Ark. 23 (1966) 308. — Type: Hansen et al. 11225, N Thailand (C; iso K).


Caudex erect; stipe 40–60 cm long, narrowly winged in its upper part, basal scales 10 mm or more long, 2 mm wide at the base, firm, marginal cells thin-walled; lamina firm, to 50 cm long, consisting of a trilobed apex which is narrowly decurrent at its base almost to the attachment of the uppermost pinnae, and 2 or 3 pairs of pinnae, all with similarly narrowly decurrent bases; buds present on rachis at the base of some pinnae on mature fronds; middle pinnae 20–25 cm long, entire or nearly so, gradually narrowed towards their bases, apex narrowly acuminate, sterile pinnae often wider than fertile, to 6 cm wide; basal pinnae of small fronds narrowed towards their base on both sides, unlobed but the lamina on the basiscopic side wider than on the acroscopic side, of larger fronds with a narrowly winged stalk and a rather long basal basiscopic lobe; pinnae-midribs and main veins reddish on the lower surface when dried and minutely hairy, upper surface glabrous; smaller veins concolorous and distinctly prominent both sides; sori small, round, in about 4 irregular rows between the main veins, not on free veinlets in areoles; indusia small, thin, glabrous, persistent. — Fig. 14g, h.

Distribution - Assam, Yunnan, Taiwan, N Thailand; in Malesia: Malay Peninsula (Pahang).

Habitat - A rheophyte growing on the rocky banks of forest streams.


Fronds dimorphous. Sterile frond: stipe to 47 cm long, mid-castaneous, very sparsely hairy, basal scales to 15 × 2 mm, firm, castaneous with paler fragile margins, those above base of stipe very narrow; lamina to 55 cm long, apex pinna-like, to 27 × 8 cm with short decurrent base or a little united with an uppermost pinna; pinnae to 4 pairs; uppermost pinnae to 24 × 4.5 cm, narrowed to cuneate bases with a bud at the base of each, apex abruptly short-acuminate; basal pinnae unlobed, to 21 × 8 cm, narrowly cuneate at their bases with stalks 5–7 mm long; main veins 10–15 mm apart
along costae, smaller veins very slender and not prominent but distinct on lower surface; surfaces glabrous except for sparse hairs near bases of upper surface of costae. **Ferite frond:** lamina to 32 cm long, its apical section sometimes trilobed; **basal pinnae** to 15 × 3.5 cm; sori small, irregularly arranged, very irregular in shape and sometimes confluent, mostly on free veinlets in areoles, small indusia sometimes present, hidden by mature sporangia. – Fig. 14d, e.

**Distribution:** **Malesia:** Philippines (Sulu Archipelago and Palawan).


*Caudex erect; fronds* of smaller plants with wholly winged rachis, the stipe also at least partly winged (width of wing variable), basal pinnae of largest plants free with slightly decurrent bases or joined to the rachis-wing (see Holttum 1955: f. 302); **stipe** of largest fronds to 60 cm long, basal scales c. 10 × 1 mm, the lowest with fragile margins; **lamina** to 60 cm long, thin, consisting of a 3–5-lobed apex and 3 pairs of pinnae or pinna-like lobes which when nearly free are narrowed towards their bases; basal pinnae sometimes with a winged stalk-like base and a large basiscopic lobe; pinnae or lobes of **ferile fronds** narrower than those of sterile ones which may be 7 cm wide; minute **hairs** present on both surfaces of costae only; main veins of pinnae 8–10 mm apart along the costa, upcurved, the cross-veins rather regular with many areoles between them; sori numerous, very irregular in shape, on free veins in areoles and also along connected veins, often coalescent to linear forms, exindustiate.

**Distribution:** Peninsular Thailand; **Malesia:** Malay Peninsula and N Sumatra.

**Habitat:** In lowland forest; see Holttum 1931 under *Aspidium maingayi*.

**Cytology:** Diploid (Manton in Holttum 1955: 626).

**Note:** This species appears to be closely allied to the fern of S China and Tonkin first named *Gymnoperis decurrens* Hook. [Hemigramma decurrens (Hook.) Copel.]. The latter has smaller, firm, fronds, the stipe never winged and all sori running along veins, almost filling the lower surface. The type of *Tectaria simulans* Ching [Acta Phytotax. Sinica 19 (1981) 129] is somewhat intermediate between *T. semipinnata* and *Gymnoperis decurrens*, having fertile fronds like the former and a frond-form like the latter.


**Caudex** and base of stipe unknown; **stipe** dark castaneous, glabrescent on abaxial surface; **fronds**
dimorphous. Sterile frond of young plant trilobate; apical lamina with cuneate base, the pinnate close to it; lamina of type 38 cm long, consisting of a rather shallowly trilobed apex with strongly cordate base and 1 pair of pinnate 10 cm below it; pinnae about 18 cm long (tips broken), shallowly bilobed with a very asymmetric base and stalks 5–7 mm long, strongly cordate on the basiscopic side, narrower and rounded on the acrosopic side, 8.5 cm wide above the basiscopic lobe; main veins widely spaced, upcurved, other veins slender, distinct on the lower surface but not prominent, areoles many with forked included veinlets; lower surface glabrous apart from sparse minute hairs on costae. Fertile frond: only known from 2 detached stalked pinnate 20 × 6 cm, base broadly rounded or slightly cordate, apex abruptly short-acuminate; sori very numerous, mostly on free veinlets in areoles, also running along other veins, very variable in shape and often confluent; no indusia.

Distribution — Malesia: Sumatra (known only from the type and a frond of a younger plant sent later to Kew, probably part of the same collection).


Stipe to 35 cm long, slender, atropurpureous, glossy, minutely hairy in the adaxial groove; lamina trilobate, the apical part trilobed with cuneate base and acuminate lobes, or 5-lobed (basal lobes small), to 25 cm long and 22 cm wide; main veins to 10 mm apart along the costae, at a wide angle, distally upcurved, cross-veins mostly almost straight with many areoles between them; short pale erect hairs present between veins on the lower surface with somewhat longer ones on costae, upper surface not seen; sori all close to the margin, 1.5 mm diameter, apparently on connected veins; indusia almost peltate, persistent.

Distribution — Malesia: Papua New Guinea (known from the type collection only).

Habitat — In damp soil under rocks near river.


Caudex short, suberect; stipe to 60 cm long, nearly black, glossy, its basal scales to 10 mm long, less than 1 mm wide, firm, entire; lamina to 50 cm long; apical part to 40 cm long, deeply multilobed, its basal lobes 25 × 5 cm, acuminate, obliquely shallowly lobulate; upper lobes entire; pinnae one pair, to 28 cm long, lobed both sides to 15 mm from the costa, basal basiscopic lobe to 15 cm long, acuminate, repand to obliquely lobulate, other lobes gradually shorter, lobes on the acrosopic side short and subequal, on largest fronds acute; main veins prominent on the lower surface, smaller veins not, areoles with included veinlets many; lower surface of costae black and glossy, bearing few minute hairs; upper surface of costae bearing hairs more than 0.5 mm long, scattered hairs also present on and between veins; sori on free veins in areoles, 3–4 mm long, 1.5–2 mm wide; indusia large, persistent, rounded to cordate at their bases, margins minutely papillose. — Fig. 14f.

Distribution — Malesia: Philippines (Luzon, Cagayan, Tayabas and Quezon Provinces).

Habitat — One specimen from stream-side at 75 m altitude, others from steep mountain slopes (no altitudes given).


Caudex erect or suberect; stipe to 50 cm long, flushed pale to deep red-brown, glabrescent, basal scales to 15 × 1 mm, their margins fringed when young; lamina rigid, dimorphous, to c. 40 cm long with 3 or 4 pairs of pinnate (rarely 7 pairs on fertile fronds), apex pinna-like, a bud rarely present at the base of uppermost pinna; basal pinnae usually unlobed and sessile; middle sterile pinnae to 18 × 5 cm, their bases peltate, wider on basiscopic than on acrosopic side, apex acuminate,
margins entire; basal sterile pinnae to 20 × 8 cm, more asymmetric than upper ones, the basiscopic margin sometimes sinuous; small veins forming many areoles between main veins, not prominent and sometimes not detectable on the lower surface; costae glabrous on both surfaces; fertile pinnae to c. 10 × 2.5 cm, sometimes with sinuous margins; sori in 2 rows between main veins, each at the end of a single veinlet in an areole (fronds of intermediate type may sometimes occur with more widely-spaced sori not on single veinlets); indusia large, broadly elliptic with an elongate receptacle.

- Fig. 14i, j.


Habitat – In Borneo found in rocky places, both sandstone and limestone, also near streams in forest; in Sabah the fertile fronds appear to be produced seasonally but no detailed records exist.

Note – When first describing this species (as A. persoriferum forma latipinna) Aldewerelt mentioned a cultivated plant from Borneo; the specimens from this are here cited as lectotype. As noted by Christensen (1934) this species is allied to T. crenata, but I have seen no evidence of hybridization.


Caudex short, suberect; stipe to 80 cm long, light castaneous, glabrescent; basal scales 1–1.5 mm wide; lamina to 90 cm long, apex usually simple or trilobed, pinnae to 8 pairs, their margins subentire to sinuous, distal pinnae adnate and slightly decurrent; middle pinnae to 30 cm long, narrowly acuminate, sterile ones to at least 4.5 cm wide, fertile ones commonly 2 cm wide (rarely to 3.5 cm); basal pinnae stalked, with at least one large basiscopic lobe, in Philippine specimens sometimes several other lobes, decreasing distally; minute hairs variably present on the lower surface of costae; sori in one row on each side of main veins, in narrower fertile pinnae distinctly immersed and sometimes on single veins in areoles, in broader pinnae hardly immersed and not on solitary veinlets; indusia peltate, quite circular on young sori, glabrous or papillate on upper surface; spores spinulose.

Distribution – Malesia: Java (?), Lesser Sunda Islands (Flores, Sumbawa), Philippines, NE Celebes, Moluccas, New Guinea; Marianas, Solomons, New Hebrides, Rotuma Is., probably Fiji.

Cytology – Plants in New Guinea diploid (T.G. Walker, in litt.).

Taxonomy – Dr. B. Zimmer has kindly examined Wildenow’s type at Berlin and confirms that the indusia are peltate.

Hybrids – Especially in the Philippines and New Guinea there appear to be hybrids between T. repanda and T. decurrens; these are variously intermediate between the two parent species.

A specimen from Luzon (Price 2245) is intermediate between T. repanda and T. hilicarpa. Its distal sori are like those of T. repanda, but those on veins nearer the costae are confluent, those nearest the costae forming continuous lines between successive main veins as in T. stifolia, differing from the latter in having conspicuous indusia, also in the absence of buds. The fronds are trilobed, the middle lobe being much elongate, the lateral lobes small (one frond has only one lateral lobe).

A specimen from NE Celebes (de la Saviére 54) has narrow fertile pinnae with peltate indusia but broader stipe-scales.


Cardiochlaena laevis Fée, Mém. Foug. 5. Gen. Filic. (1852) 316. — Type: Cuming s.n., Philippines (not seen).

Cardiochlaena sinuosa Fée, Mém. Foug. 5. Gen. Filic. (1852) 316. — Type: Cuming s.n., Philippines (not seen).

Aspidium heptaphyllum Baker, J. Bot. 17 (1879) 246. — Tectaria heptaphylla (Baker) C.Chr., Index Filic. Suppl. 3 (1934) 180. — Type: Horne 20, Fiji (K).


Caudex suberect; stipe to 70 cm long, castaneous, its basal scales to 15 mm long, 2 mm or more wide; lamina to 70 cm long, its apical section deeply multilobed, the lower lobes grading to adnate or sessile pinnae; middle pinnae to 30 cm long, short-acuminate, of sterile fronds to 8 cm wide, of fertile fronds 3–5 cm wide (of type 4.5 cm), firm, drying brown-olivaceous, margins crenate to almost entire; basal pinnae distinctly stalked and bearing a large basiscopic lobe; main veins in pinnae 7–10 mm apart along the costa, in fertile fronds with 2 fairly regular rows of areoles between them; minute hairs variously present on lower surface of costae, upper surface of costae glabrous or nearly so; sori on free veinlets in areoles, rather large; indusia firm, slightly reniform, attached to a linear receptacle 0.5 mm long; spores with irregular thin fimbriate wings; plants in Malay Peninsula diploid (Hottot 1955: 626).


Habitat — In lowland and mid-mountain forest.

Possible hybrids — This species appears to intergrade with T. repanda in the Philippines. One specimen from the Malay Peninsula may represent a hybrid with T. angulata; it has some irregular small sori in addition to the two rows normal for T. crenata, also buds at the bases of some pinnae.


Caudex short, suberect; stipe commonly 15–20 cm long (to 30 cm), very dark, hairless, densely scaly in basal 4 cm, basal scales very dark, less than 1 mm wide, to 0.5 mm long, upper ones paler, all with thinner entire margins; lamina to 35 cm long with up to 6 pairs of pinnae, very firm, apex pinna-like or joined to uppermost pinna; middle pinnae 10–12 × 2–3 cm, short-stalked, short-acuminate, margins entire to irregularly repand, base rounded to broadly cuneate; basal pinnae not or little longer than the next pair, with a large acute basiscopic lobe, the lobe on largest fronds sometimes almost free, the acrosopic base rounded or in largest fronds forming an obtuse almost free lobe 8 × 4 mm; all surfaces almost glabrous, minute hairs sometimes present on lower surface of veins and near base of upper surface of costae; lateral veins of pinnae flexuous, prominent on the lower surface, smaller veins usually also prominent; sori on short veinlets in areoles, in one row on each side of lateral veins, not impressed; indusia firm, about circular, attached along a line from centre to base, bearing a few minute hairs.


Habitat — On limestone cliffs at altitudes to 1300 m.

Note — The Kew isotype is a rather immature frond which has a mid-castaneous stipe and rachis and young sori. All other specimens from both Western and Eastern New Guinea, have a very dark stipe and rachis. Young plants have deeply 5-lobed fronds which may sometimes bear a few sori.

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*Caudex* short, erect; *stipes* to 25 cm long (sterile fronds) or 37 cm (fertile), dark, glossy on abaxial surface, basal scales very dark, rigid, to 12 mm long, less than 1 mm wide, much contorted; *lamina* to 25 cm long, isomorphous, firm, consisting of a trilobed apex and 2 pairs of pinnae; *upper pinnae* sessile, to c. 17 × 5 cm, base subcordate on basiscopic side, cuneate and not auricled on acroscopic side, margins subentire, apex not acuminate; lower surface quite glabrous; *basal pinnae* with one large basiscopic lobe; main veins c. 15 mm apart along costae, sinuous; *sori* in one row on each side of main veins, on terminal veinlets in areoles, rather large, slightly impressed (with prominences on the upper surface); indusia firm, round-reniform (not peltate).

Distribution – *Malesia*: New Guinea (known only from the type collection).

Habitat – On limestone, found at an altitude of 175 m.


*Caudex* quite prostrate, c. 5 mm diameter; *stipe* to 50 cm long, glabrescent, dull reddish, basal scales to 5 mm long, narrow, not persistent; *lamina* of young plants simple, of mature plants trifoliate or with a deeply trilobed apex and one pair of unlobed pinnae; *apical lamina* or simple frond to 28 × 8 cm, margins entire, base narrowly cuneate, apex abruptly caudate-acuminate; *pinnae* to 20 × 5 cm, sessile, with a bud at the base of each on old fronds, unlobed, shape as apical lamina but sometimes wider on the basiscopic side of the costa than on the acroscopic side; *costae* sparsely short-hairy near their bases on lower surface only; main veins to 10 mm apart along costae, upcurved, slender, cross-veins irregular with 3 or 4 series of areoles between them, smaller veins slender and distinctly prominent when dried; *sori* in a rather uneven row on each side of main veins, often with many additional ones between the rows, not on free veinlets; indusia firm, persistent, slightly reniform.

Distribution – *Malesia*: throughout Borneo.

Habitat – In forest to about 300 m, often on rocks and sometimes beside streams, also on steeply sloping ground.


*Caudex* erect or suberect; *stipe* to 30 cm long, base very dark, above base castaneous, minutely hairy, glabrescent; basal scales to 10 × 1.5 mm, firm with thinner margins; *lamina* of young plants multilobed, of mature plants to 45 cm long, texture very firm, consisting of a 5-lobed broadly triangular apex and 3 or 4 pairs of subopposite pinnae; *pinnae* gradually larger towards the base of the frond, short-stalked, with cordate basiscopic and rounded to cuneate acroscopic base, margins repand-
sinuate, gradually narrowed to an acuminate apex; basal pinnae 18–25 cm long (stalks 15 mm), 2 cm wide on acrosopic side of costa, on basiscopic side a basal lobe 11 cm long and another 9 cm, both acuminated with repand margins, apical part of pinnae irregularly obliquely bluntly lobed on the basiscopic side; main veins to 10 mm apart along the costa, upcurved, prominent on the lower surface, cross-veins irregular with many areoles between them, smaller veins distinct but not prominent; lower surface of costae sparsely short-hairy, upper surface of rachis and costae densely covered with thicker short hairs, rest of the surface glabrous; sori rather large, in a rather uneven row on each side of main veins with a few additional ones, not impressed, mostly not on free veinlets; indusia large, thin and shrivelling, slightly reniform, minutely hairy, glabrescent.

Distribution — Malesia: Philippines (Palawan, also eastern Mindanao).

Habitat — In forest on limestone rocks at low altitudes.


Stipe 65 cm long, nearly black, glossy, rachis similar; lamina c. 50 cm long, firm but not rigid, consisting of a tri lobed apex and 3 pairs of pinnae; apical lamina 22 cm long, its midlobe 7.5 cm wide with obliquely shallowly lobed margins, lateral lobes c. 17 × 5 cm; middle pinnae 26 cm long (stalk 5–7 mm), their acrosopic bases cuneate at 45° and then rounded, basiscopic bases truncate to subcordate, 15 mm wide, then gradually wider, margins almost entire; basal pinnae 25 cm long (stalk 12 mm), bilobed, basiscopic lobe 19 cm long, abruptly short-acuminate, 5.3 cm wide, its basiscopic margin undulate-subcuneate in its widest part; main veins to 12 mm apart along costae, sinuous, upcurved, cross-veins irregular, smaller veins concolorous, distinct on both surfaces; lower surface wholly glabrous, upper surface minutely hairy on costae only; sori in a row on each side of main veins (no additional ones present), mostly not on free veins in areoles, somewhat impressed; indusia apparently peltate (all old and distorted on type).

Distribution — New Ireland; known only from the type collection.

Habitat — On limestone in lowland hill forest.


Caudex short-creeping, thick; stipe to 55 cm long, castaneous, minutely hairy, glabrescent; lamina to 45 cm long, thin, glabrous, consisting of a deeply tri lobed apex and 4 pairs of pinnae; uppermost pinnae sessile, to 13 × 3.5 cm, base rather narrowly cuneate on the acrosopic side, more broadly on basiscopic side, margins subentire; second pair of pinnae similar but larger with ± sinuous margins; third pair much wider on basiscopic than on acrosopic side of costa, basiscopic margin irregularly shallowly lobed; basal pinnae 22 cm long (stalks 10 mm) with 2 large acuminate lobes on basiscopic side, basiscopic margin obliquely obtusely lobed to a depth of 3–4 mm; main veins upcurved, not sinuous, with irregular areoles between them; sori in a regular row on each side of main veins with a few additional ones, slightly impressed, mostly not on free veins in areoles; indusia minute, apparently reniform and soon caducous.

Distribution — Malesia: Lesser Sunda Islands (besides the type from Timor, a frond of a smaller plant from Flores probably belongs to this species).


Caudex short, erect, bearing a tuft of many stipes; stipe c. 20 cm long, dull castaneous, minutely hairy on the abaxial surface; basal scales to 8 mm long, less than 1 mm wide, dark with paler margins; lamina c. 20 cm long, apex very deeply tri lobed or simple with a pair of pinnae close below it; pinnae 2 or 3 pairs, upper ones 10 × 2 cm, almost sessile, entire, base rather narrowly cuneate, apex acuminate; basal pinnae to 12 × 2 cm with a basiscopic lobe 8 × 1.5 cm; main veins in pinnae 5 mm apart along the costa, at 45°, red-brown and prominent on the lower surface, cross-veins similar with 2 irregular series of areoles between them; lower
Fig. 15. *Tectaria siifolia* (Willd.) Copel. a. Venation of a middle pinna (sori removed on the right, to show attachment), x 2.2. — *T. rheophytica* Holttum. b. Fertile frond, x 0.33; c. detail of b, x 4. — *T. schultzei* (Brause) C. Chr. d. Middle of a lateral lobe, x 4. — *T. tricuspis* (Bedd.) Copel. e. Middle of a lateral lobe (venation details only shown in centre), x 2.2; f. single sorus showing indusium with stiff hairs, x 23 (a: Teijsmann s.n., Sumatra; b, c: Croft 1681; d: Croxall & Parris 5963; e, f: Iwatsuki et al. B-762).


Surface of costae and veins bearing sparse minute hairs, upper surface of costae closely covered with short hairs, no other hairs present; sori rather irregularly spaced, often confluent or elongate to form lines parallel to the main veins (not to costae); indusia very small and thin, not covering sori.

Distribution — *Malesia*: Irian Jaya (apart from the type, one collection from lowland forest in NW Irian Jaya, Sorong Dist.).
Dryopteris xanthomelas (C. Chr.) C. Chr., Index Filic. Suppl. 3 (1934) 183. — Type: Treub 232, New Guinea, Skroo (BO; iso K, L).


Caudex short-creeping; fronds dimorphous, sterile ones with shorter stipe and broader pinnae than fertile, pinnae to 4 pairs; fronds of young plants ovate-acute with strongly cordate base. Sterile fronds: stipe to 30 cm long, glabrous, basal scales to 10 mm long, dark with thinner pale margins; apical lamina often trilobed, the middle lobe sometimes with sinuous margins; buds present at bases of pinnae on old fronds; basal pinnae to 20 cm long, to 7 cm wide above the basal lobe, abruptly short-acuminate; middle pinnae broader on basiscopically than on acropetally side of the costa; main veins to 10 mm apart along costae; upper surface of costa glabrous except near their base in Sumatra, closely short-hairy in Celebes and Philippines, lower surfaces glabrous. Fertile fronds: stipe to 50 cm long; middle pinnae to c. 12 × 4 cm with main veins to 6 mm apart along costae, areoles between main veins fewer than in sterile pinnae and in smaller pinnae lacking included veinlets; sori on the outer veins of areoles, in a row on each side of main veins, usually rather large, those near the costa elongate and often coalescing to form lines parallel to the costa; indusia thin, soon caducous. — Fig. 15a.

Distribution — Malesia: throughout, but local in occurrence.

Habitat — In Sumatra and the Malay Peninsula associated with limestone and seasonal in producing fertile fronds; no good records elsewhere.


Caudex short, erect, sometimes branching near its base; stipe to 60 cm long, glabrous and glossy above its base, usually dark, basal scales to 15 × 1.5 mm, stiff, not very dark, fringed when young; lamina to 60 cm long consisting of a rather shallowly trilobed apex and 1–4 pairs of pinnae, thin, drying brownish; apical lamina to 25 cm long, its...
base not decurrent, 1 or more buds present on the upper surface of its costa near bases of main veins; pinnae more broadly rounded at their bases on the basiscopic than acroscopic side, middle ones commonly 15–18 x 5–6 cm, basal pinnae with stalks to 2 cm long and a broad basiscopic lobe; main veins 10–15 mm apart along costa of pinnae, at 45°, little upcurved, cross-veins not regular, smaller veins distinct but not prominent, forming areoles containing copious branched free veinlets; lower surface glabrous, upper surface of costae densely short-hairy; sori small, mostly at ends of veinlets in areoles, nearly round but on some fronds variously a little elongate; indusia small, reniform, sometimes lacking.

Distribution – Peninsular Thailand; throughout Malesia; Solomon Islands.

Habitat – In lowland forest near streams, usually on rocks but not in the flood zone of swiftly flowing streams.

Note – There is considerable variation in the development of indusia and in the abundance of ± elongate sori. Indusia are best developed on specimens from Perak in the Malay Peninsula. Some specimens from Sarawak and Celebes have buds at the bases of pinnae in addition to those on the costa of the apical lamina. Buds may be prolific on plants in very humid positions (e.g. spray of waterfalls). One plant from ‘alluvial forest’ in the G. Mulu National Park, Sarawak, has pinnae with very broad bases, subcordate on the basiscopic side. Under T. trifolia, Copeland (l.c. 1960) appears to have included specimens of T. polymorpha.

70. Tectaria croftii Holttum, Blumea 35 (1991) 548. — Type: J.R. Croft 1734, Papua New Guinea, W Sepik, N slopes of Bewani Mts, 300 m, on vertical limestone face (K; iso LAE, L).

Caudex short, erect; stipe to 40 cm long, dull castaneous, minutely hairy throughout; basal scales 15–20 mm long, abundant, firm and ± twisted, distal scales and those on rachis and lower surface of costa all much shorter and very narrow; lamina to 34 cm long; apical section trilobed, 27 cm long, base short-decurrent, midlobe 11 cm wide, entire, short-acuminate, narrowed at base to 8 cm, lateral lobes upcurved, 15 cm long from bases of their costa, 5.5 cm wide; pinnae 15 cm long with stalks 3 mm long and abrupt acute apices, each with one short abruptly acute basiscopic lobe; main veins in pinnae upcurved, 10–15 mm apart along costae, cross-veins irregular, small veins forming many areoles between them with fewer free veinlets than in T. angulata; lower surface of costae and veins copiously hairy, slender hairs between veins; upper surface of pinna-midrib densely covered with thick hairs 0.3 mm long, fewer similar hairs on main and smaller veins, a few thick hairs 0.5 mm long between veins; sori small, scattered irregularly, ex-indusiate, mostly not on free veinlets.

Distribution – Malesia: Northern Papua New Guinea (W Sepik), Manus Is.

Habitat – The type and Sands 2629 from Manus Is. were collected from limestone. A plant cultivated at Kew, brought from near Lae in 1969, is similar but did not originate from limestone.


Caudex short, erect; stipe to 30 cm long, distally light-castaneous, glabrous and glossy on abaxial surface, basal scales 7 mm long, no scales above base; lamina firm, to 40 cm long, consisting of a ± deeply trilobed apical section and one or two pairs of pinnae; upper pinnae short-stalked, to 14 x 5 cm, apex narrowly acuminate, base broadly corotate on basiscopic side; basal pinnae to 15 cm long, each with a large basiscopic lobe, stalks to 5 mm long; main veins at 45° to costae and 10–12 mm apart along it, cross-veins and areoles very irregular, smaller veins slender but distinct; surfaces, including costae, quite glabrous; sori many, small, very irregularly scattered, sometimes confluent, some on free veinlets in areoles but many on connected veins, no indusia seen.

Distribution – Malesia: Lesser Sunda Islands (Flores, Obi Is.).

Habitat – On limestone rocks on shaded stream-banks, just above normal water level, sometimes flooded, altitude 100–200 m (information from Dr. Schmutz).

Note – The type of Aspidium trifolium var. comptale is a young plant. The fronds consist of a simple or slightly trilobed lamina shaped as in immature plants of T. schmutzii; there are few sori.


*Aspidium burchardii* Rosenst., Meded. Rijksherb. 31 (1917) 3. — *Tectaria burchardii* (Rosenst.) C.Chr., Index Filic. Suppl. 3 (1934) 177. — Type: *Burchard s.n.*, Sumatra (L).


*Caudex* short, suberect; *stipe* to 70 cm long, mid-castaneous, glabrescent, basal scales to 15 × 2 mm, firm, glossy, twisted distally, fringed when young; *lamina* to 100 cm long consisting of 1–5 pairs of pinnae and pinna-like apex which may be joined to the uppermost pair of pinnae; *pinnae* to 25 × 6 cm, entire with narrowly cuneate base and caudate-acuminate apex; basal pinnae (sometimes 2 pairs) with stalk 2–3 cm long and a basiscopic lobe which may be more than 20 cm long; *main veins* 6–10 mm apart along costae and at a broad angle to them, distally upcurved; cross-veins rather regular, between them 2 irregular rows of areoles with included veinlets; *lower surface* of costa and main veins variably minutely hairy, upper surface usually quite glabrous; *sori* mostly on veins surrounding areoles, in a row on each side of a cross-vein, usually 4–6 in a row in the middle of a large pinna; indusia reniform, firm, persistent.

**Distribution** — *Malesia*: Sumatra, Malay Peninsula, Java, Borneo.

**Habitat** — In lowland forest, occasionally up to 1200 m.


*Caudex* suberect; *stipe* to 45 cm long, dull reddish, minutely hairy, basal scales to 10 × 1.5 mm, dark with a thinner ± fringed margin; *lamina* to 50 cm long consisting of a pinna-like apex (sometimes fused with the uppermost pinnae) and 1–4 pairs of opposite pinnae; *middle pinnae* to 25 × 5 cm, short-stalked, rounded to subcordate on their basiscopic bases, more narrowly rounded on the acroscopic side, apex abruptly short-acuminate, margins entire; *basal pinnae* with stalks 15 mm long, bearing a large basiscopic lobe; *main veins* 6–8 mm apart along costae, at a broad angle and upcurved, cross-veins rather regular between them; *lower surface* of costae and main veins short-hairy, short erect hairs also present between veins, upper surface of costae glabrous or sparsely hairy; *sori* small, at maximum development 4 or 5 in a row on each side of cross-veins, mainly on veins which surround areoles; indusia thin, rather small, shrivelling; n = 80 in Sri Lanka and S India.

**Distribution** — Nepal to Yunnan and to N Thailand and Tonkin, Taiwan, S India and Sri Lanka; in *Malesia*: E Java, Lesser Sunda Islands (Timor), Philippines (Luzon), and Celebes.

*Caudek* short, erect, with long tough roots; *stipe* 33 cm long, glabrous, basal scales not seen; *lamina* 33 cm long, firm, its apical section 19 × 1.8 cm joined at its base with the uppermost pinnae; pinnae all with narrowly cuneate bases and acuminate apices, upper ones 12.5 × 1 cm, third pair 16.2 × 1.4 cm, fourth pair 18 × 1.6 cm, basal pair 18 cm long (stalk 7 mm), 1.8 cm wide above its base with a basiscopic lobe 12 × 0.8 cm; *veins* about as in *T. lobbii*; both *surfaces* glabrous apart from sparse short hairs on lower surface of main veins; *sori* irregular in size and arrangement, inducia very small, reniform.

Distribution — **Malesia**: E Java, known only from the type.

Habitat — River bank; evidently a rheophyte, as *T. lobbii*.


*Caudek* short, erect, bearing a close tuft of stipes and many strong roots; *stipe* to 20 cm long, ± flushed with red, sometimes very dark, its basal scales flaccid, to 7 × 1 mm; *lamina* of young plants 3–5-lobed, of mature plants with 2 pairs of pinnae and a simple or trilobed apical lamina, not or little dimorphous; *apical lamina*, if simple, commonly 12 × 3 cm (to 17 × 6 cm), acuminate, margins entire or ± sinuous, a bud present on the upper surface near middle of the costa, if trilobed broadly cuneate at its base; *basal pinnae* commonly to 10 × 2 cm (to 17 × 2 cm), acuminate, with a narrower basiscopic lobe, on largest fronds the basiscopic lobe almost free and a small acroscopic lobe present also; *main veins* 6–7 mm apart along the costa, at 45°, sinuous, hardly prominent, smaller veins very slender but distinct; *lower surface* of costa sparsely short-hairy, upper surface densely; *sori* small, irregularly scattered, often ± elongate and confluent, usually on free branched veinlets in areoles, inducia very small, apparently lacking in some sori.

Distribution — **Malesia**: Philippines (Luzon, Samar).

Habitat — On rocks in stream-beds, apparently a true rheophyte.

76. **Tectaria rheophytica** Holttum, Blumea 35 (1991) 554. — Type: *J.R. Croft* 1681, Papua New Guinea, W Sepik, Blackwater Creek logging area (K; iso LAE).

*Caudek* short, erect; *stipe* to 28 cm long, sparsely minutely hairy, glabrescent and glossy, dark purplish brown; basal scales c. 10 × 1 mm, rigid, dark, persistent, narrower scales above base caducous; *lamina* to 25 cm long, rigid, consisting of a trilobed apex and 1 pair of pinnae; *apical lamina* to 20 cm long, its base rather narrowly decurrent, midlobe 3–4 cm wide, entire or with sinuous margins and narrowed to 2.5 cm wide at its base, lateral lobes to 10 × 1.2 cm, often unequal, their costae at 45° to the midlobe; *pinnae* 15 cm long with stalks to 7 mm long, somewhat dimorphous, sterile ones to 2.5 cm wide, fertile to 1.7 cm; each with a basiscopic lobe to 10 × 0.8–1.2 cm; *main veins* prominent on lower surface, other veins not prominent, distinct on young fronds only; *lower surface* glabrous, upper surface of costa and main veins sparsely hairy; *sori* small, irregularly scattered, exindusiate, many ± along veins but others on free veinlets in areoles. — **Fig. 15b**.

Distribution — **Malesia**: New Guinea (known only from the type and *Croft* 1623, foot of Mt Bougainville near West Irian border).

Habitat — On rocky or gritty clay river banks in the flood zone.

Note — The *sori* are arranged as in *T. christovalensis* (C.Chr.) Alston but the frond-form is different; the latter species is not a rheophyte.

Polydictyum plants

New pair nae,ing with ported than lamina
found a glabrous, connected when rheophyte;


Habitat Distribution 40 of of filiform 20-50
Type: scales;

— Jahrb. — Bot. 259; Aspidium

X scaly with dried, — Bot. Jahrb. Syst. 23 (1896) 354, non Kunze 1847. — Tectaria juglandifolia (Baker) C. Chr., Index Filic. Suppl. 3 (1934) 180. — Type: Horne s.n., Fiji.

Caudex long-creeping, commonly 3–5 mm diameter when dried (to 8 mm in New Guinea); stipe 20–50 cm long, lightly flushed reddish, glabrous, scaly near base only, scales c. 5 mm long with filiform apex and widened base; lamina not or little dimorphous, to 50 cm or more long, consisting of a pinna-like apex and 1–4(–6) pairs of pinnae, texture firm; apex commonly 20 × 3–4 cm (to 40 × 4 cm), sometimes united to uppermost pair of pinnae; basal pinnae usually unlobed (some New Guinea specimens have a small basiscopic lobe), commonly 24 × 3 cm (to 35 × 3.5 cm) with stalk 10 mm long, gradually narrowed to base and apex, usually entire; main veins 6–8 mm apart along costae, at 45° and upcurved, slender, cross-veins irregular, small veins slightly prominent when dried; both surfaces glabrous; sori small, on connected veins, mostly in 2 rather irregular rows between main veins with some additional ones especially towards the margin; indusia small, thin, glabrous, reeniform.

Habitat – In lowland forest, several times reported on or near stream banks but apparently not a rheophyte; several New Guinea specimens were found on limestone.

Note – Young plants have simple fronds, the lamina to 25 × 4.5 cm and fertile. New Guinea plants often have a thicker caudex and larger fronds than those from the Philippines, also very dark basal scales; scales on Philippine plants are dull brown with paler filiform tips.


Caudex long-creeping, 6–10 mm diameter when dried, bearing stipes c. 1.5 cm apart, scales 5 × 1 mm, base cordate, dark glossy with paler fragile edges; stipe 30–80 cm long, lightly flushed with red, glabrescent, scales near base as those of caudex but 10 mm long; lamina consisting of 1–4 pairs of pinnae and pinna-like apex; apex to 21 × 11 cm, entire, base cuneate, apex abruptly short-acuminate; upper pinnae sessile, to 21 × 6 cm with asymmetric base rounded on the basiscopic side; basal pinnae stalked, to 30 × 10 cm, asymmetric with a single basiscopic lobe to 20 × 6 cm (largest fronds may have 2 pairs of pinnae with basal lobes); main veins pale on lower surface, 8–10 mm apart along costae, at a wide angle and upcurved, cross-veins irregular; lower surface of costae and main veins bearing sparse short hairs, upper surface of costae densely short-hairy; sori mostly not on free veins in areoles, rather small, in a single row on each side of main veins but with additional ones irregularly between the rows; indusia thin, shrivelling but persistent.

Distribution – Thailand, Burma, Bangladesh; in Malesia: Malay Peninsula (Perak).
Habitat – Spreading over humus-covered rocks in steep rocky forest (type); some specimens from Thailand found on limestone.

79. Tectaria taccifolia (Fée) M.G. Price, Kali-

Caudex short, subectect, fronds strongly dimor- phous. Sterile frond: stipe 20–35 cm long (Cope-
land); lamina to 36 cm long; pinnae one pair, to 22 cm long, 4.5 cm wide, narrowed to base and apex, margins ± sinuous, a basiscopic lobe 14 ×
3.5 cm arising 3 cm above its base; rest of frond lobed to a narrow wing on each side of the rachis, the lobes 3 pairs, narrowed at their bases, apex of lamina conform with the upper lobes, the basal lobes 21 × 4.5 cm with short basiscopic lobules like the lobes of basal pinnae but shorter. **Fertile frond:** stipe to 50 cm long (Copeland); **lamina** to 30 cm long, divided as sterile frond but its lobes and pinnae not over 4 mm wide; pinnae of type 19 cm long with lobes 13 cm long; venation consisting of few narrow areoles, the veins bearing densely packed spongia throughout, so that the lower surface appears to be covered by them.

**Distribution** — **Malesia:** Philippines (Mindoro only).


**Aspidium pteropus** Kunze, Bot. Zeitung (Berlin) 4 (1846) 462; Mett., Farngatt. IV (1858) 120. — **Sagenia pteropus** (Kunze) T. Moore, Index Filic. (1858) 89; Bedd., Ferns S India (1863) pl. 82. — **Type:** *Cuming 148*, Luzon (holotype lost; isotypes BM, K, L, SING, Z).

**Cardiochaena alata** Fée, Mém. Foug. 5. Gen. Filic. (1852) 315. — **Type:** *Cuming 148*, Luzon (RB).

**Sagenia mamillosa** Moore, Ill. Hort. IV, 6 (1886) t. 598. — **Aspidium decurrens** var. *mamillosum* (Moore) Alderw., Malayan Ferns (1908) 247. — **Type:** Cult. ex Moluccas (K).

**Aspidium heterodon** Copel. in Perkins, Fragm. Fl. Philipp. (1905) 177, non Blume 1828. — **Type:** *Copeland 951*, Mindanao (MICH).

**Asplenium alatum** Ridley, Trans. Linn. Soc. Lond. 9 (1916) 225. — **Aspidium ridleyanum** Alderw., Malayan Ferns (1917) 505. — **Tectaria ridleyana** (Alderw.) C.Chr., Index Filic. Suppl. 3 (1934) 184. — **Type:** *C.B. Kloss s.n.*, W New Guinea, Mt Carstensz Exp. (K).

**Tectaria peralata** Copel., Philipp. J. Sci. 83 (1954) 98, t. 4. — **Type:** *Edano PNH 12297*, Luzon (MICH; iso BM).

**Aspidium macrophyllum** auct. non Sw. (1806): Blume, Enum. Fl. Javae (1828) 144.

**Caudex** short, erect; stipe to 50 cm long, winged except in basal 2–10 cm, the wing 5–10 mm wide on each side distally, basal scales 10 mm long, 1.5–2 mm wide at their bases, firm, distal scales narrow; **lamina** thin, lobed, to 60 cm long, the lobes 2–7 pairs joined by a wing, sterile ones to 7 cm wide, fertile narrower and sometimes with sinuous or irregularly lobulate margins, basal lobes sometimes bilobate; main lateral **veins** in lobes c. 10 mm apart along the costa, prominent on the lower surface, smaller veins amply anastomosing in sterile fronds, fertile ones with closer main veins and smaller areoles; **lower surface** of costae and main veins minutely hairy, minute hairs also sometimes present between veins, narrow scales ± abundant on lower surface of rachis and sometimes on costae of lobes (such scales apparently rare in W Malesia); upper surface quite glabrous; **sori** in a row on each side of main veins in lobes of the frond, also on rachis-wings, on free veinlets in areoles, variably somewhat immersed with corresponding projections on the upper surface; indusia large (crumpled when old), glabrous, round or elliptic, sometimes apparently peltate but more usually attached along a line from the centre to the base; **spores** spinulose.

**Distribution** — Widely in tropical mainland Asia; **Malesia:** W Malay Peninsula (in Perak only), Philippines, New Guinea; in the Pacific eastwards to Tahiti.

**Habitat** — In forest at low and medium altitudes.

**Note** — Young plants collected by M.G. Price in Luzon have unlobed linear fronds to about 30 cm long; such fronds may be fertile, the smallest fertile ones seen 9 cm long.

**Cytology** — T.G. Walker found that three plants in New Guinea were diploids; Manton found tetraploids in Sri Lanka. Structural differences between diploid and tetraploid have not been established.

**Possible hybrids** — In the Philippines and in New Guinea are intermediates between this species and
T. repanda; they have narrow fertile pinnae decurrent to a narrow wing on the rachis and a short stipe-wing.


Stipe to more than 70 cm long, dark castaneous, distal part narrowly winged, basal scales to more than 3 mm wide; lamina to 110 cm long, pinnatisect throughout to a wing along the rachis, wing above lowest lobes 4 mm wide on each side, wider in distal part of frond; lobes many, closely placed, entire, to c. 30 × 6 cm (both sterile and fertile), basal ones with a large lobe on the basiscopic side; lower surface of rachis and costae minutely hairy, upper surface glabrous throughout; veins anastomosing as in T. decurrens, the main lateral veins mostly ± sinuous, smaller veins distinct but hardly prominent on dried fronds; sori in one row on each side of main veins, some on free veins in areoles; indusia reniform.

Distribution — Malesia: Philippines (Luzon, Panay, Negros, Mindanao).

Habitat — In forest, to 1200 m altitude.

Note — M.G. Price, who has seen living plants on Mt Makiling, regards this as a distinct species, in frond-form between T. decurrens and T. crenata. It differs from the former in the firmer texture of the narrow rachis-wing which extends only a short distance below the lowest lobes of the lamina, in the more numerous and closer lamina-lobes, darker stipe and rachis and broad stipe-scales. The type of T. loheri Copel., though consisting of an almost complete frond, is imperfectly developed; that of T. sulitii is much better and is therefore preferred; they were published simultaneously. There may be intermediates between T. sulitii and T. crenata.


Nephrodium everettiæ Baker, Kew Bull. (1896) 41. — Aspidium everettiæ (Baker) C. Chr., Index Filic. (1905) 73; Alderw., Malayan Ferns (1908) 241. — Tectaria everettiæ (Baker) C. Chr., Index Filic. Suppl. 3 (1934) 179. — Type: Everetti s.n., Natuna Is. (K).

Tectaria clemensiae Copel., Brittonia 1 (1931) 73. — Type: Clemens 22078, Sarawak, Lundu (UC; iso K, NY).

Caudex short, erect; stipe usually winged in its distal part (wing 2–8 mm wide on each side in the type), basal scales to 10 mm long, 1.5 mm wide at base, firm and dark with paler margins; lamina on young plants trilobed, on mature plants consisting of a trilobed apical part decurrent by a narrow wing along the rachis which may or may not join with a pair of pinnae, lobes of pinnae usually wider in sterile than in fertile fronds; pinnae to 20 cm long, to 8 cm wide (sterile) or 4 cm (fertile), entire, acuminate, lacking basiscopic lobes, a small scaly bud sometimes present at base of costa on lower surface; venation similar in sterile and fertile fronds, forming many areoles containing branched free veinlets, the cross-veins between main veins very regular; lower surface of costa and main veins bearing sparse very short hairs, upper surface densely covered with thicker hairs; sori in 2 rows between cross-veins (4–5 irregular rows between main veins) on veins which surround areoles, some sori present also on rachis-wing; indusia reniform but when dried sometimes apparently peltate, bearing stiff hairs 0.3 mm long on their upper surface. — Fig. 15e, f.

Distribution — Malesia: Malayan Peninsula (Perak, Natuna Is.), Borneo (Sarawak, Kalimantan).

Habitat — In forest at low altitudes.

Note — There is much variation in width of lobes and pinnae and of the rachis-wing in different specimens. Buds at the bases of lateral lobes (of trilobed fronds) or pinnae occur on the types of A. tricuspe Bedd. and T. clemensiae Copel..

Hora: 39x252 Aspidium rowed mina long, winged between wide and spaced; ate, numerous, very short-hairy, lower ones more widely spaced; main veins in lobes connected by rather regular outwardly curved cross-veins, the areoles between them forming a very fine reticulum; lower surface of costae short-hairy, small scales sometimes present, short hairs also present on veins and very short slender ones between veins; sori very numerous, consisting of few sporangia, exindusiate, scattered irregularly on the smaller veins. –

Fig. 15d.


Habitat – In forest at low altitudes, to 900 m.


Caudex short-creeping; stipe to 40 cm long, winged except near its base, basal scales 10 mm long, less than 1 mm wide, their apices filiform, narrow scales ± abundant above base of stipe; lamina to 75 cm long, consisting of an elliptic apex and up to 6 pairs of lobes connected by a wing which is 8–10 mm wide distally and 3–4 mm wide near base of frond, lobes to 30 × 6 cm, narrowed towards their bases, lower ones more widely spaced; main veins in lobes connected by rather regular outwardly curved cross-veins, the areoles between them forming a very fine reticulum; lower surface of costae short-hairy, small scales sometimes present, short hairs also present on veins and very short slender ones between veins; sori very numerous, consisting of few sporangia, exindusiate, scattered irregularly on the smaller veins.

With sparse very short hairs; sori small, numerous, rather irregularly arranged on veins which surround areoles; indusia distinct, thin, ± reniform, their margins usually short-fringed when young.

Distribution – Assam and W Yunnan southwards to Burma and Thailand; W Malesia.

Habitat – In lowland forest.

Note – The type of T. decurrenti-alata is an unusually large specimen but not much larger than some from Assam and does not differ appreciably in other ways.


Frons of young plants lanceolate with undulate margins, the lamina c. 20 × 2.5 cm on a slender stipe 8 cm long, successive fronds longer and more deeply lobed, the lobes decurrent both towards base and apex; mature plants with short erect caudex, stipes to 60 cm long, their upper part winged, a deeply lobed lamina to c. 85 cm long, lower lobes a little decurrent and gradually more widely spaced than the upper ones, the rachis-wing c. 5 mm wide each side at the base, 10–15 mm distally; largest lobes c. 20 × 3 cm, hardly narrowed at their base, very gradually narrowed distally, margins entire near the base, minutely crenate-dentate distally; venation prominent on both sides when dried, forming many areoles between main veins; lower surface of costae and veins bearing minute hairs, upper surface quite glabrous; sori small, numerous, exindusiate, irregularly scattered, mostly on connected veins, rarely terminal on free veinlets in areoles; branched paraphyses as long as the sporangia present; spores with translucent wing and few cross-wings.

Distribution – Malesia: Sumatra, Malay Peninsula, Borneo (Sarawak).
Habitat – On rocks in forest, not on stream banks; fronds of mature plants pendulous.

86. Tectaria beccariana (Cesati) C. Chr., Index Filic. Suppl. 3 (1934) 177; C. Chr., Dansk Bot. Ark. 9, 3 (1937) 51; Copel., Philipp. J. Sci. 78 (1951) 419; Fern Fl. Philipp. (1960) 308.


Tectaria celebica C. Chr., Bot. Jahrb. Syst. 66 (1933) 49. — Type: Kjellberg 418, SE Celebes (5; BO).

Very near Tectaria vasta (Blume) Copel., differing in firmer texture of fronds with all veins prominent on lower surface, wider wing on stipe (to 2 cm wide on each side) and rachis, wider laminas; lobes on largest fronds (to 10 cm wide), basal ones of large fronds always with a large basiscopic lobe, sori exindusiate or rarely with very small indusia.

— Fig. 16f, g.

Distribution – Malesia: Borneo (Sabah), Philippines (Luzon, Negros, Samar, Mindanao), SE Celebes, widely in New Guinea.

Habitat – In forest at low to medium altitudes.

Notes – The relationship of this species to T. vasta needs experimental study. The widely distributed indusiate T. vasta must be the more primitive of the two; it does not occur in Taiwan, so that the Philippine T. beccariana may be an eastern development from T. vasta in Vietnam. In Sabah are possible hybrids between the two species.

The type of T. celebica is an immature plant; the lamina of its largest frond is 50 x 9 cm with entire or subreptand margins, fertile, with sori as in T. beccariana.

87. Tectaria novoguineensis (Rosenst.) C. Chr., Index Filic. Suppl. 3 (1934) 182. — Aspidium novoguineense Rosenst., Meded. Rijksinst. Fl. 31 (1917) 4. — Type: Zippel s.n., W New Guinea (L 908,302-327).

Caudex short, erect or suberect; stipe to 17 cm long, very dark, minutely hairy throughout, basal scales 5 mm long, very narrow; lamina simple, of young plants ovate-acute with deeply cordate base and irregularly shallowly lobed margin, of mature plants firm, 3-lobed to sub-5-lobed, to 12 cm long from top of stipe to apex and 11 cm wide, the lobes obtuse, irregularly slightly lobulate; both surfaces bearing many short slender erect hairs throughout; sori on free veinlets in areoles, rather large, irregularly arranged; indusia hairy.


Habitat – The second collection is from crevices in limestone on the north coast, near the border between W Irian and Papua New Guinea (Croft 1600). The type was probably also from limestone (some other Zippel collections certainly are).


Caudex short, suberect, its apex covered with narrow light brown scales; stipe very dark, glabrous, 25 cm long; lamina to 20 cm long and wide, its base subcordate, near base lobed halfway to the costa, less deeply distally, lobes subcaudate, the lowest largest and sometimes with a basiscopic acuminate lobule; lower surface rather densely covered with rufous hairs 0.2 mm long which are more dense near the margin, upper surface glabrous except near the margin; sori small, irregularly scattered, mostly not on free veinlets; indusia firm,
Fig. 16. Tectaria christovalensis (C. Chr.) Alston. a. Outline of a fertile frond, × 0.22; b. detail of a, showing pattern of sori mostly on free veins in areoles, × 2.2. — T. inopinata Holttum. c. Outline of a frond, × 0.4; d. detail of c, showing few simple included veinlets in costal areoles, × 1.7. — T. kehdingiana (Kuhn) M.G. Price. e. Portion of a fertile frond, with indusia removed on right side, × 2.6. — T. beccariana (Cesati) C. Chr. f. Outline of frond, × 0.16; g. detail of soral pattern in rachis-ring, × 1.7 (a, b: von Mueller coll. 1879; c, d: Matthew s.n., 29-11-1912; e: Boden Kloss 14766; f, g: Millar & Holttum NGF 15863).
dark, persistent, subpeltate, bearing a few hairs like those on the lower surface between veins:

Distribution – *Malesia*: Borneo (known only from the type).

Habitat – In forest at 650 m, 'epiphyte' (collector's label, but no other *Tectaria* species are thus reported).

89. *Tectaria nitens* Copel., Philipp. J. Sci. 56 (1935) 475, t. 6 — Type: *Clemens* 40652, Sabah, Mt Kinabalu (holotype PNH destroyed; iso MICH).

*Caudex* short, suberect, its apex densely covered with mid-brown narrow scales 5 mm long; *stipe* 20 cm long, very dark, glossy; *lamina* ovate in outline, to 18 × 12 cm, base deeply cordate with the basal lobes overlapping, near base lobed 1/3 towards the midrib, distally less deeply, the lobes contiguous, larger ones falcate and abruptly sub-caudate; *lower surface* quite glabrous, upper surface with some short hairs near the margin; *sori* irregularly arranged, not on free veins in areoles; indusia persistent, entire, reniform to peltate.

Distribution – *Malesia*: Borneo (known only from the type).

Habitat – Jungle hillside under cliff, 1200 m.


*Caudex* short with tufted stipes; *stipe* to 40 cm long, atropurpureous; basal scales to 12 × 2 mm, margins conform; *lamina* deltoid in outline, to 35 cm long and 30 cm wide at its base, deeply 3–5-lobed, the basal lobes with basal basiscopic lobes on the largest fronds; *apical lobe* narrowly acuminate, its margins sinuous on small fronds, lobulate with acuminate lobules on large fronds, basal lobes similar, their apices upcurved; *costae* beneath dark at their bases, paler distally, main veins slender, slightly prominent, at c. 45°, almost straight, smaller veins very slender and not prominent; *both surfaces* glabrous except for a few hairs near base of the midrib on the upper surface; *sori* rather irregularly arranged, irregular in outline, not on free veins in the areoles; indusia thin, small, persistent, with a fringe of short slender hairs and some on the upper surface, the hairs rarely conspicuous.

Distribution – *Malesia*: Philippines (type locality only).

Habitat – On dripping limestone cliffs, the fronds pendulous.


KEY TO THE VARIETIES

1a. Fertile fronds isomorphous with sterile ones, or nearly so, their lower surface glabrous between veins

2b. Fertile fronds much contracted, their lower surface bearing many hairs between veins

d. var. *dimorpha*

2a. Indusia distinct on all sori

3b. Indusia very small, hidden by sporangia, or lacking

c. var. *platanifolia*

3a. Costae densely short-hairy on upper surface

a. var. *palmata*

b. Costae glabrous on upper surface

b. var. *sumatrana*

1a. var. *palmata*

*Caudex* suberect with tufted stipes, its scales narrow distally; *stipe* very dark, minutely hairy (glabrescent), to 45 cm long, longer on fertile than on sterile fronds; *lamina* on young plants (sometimes fertile) elongate, unlobed, with cordate base and acuminate apex, on mature plants deeply 5-lobed, to c. 20 cm long and wide, the lobes entire, acuminate, a scaly bud present near the base on the upper surface; *costae* beneath minutely hairy near their bases, densely short-hairy on the upper surface; *sori* numerous, small, either on veins surrounding areoles or on free veinlets in areoles; *indusia* less than 1 mm diameter, reniform, persistent, with minutely papillose margins.

Distribution – *Malesia*: Borneo (Central & SE Kalimantan).

Differs from the typical variety in the costae being entirely glabrous and lightly sulcate above.
Distribution — **Malesia**: Sumatra (known only from the type).


Differs from var. *palmata*: sori much smaller and more numerous, exindusiate or with very small indusia hidden by sporangia, those on veins near costae sometimes a little elongate or confluent.
Distribution — **Malesia**: Borneo (Sarawak, many collections; E Kalimantan).

Habitat — In lowland forest, in some cases reported from wet ground.


Differs from the typical variety in the stipe being up to 20 cm long and in the contracted fertile fronds clothed with many 0.5 mm long or longer hairs between the veins.
Distribution — **Malesia**: Borneo (known only from the type locality).

Habitat — In wet ground by stream in shade; altitude 100–150 m.

Notes — The indusia of var. *dimorpha* are rather smaller than those on specimens of var. *palmata* and have papillae on the upper surface as well as on the margins; the sori are close together on the contracted lamina.

In both var. *platanifolia* and var. *dimorpha* a scaly bud is sometimes present at the base of the lamina, on the upper surface of the costa; such buds have not been seen in var. *palmata*.


*Caudex* short, erect, its apex covered with narrow scales which have filiform apices each consisting of a row of 10 or more cells; *stipe* to 18 cm long, slender, mid-castaneous, glabrous; *lamina* of fronds of young plants elongate and slightly tri-lobed, its margins ± sinus distally, of mature plants subequally tri-lobed, to 14 cm long, base shortly cordate, lobes entire, acuminate, midlobe to 5.5 cm wide, lateral lobes to 3 cm; *lower surface* bearing very short slender hairs throughout between veins, upper surface glabrous including costae of lobes; *main veins* of midlobe 8–10 mm apart along the costa, at a wide angle, slender, small veins forming areoles between them distinct but not prominent; *sori* small, irregularly scattered, mostly not on free veins in areoles, occasionally ± elongate, exindusiate.
Distribution — **Malesia**: Java, known from *Lobb 258 & 259* only.

Note — Thomas Lobb collected for Veitch in W Java in 1845–46; if these specimens in fact came thence, the species is now perhaps extinct.


*Caudex* short, erect or suberect; *stipe* dark castaneous, minutely hairy, to at least 22 cm long, basal scales to 7 mm long, not hair-pointed; *lamina* thin, to 28 cm long, deeply tri-lobed, its base not cordate, midlobe to 7 cm wide, narrowed to 1.2 cm at its base, lateral lobes to 18 x 5 cm, entire, short-acuminata; *smaller veins* concolorous on both surfaces, ± prominent; no *bud* present at base of frond; *lower surface* of costae and main veins minutely hairy, very short hairs variably present between veins, upper surface glabrous; *sori* small, mostly not on free veins in areoles, sometimes a little elongate; *indusia* very small and apparently variable in shape, bearing many un cellular acicular hairs.
Distribution — **Malesia**: New Guinea (known only from the type collection).

Habitat — On vertical clay bank in lowland forest; fronds horizontal or pendulous.

Note — Young plants have an almost evenly elliptic lamina with rounded apex and broadly cuneate base (those seen 3.9 x 2.5 cm).

Caudex short, erect, its apex covered with narrow shortly hair-pointed scales 5 mm long; stipe atrocastaneous, minutely hairy, of sterile fronds to 23 cm long, of fertile to 42 cm; sterile lamina very firm, rather narrowly ovate, acute, to 14.5 cm long, its base cordate, with a short acute lobe on each side near the base, width above the lobes 9.5 cm; fertile lamina similar in shape but somewhat smaller; lower surface of costae and main veins sparsely minutely hairy, between veins glabrous; upper surface of costae densely short-hairy, fewer hairs on main veins; sori small, abundant, irregularly scattered, exindusiate, often on veinlets in areoles but also on veins surrounding areoles, often ± elongate or coalescent.

Distribution — Malesia: Celebes (known only from the type collection).

Habitat — Ultradacical area, roadside on forest margin near a small waterfall.


Caudex short, erect; stipe of fertile fronds to 35 cm long, of sterile shorter, very dark, glabrescent; basal scales to 7 mm long, firm, not hair-pointed; lamina firm, commonly to 15 cm long (largest seen 25 cm), very deeply trilobed, the lateral lobes, especially on fertile fronds, usually with small basiscopical lobules of variable size, base of lamina not cordate; apical lobe of fertile fronds commonly 3–4 cm wide, of sterile variably wider; a scaly bud often present near the base of a lateral costa on the lower surface; small veins concolorous on lower surface, sometimes hardly distinct though evident by transmitted light; lower surface glabrous; upper surface of costae densely short-hairy near their bases, less so distally; sori mostly on free veins in areoles, exindusiate, often ± elongate or confluent. — Fig. 16a, b.

Distribution — Malesia: New Guinea; Solomon Is. (San Cristobal, Malaita).

Habitat — In lowland forest, sometimes on steep slopes; on limestone in Malaita Is.

Note — In Herb. Kew is a specimen from New Ireland which has the apical lobe deeply trilobed, agreeing in other respects.


Caudex short, suberect, scales narrow, to 3 mm long; stipe to 4.5 cm long, slender, dark, minutely hairy; lamina firm, ovate, base cordate, apex rounded, margins broadly crenate, to 4 cm long and 2.7 cm wide; both surfaces glabrous, including upper surface of costa; main veins not prominent, not reaching margin, smaller veins forming areoles with few included veinlets; sori sparse, some at the ends of veinlets in areoles; indusia round-reniform, persistent.

Distribution — Malesia: New Guinea (known only from the type).

Note — The type consists of one plant bearing a tuft of about 10 fronds, several of the larger ones fertile and similar in size.


Caudex suberect or partly decumbent; stipe 20–40 cm long, dark castaneous, minutely hairy at the base, basal scales to 8 mm long, narrow, with long slender tips; lamina broadly ovate, its base strongly cordate, apex very shortly apiculate, margins broadly and shallowly lobed (rarely distinctly trilobed) to sinuous, largest seen 18 × 12 cm,
smallest fertile 9 × 7 cm; main veins prominent on both surfaces, distinct to the margin, rather widely spaced, smaller veins forming many areoles with included veinlets; lower surface densely covered with slender erect hairs 0.5 mm or more long between veins, the hairs brownish when dried, upper surface more sparsely hairy; sori small, exindusiate, sometimes a little elongate, mostly on free veinlets in areoles.

Distribution – Malesia: Borneo (Sarawak and Kalimantan).

Habitat – On limestone, in rock crevices.

Notes – Hooker received two collections of specimens from limestone in Sarawak made by Thomas Lobb in 1857. They are mounted on separate sheets and evidently Lobb recognized them as distinct. But Hooker included both in one species; his t. 285B shows a frond from each sheet. He wrote the name Polypodium labrusca on one sheet only; which is now marked as lectotype; the specimens on the other sheet represent T. brooksi. Hooker omitted reference to hairs on the fronds, but Baker (1868) stated that the fronds are glabrous, thus misleading Raciborski who gave the new name Nephrodium vitis to a specimen of the true T. labrusca and was copied by Alderwerelt. See further comment under T. brooksi.

Probable hybrid: M. Kato et al. B5492 from Kalimantan has almost entire fronds, as in T. brooksi and shorter and more sparse hairs on the lower surface than in T. labrusca; it looks like a hybrid. The two species grow together, as noted by Brooks.

98. Tectaria brooksi Copel., Philipp. J. Sci. 6 (1911) Bot. 137, pl. 20b. – Aspidium brooksi (Copel.) C. Chr., Index Filic. Suppl. 1 (1913) 7. – Dicthyopteris brooksi (Copel.) Alderw., Malay. Ferns Suppl. (1917) 322. – Type: C.J. Brooks 26a, Bidi, Sarawak (MICH; iso BM).


Caudex short, erect or suberect; stipe dark near its base, less so distally, commonly 15 cm long, basal scales to 5 mm long and to almost 1 mm wide at base; lamina firm to rigid, simple, broadly ovate with strongly cordate base, apex short-acuminate, margins entire or irregularly slightly sinuous, commonly 8 × 5 cm, largest seen 17 × 10.5 cm, rarely ± trilobed; main veins sinuous, hardly prominent, upcurved; lower surface glabrous, upper surface of costa variably short-hairy, at least near the base of the lamina; sori irregularly scattered, mostly punctate but often ± elongate or confluent, exindusiate, on both free veinlets in areoles and on veins surrounding areoles.


Habitat – On limestone, at 0–1200 m, in rock crevices, sometimes growing with T. labrusca.

Note – See comment under T. labrusca. Cope- land (I.c. 1911) was the first person to note Aspidium labrusca sensu Hook. (1864) was based on specimens of two species; he distinguished between them in the brief diagnosis of his species.


In shape of lamina very near T. brooksi Copel., but thinner; basal scales to 8 mm long, very narrowly attenuate; largest lamina seen 16 cm long from attachment to stipe to the rather narrowly acuminate apex; free veinlets lacking in costal and costular areoles and very few, unbranched, in other areoles; sori exindusiate, irregular, nearly all ± elongate along veins, those on the outer veins of costal areoles longest. – Fig. 16c, d.

Distribution – Malesia: Borneo, known only from the type locality (two collections) and from G. Matang, Sarawak.

Habitat – In forest, not on limestone, on sloping ground.


Caudex short, erect; fronds very dimorphous. Sterile frond: stipe commonly less than 5 mm long (to c. 30 mm); lamina commonly to 15 × 6 cm (largest seen 24 × 7 cm), base ± cordate where stipe is short, cuneate where stipe is longer, margins entire or ± sinuous, not deeply lobed, apex obtuse; all small veins distinct on both surfaces; both surfaces quite glabrous. Fertile frond: stipe to 15 cm long, ± persistently scaly, scales thin, light brown, to 7 mm long and 0.5 mm wide; lamina to 12 cm long, commonly 8 mm wide, very gradually narrowed to base and to apex; margins often ± sinuous; very narrow scales present on lower surface of costa; venation much reduced and lacking included veinlets in areoles, the main veins very oblique, connected by simple cross-veins; sori spreading all along cross-veins.

Distribution – Malesia: Java, SW Celebes, Moluccas (Tanimbar Is., Ambon).

Habitat – On steep earth banks in shaded places, especially near streams, at low altitudes.


Gymnopteris trilobata J. Sm. ex Hook., Icon. Pl. 10 (1854) t. 7. — Lectotype (selected here): T. Lobb s.n., Luzon (K).


Closely related to T. zollingeri, differing as follows: lamina of sterile fronds of larger plants variably ± deeply lobed, sometimes very deeply, with lamina to 30 cm long having several pairs of lobes to 14 × 3.5 cm connected by a narrow wing along the midrib, the wing decurrent below the lowest lobes; lower surface of midrib of frond, costae of lobes and main veins always bearing many short hairs; lamina of simple fertile fronds to 3 mm wide and up to 15 cm long, larger fertile fronds irregularly lobed as sterile, the lobes commonly 3 mm wide (intermediates between sterile and fertile fronds, with wider lobes, may occur).

Distribution – Malesia: N Borneo, Philippines (Luzon, Leyte, Panay, Mindanao).

Habitat – On damp clay banks in shade, low country (C.G. Matthew).

Note – Under Hemionitis gymnopteroidea Copeland briefly described forma major, based on a plant with large simple sterile fronds, Copeland 1398, of which no specimens now exist (M.G. Price). Christ’s new name Hemigramma zollingeri var. major was based on Copeland’s Hemionitis gymnopteroidea forma major, but Christ described deeply lobed fronds and cited other specimens.


Caudex short, erect; fronds strongly dimorphous. Sterile frond: stipe c. 5 cm long, basal scales less than 1 mm wide; lamina to 35 × 5 cm, widest above the middle, narrowed very gradually towards the base, apex hardly acuminate; main veins hardly prominent on the lower surface, always ± sinuous, free veinlets present in areoles between them; both surfaces glabrous. Fertile frond: stipe c. 25 cm long, lamina to 25 × 2 cm; veins forming 3 rows of ± hexagonal areoles between midrib and margin, one free vein in each areole; sori on free veins in
areoles; *indusia* elliptic in outline, c. 3–4 × 2 mm when young, firm and persistent. — **Fig. 16e**.

Distribution — *Malesia*: Sumatra (NE and Mentawai Is.).

Habitat — Low altitude; no details.


Fronds simple, differing from those of *T. singaporeana* as follows: *caudex* perhaps not erect; unwinged stipes of fertile fronds to 4 cm long; *lamina* of fertile fronds c. 30 cm long, 10–13 cm wide, abruptly narrowed near the base to a wing 1–2 cm wide on each side of the midrib; upper surface of *midrib* densely short-hairy, fewer similar hairs on main veins.

Distribution — *Malesia*: Borneo (known from the type only).

Habitat — In forest at 180 m altitude.


*Caudox* erect, to 10 cm tall; fronds somewhat dimorphous; *stipe* of sterile fronds commonly to 10 cm long, of fertile ones to 25 cm, basal scales 8 mm long, mid-castaneous, narrow, rather closely fringed when young; *lamina* simple, widest about 1/3 from the base, sterile to 40 × 12 cm, fertile to 7 cm wide, margins entire, apex short-acuminate, base ± abruptly narrowed (more abruptly in sterile than in fertile fronds) and narrowly decurrent for a short distance; *main veins* c. 10 mm apart near base of lamina, cross-veins between them rather regular, 2 rows of areoles between cross-veins; both surfaces glabrous including midrib; *sori* to 6 in a row on each side of cross-veins, not on free veins in areoles; *indusia* petalate or nearly so, entire, sometimes with a few short hairs on upper surface.

Distribution — Peninsular Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo.

Habitat — In lowland forest, rather common in the Peninsula but little collected elsewhere.


Similar in habit and frond-form to *T. singaporeana*, differing as follows: *fronds* smaller, sterile ones little wider than fertile; largest fertile lamina 18 × 3 cm, its narrowly decurrent base 10–15 mm long; margins rather regularly sinuate-crenate (one main vein to each lobe) to a depth of 2–3 mm; *main veins* c. 6 mm apart along midrib, cross-veins very irregular; lower surface of midrib minutely hairy, upper surface more copiously so; *sori* fewer, rather irregular; *indusia* apparently mostly reniform.

Distribution — *Malesia*: Sumatra (known from type collection only).

Habitat — In forest at 150 m.

**PSOMIOCARPA**


Habit, scales and frond-form as *Tectaria ramosii* but fronds smaller and strongly dimorphous; leaflets of fertile fronds much contracted, almost circular, their convex lower surface densely covered with sporangia which obscure the small upper surface. — **Fig. 17**.

Distribution — *Malesia*: One species, widely distributed in the Philippines.

Cytology — Chromosome number n = 40 (see the species).
Note — John Smith published the name *Polybotrya apiifolia* for Cuming 26, but no description; Kunze published the first description under the same name. Presl proposed the new generic name *Psomiocarpa*, including also three other species now generally retained in *Polybotrya*, and stated that they differed from *Polybotrya* in bearing sporangia all over the upper surface of fertile leaflets or lobes, though Kunze had stated that an upper surface free from sporangia was visible. The species *P. apiifolia* was transferred to *Acrostichum* by Hooker and the genus was ignored by other authors until Copeland, who, however, repeated the erroneous statement that sporangia are borne on both surfaces. In 1947 Copeland regarded *Psomiocarpa* as 'in every respect except its dimorphism ... a typical *Ctenitis*', but Zamora and Chandra noted resemblances to free-veined *Tectaria* species and anatomical differences from *Ctenitis* (but no species of the latter mentioned). The close relationship to *Tectaria ramosii* is confirmed by the existence of hybrids. *Tectaria ramosii* also hybridizes with *T. aurita* (Sw.) Chandra (type species of *Stenosemia*).

The retention of *Psomiocarpa* as a genus distinct from *Tectaria* is based on the very specialized structure of its fertile leaflets, a structure which still needs a detailed study.

![Figure 17](image-url)

**Fig. 17. Psomiocarpa apiifolia** (Kunze) Presl. a. Outline of a sterile basal pinna, × 0.6; b. enlargement of upper surface of a pinnule, × 4; c. outline of a fertile frond, × 0.6; h. enlargement of base of basal pinna, × 20 (a, b: *Matthew* s.n., 28-11-1906; c, d: *Price* 1543, cult. Kew).


_Caudex_ short, erect; scales 3–4 mm long, narrow, dark; fronds strongly dimorphous. **Sterile frond**: stipe to 7 cm long, covered with hairs 1 mm long and very narrow scales; _lamina_ to 13 cm long, bipinnate above base, deltoid-pentagonal in outline; pinnate, pinnae to 6 pairs, middle ones bearing 3 or 4 pairs of sessile or adnate deeply lobed pinnules, basiscopic basal veins in larger adnate
ones arising from the major axis; *basal pinnae* to 6.5 cm long, their basal basiscropic pinnules to 2.8 × 1.3 cm, very deeply lobed above a pair of free basal leaflets; *veins* all free; thick hairs present between veins on upper surface. *Fertile frond*: stipe to 25 cm long; *lamina* to 10 cm long, shaped as sterile but all parts much contracted; *basal pinnae* to 4 cm long, basal basiscopic pinnule to 1.2 cm long, pinnules on acrosopic side to 1.5 × 1.5 mm, each with a narrow firm upper surface free from sporangia and a swollen lower surface covered with them, veins not detectable externally; spores with finely reticulate crests. — Fig. 17.

**AENIGMOPTERIS**


*Caudex* suberect; scales *Tectaria*-like; *lamina* of fronds much longer than wide, bipinnate; basal pinnae little longer than the next pair with elongate basal pinnules; middle pinnae with many subequal deeply lobed pinnules or pinna-lobes which are decurrent at their bases to form a very narrow wing along the pinna-rachis; *veins* free, not reaching the margin, pinnate in pinnules, the basal basiscopic veins not arising from the pinna-rachis; scales on smaller axes few, linear or the smallest ovate, not thin nor with isodiametric cells; scattered thick hairs present on upper surface of lamina between veins; small sub-spherical unicellular glands present on lower surfaces of veins but not elongate cylindric ones; *sori* at the apices of veins (distal ones sometimes apical on short lateral veins); *indusia* firm, dark, persistent, of sori near the bases of lobes reniform, of distal sori variously asymmetric; sporangia sometimes bearing a short hair near the annulus; perispore forming thin ridges or crests with spinulose margins, the ridges forming a few irregular areoles, the surface within areoles bearing irregular short projections. — Fig. 18.

Distribution — *Malesia*: Five known species in the Philippines, Western New Guinea and Borneo.

**KEY TO THE SPECIES**

1a. Upper surface of pinna-rachis, at least distally, prominent and bearing short hairs; scales of pinna-rachis broad at the base, tapering distally, not dark ... 1. *A. dubia*
b. Upper surface of pinna-rachis slightly grooved, the groove filled with many short hairs; scales on pinna-rachis dark and narrow ........................................... 2

2a. Pinnules of middle pinnae c. 4 mm wide, their lobes c. 1 mm wide ... 2. *A. pulchra*
b. Pinnules of middle pinnae c. 7 mm wide, their lobes c. 2 mm wide ............... 3

3a. Thick hairs c. 1 mm long on lower surface of veins ....... 3. *A. mindanaensis*
b. Thick hairs lacking on lower surface of veins ........................................ 4

Distribution — *Malesia*: Philippines.

Variability (see Holttum 1984) — M.G. Price, who saw many plants in the field, reports that there are two forms of this species, a larger one with erect sterile fronds and a smaller one with horizontal sterile fronds, also that spores of the two differ. Herbarium specimens do not show this difference clearly. Further field studies are needed.

Cytology — Chromosome number 41 was reported by T.G. Walker in Bot. J. Linn. Soc., Suppl. 1, 67 (1973) 109, but Dr Walker in 1987 has written to correct this to 40, thus agreeing with *Tectaria*.
4a. Pinnule-lobes on first suprabasal pinnae deeply lobed; the thick hairs present on upper surface rigid, more than 1 mm long, short hairs also present ... 4. A. katoi
b. Pinnule-lobes on first suprabasal pinnae not deeply lobed; thick hairs between veins on upper surface not rigid, no other hairs present ............... 5. A. elegans


Caudex suberect, bearing few fronds, its apex covered with dull brown scales 10 x 1 mm; stipes to 30 cm long, dark castaneous, bearing ± persistent scales throughout, also short ctenitoid hairs in the groove; lamina to 55 cm long and 24 cm wide; free pinnae to 7 pairs, adnate pinnae to 7 or more pairs, the distal ones with very narrowly decurrent bases merging into the apical lamina of the frond the axis of which is very narrowly winged, as is the greater part of every pinna-rachis; a bud sometimes present at the base of an upper pinna; basal pinnae to 14 cm long bearing 4 pairs of free pinnales, rest of pinnae lobed to a very narrow wing along the rachis; basal basiscopic pinnae to 7.5 cm long, nearly 3 cm wide, bearing several pairs of well-spaced tertiary leaflets, all deeply obliquely lobed with narrowly decurrent bases; basal acroscoptic pinnae to 3.5 x 1.1 cm, only its basal lobes lobulate; second pinnae to 11 cm long with 1 pair free pinnales and others adnate; pinnales and larger pinna-lobes of middle pinnae like tertiary leaflets of basal pinnae; lower surface of pinna-rachis bearing thick ctenitoid hairs 0.5-1 mm long and a few ovate-acuminate scales, smallest scales ovate; lower surface of pinna-lobes bearing a few thick hairs on costules and veins; upper surface of pinna-rachis prominent, glabrous, of lamina between veins and of rachis-wing bearing scattered very thick hairs 0.5-1 mm long; sori in lobules of pinna-lobes, apical on veins; indusia firm, reniform, glabrous, those of distal sori asymmetric.

Distribution — Malesia: New Guinea (known only from the Idenburg River; 2 collections).

Habitat — On banks of stream in forest at 850 and 1150 m.


Stipe c. 30 cm long, dull castaneous, bearing long hairs in the groove; basal scales 13 mm long, less than 1 mm wide, very firm, dark; scales above base gradually smaller; rachis bearing rather sparse scales abaxially, adaxially hairs more than 1 mm long; lamina to 45 cm long and 24 cm wide, firm; free pinnae c. 15 pairs, contiguous, distal ones grading into the apical lamina; basal pinnae to 13.5 cm long with 1 pair of free pinnales and several with decurrent bases, all acuminate and deeply lobed with well-spaced, narrow, oblique lobes which are deeply and obliquely lobulate; basal basiscopic pinnae 5.2 x 1.6 cm, acuminate, its lobulate bases 9 x 3.5 mm, their bases 4 mm apart, their lobules 1 mm wide; basal acroscoptic pinnae 3.4 x 1.4 cm; second pair of pinnae with subequal basal pinnales; fourth pair of pinnae 12 x 3.5 cm; pinnales of middle pinnae 4 mm wide, their lobes 1 mm wide; lower surface of pinna-rachis bearing many thick hairs and sparse narrow scales, of costae of pinnales similarly but more sparse hairy, of costules of pinna-lobes and on veins a few smaller hairs and small spherical glands; upper surface of pinna-rachis bearing many small hairs and scattered very thick ones more than 1 mm long, similar long hairs present on pinna-lobes between the veins; sori as in A. dubia; indusia sometimes papillate.

Distribution — Malesia: New Guinea (known only from the Idenburg River; 2 collections).

Habitat — On banks of stream in forest at 850 and 1150 m.


Stipe 30 cm long; lamina 35 cm long, agreeing with that of A. dubia but with pinnales or pinna-lobes more closely placed and the pinna-lobes less
deeply lobulate; upper surface of pinna-rachis slightly grooved and covered with very short hairs; long thick hairs like those between the veins of leaflets also occurring on the wing of the pinna-rachis and sometimes on the margins of the rachis itself with the short hairs; scales on pinna-rachis few, all linear; sori as in A. dubia.

Distribution - Malesia: Philippines (known only from the type collection).

Note - Specimens of the type collection were distributed from Manila as Dennstaedtia sp.


Caudex c. 8 mm diameter, bearing stipes in a lax spiral; shape of pinnae and pinnules as in A. mindanaensis; hairs on upper surface of leaflets between veins very thick, rigid (cell-walls not collapsing on drying), tapering to an acute apex, to 1 mm long and consisting of 5 or 6 cells, short suberect hairs also present; no long hairs on lower surface of costules and veins.

Distribution - Malesia: Borneo (known only from the type collection).

Habitat - In forest, in humus-rich soil, 800–1400 m.

5. **Aenigmopteris elegans** Holttum, Blumea 30 (1984) 8, f. 1b, c, pl. 1b. — Type: Parris & Croxall 9135, Sabah, Mt Kinabalu (K).

Stipe 32 cm long, dark castaneous, bearing throughout narrow dark scales and sparse rather thin hairs to 1 mm long; basal scales to 12 mm long, less than 1 mm wide, rachis similarly scaly; lamina c. 40 cm long; free pinnae 4 pairs, then c. 10 pairs with adnate decurrent bases, the upper ones grading into the apical lamina in which the deeply lobed lobes are connected by a narrow wing along the rachis; a bud sometimes present at the base of one or more pinnae; basal pinnae 12–13 cm long including stalk of 5 mm; basal basiscopic pinnule to 6.5 × 2 cm, lobed to a narrow wing throughout, the costules of its lobes (or tertiary leaflets) 5 mm apart, the lobes oblique with obtuse apex, to 11 × 4 mm, deeply lobulate with 3 or 4
pairs of very oblique lobules 1 mm wide; the successive basiscopic lobes of basal pinnae gradually smaller and with less deeply lobulate lobes; basal acroscopic pinnule 3.3 x 1.2 cm; middle pinnae sessile, c. 10 x 3 cm, lobed throughout to a narrow wing, the lobes almost all deeply and obliquely lobulate, those of the acroscopic and basiscopic sides nearly equal, the basal acroscopic lobules of the largest lobes only slightly crenate; the lower surface of pinna-rachis bearing many short hairs and a few narrow dark scales, of costae of pinna-lobes sparsely short-hairy, of costules of lobules bearing minute spherical glands; the upper surface of pinna-rachis shallowly grooved and bearing many short hairs with a few long ones, of the surface of the lobes between veins bearing thick flaccid hairs consisting of up to 8 cells; sori as in A. dubia; sporangia sometimes bearing a very short hair consisting of a few cells, near the annulus. — Fig. 18.

Distribution — Malesia: Borneo (Mt Kinabalu, Sabah).

Habitat — In forest at 1400–1600 m, the type from a ridge slope.

HETEROGONIUM


Tectaria auct.: C. Chr., Index Filic. Suppl. 3 (1934) 176, p.p.

Caudex short, erect; stipe and rachis usually blackish; lamina simply pinnate with deeply lobed pinnae; basal pinnae widest in the middle of the basiscopic side and on that side narrowed to the base, rarely with a pair of free pinnules; veins free or forming a series of costal and costular areoles, in species with broad pinnae more amply anastomosing, free veins in the areoles none or few, never forked; basal basiscopic vein of each vein-group, whether free or not, arising from the costa or from the very base of the costule; upper surface of rachis and costae bearing short multicellular hairs, longer thick multicellular hairs variously present on the upper surface on and between veins (often fewer in fertile than in sterile fronds); fertile fronds usually with narrower pinnae than sterile, in a few cases much contracted and covered beneath with sori; sori round with reniform indusia, or exindusiate and then sometimes spreading along the veins, on free veins where these are present in the pinna-lobes, or on connected veins. — Fig. 19.

Distribution — Burma to South China; Malesia; Mauritius; 22 known species.

Cytology — Chromosome number n = 41.

Taxonomy — In the 19th century the species here brought together were very variously treated by different authors. Specimens of the type species were assigned to the genera Stenosemia, Gymnogramma, Digrammaria, Phegopteris and Aspidium, of other species to Nephrodium, Dryopteris, Lastrea, Polypodium, Acrostichum, Polybotrya and Pleocnemia. As here construed (following Holttum 1949 and 1975) Heterogonium might rank as a subgenus of Tectaria. As in Tectaria, it comprises species with free and anastomosing veins, but differs constantly in the shape of basal pinnae and in the venation of species which have broad pinnae, also in a more frequent tendency to the exindusiate condition
with sori more or less spreading along veins, and to an apparently acrostichoid condition where the fertile pinnae are greatly contracted.

Presl’s type species has the venation of Sagenia Presl with exindusiate sori spreading a variable distance along the veins. The genus was ignored by other authors until Copeland added another species in 1929. Copeland failed to notice the form of basal pinnae. Christensen added two more species in 1934; these are here united as H. stenosemioides which, having free veins, does not correspond to Copeland’s definition of 1947 and was ignored by him.

In 1938 Ching made the first attempt to deal with Ctenitis in Asia. In the New World Christensen had found that Tectaria and Ctenitis agree in having hairs of a peculiar type (a character ignored in the 19th century) and remarked that they were distinct in the anastomosing veins of Tectaria and the free ones of Ctenitis. But in Asia Ching found that there were free-veined species which agreed with Tectaria, not Ctenitis, in some details of venation, and proposed for them the new genus Ctenitopsis. In it he included six species which have basal pinnae as in Tectaria and two with basal pinnae of the Heterogonium form here recognized; all those published before 1905 had been included in Dryopteris in Christensen’s Index Filicum. Copeland (1947) included Ctenitopsis in Ctenitus, without comment on basal pinnae.

Holttum (1949 and 1975) contended that the recognition of the form of basal pinnae as a distinctive character separated Heterogonium as a natural group from Tectaria when all relevant species are considered. But there is one known case of apparent hybridization between a species having basal pinnae as in Tectaria (T. aurita) with one having basal pinnae as in Heterogonium (H. pinnatum). Experimental study of the relationships between these and other species of the two genera is needed.

Note on using the key — In nearly all species the pinnae of fertile fronds are ± reduced as compared with pinnae of sterile fronds. In species which normally have much-contracted fertile pinnae intermediates between this condition and sterile pinnae may occur, and these may mislead users of the key. In some species also, notably H. profereoides, young plants which do not show the normal frond form and size may be fertile.

KEY TO THE SPECIES

1a. Veins free or with irregular slight anastomosis ........................................ 2  
b. Veins anastomosing in sterile fronds ......................................................... 12  
2a. Pinnae c. 3 cm long; veins 3 or 4 pairs, nearly all simple ............................. 1. H. ceramense  
b. Pinnae much longer; veins 6 or more pairs, mostly forked .............................. 3  
3a. Sori indusiate ............................................................................................... 4  
b. Sori exindusiate ............................................................................................. 8  
4a. Hairs between veins scattered all over upper surface ...................................... 5  
b. Hairs between veins on upper surface present only near sinuses and margins of pinna-lobes ................................................................. 6. H. subglabrum  
5a. Pinna-lobes at most crenate ........................................................................... 6  
b. Pinna-lobes, except those of distal pinnae, distinctly lobulate .......................... 5. H. lobulatum
6a. Lamina of largest fronds 30–40 cm long; suprabasal fertile pinnae to 12 × 2.5 cm

2. H. sagenioides

b. Lamina of largest fronds 50–75 cm long; suprabasal fertile pinnae to 15 cm or more long, 2.5–4 cm wide. .................................................. 7

7a. Stipes rusty brown, not glossy ............................................ 3. H. rufescens

b. Stipes nearly black, glossy ................................................. 4. H. wigmanii

8a. Fertile pinnae not greatly contracted; most sori separate ........................................ 10

b. Fertile pinnae with lobes much contracted ........... 10. H. stenosemioides

9a. Basal pinnae of fertile fronds bearing deeply lobed pinnules .... 7. H. wenzelii

b. Basal pinnae of fertile fronds wholly pinnatifid .............. 10

10a. Lobes of suprabasal pinnae entire or nearly so ................. 11

b. Lobes of suprabasal pinnae distinctly crenate ................. 9. H. novoguineense

11a. Several pairs of pinnae with stalks 3–4 mm long; all pinnae lobed to 3–4 mm from costules ...................................................... 8. H. calcicola

b. Pinnae mostly sessile, lobed more deeply ............... 2. H. sagenioides

12a. Young fertile fronds with distinctly separate sori ............. 13

b. Young fertile fronds with sporangia running along all veins and at maturity covering lower surface of pinna-lobes ................. 18

13a. Young sori round, indusiate, on pinna-lobes 1.5–2.5 mm wide, completely covering lobes when mature ..................................... 11. H. alderwereltii

b. Young sori of varied form; if indusiate on much wider pinna-lobes which they do not cover when mature .................................. 14

14a. Sori all irregularly elongate along veins, exindusiate ........ 15

b. Sori all round to elliptic, not linear, indusiate or not .......... 16

15a. Suprabasal pinnae of mature plants to 13 × 2.5 cm, lacking costular areoles; no buds on upper surface of sterile fronds .... 12. H. aspidioides

b. Suprabasal fertile pinnae of mature plants to 25 × 5 cm; several pairs of costular areoles present; buds present on upper surface of some costae of sterile fronds near the rachis .......................................... 13. H. profereoides

16a. Sori in one row on each side of costules of pinna-lobes ........ 17

b. Sori on each side of veins which run to crenatures on margins of pinna-lobes .......................... 15. H. pluriseriatum

17a. Basal pinnae of fertile fronds bearing 1 pair of free pinnules and 2 or 3 pairs adnate .... 7. H. wenzelii

b. Basal pinnae of fertile fronds lacking pinnules ............... 14. H. giganteum

18a. Fronds to 70 cm long; sterile pinnae to 21 × 4 cm ....... 16. H. teysmannianum

b. Fronds to 30 cm long; sterile pinnae much smaller .......... 17. H. pinnatum

1. Heterogonium ceramense Holtum, Kali-
kasan 4 (1975) 217 — Type: Buwalda 5711,
Central Ceram, Mt Solagor, 600 m (K; iso L).

Stipe to 10 cm long, slender, dark brown, near base bearing narrow scales 4–5 mm long; fronds isomorphous; lamina to 17 cm long; free pinnae 9 pairs, short-stalked; basal pinnae slightly shorter than those next above them, their middle width 1.1 cm; largest suprabasal pinnae 3 × 1 cm, lobed 2/3 or more towards the costa, lobes slightly crenate distally; veins 3 or 4 pairs, mostly simple; lower
surface bearing few hairs on costa and costules only; upper surface of costae densely hairy, a few thick hairs present between veins especially near sinuses; sori small, subterminal on veins; indusia small, caducous.

Distribution – Malesia: Moluccas (Ceram; only known from two collections).

Habitat – In limestone crevices, in light shade.


Stenosemia aurita auct.: Hook., Gen. Fil. (1842) t. 94, for f. 5 & 6 only.

Aspidium membranifolium auct.: Kunze, Bot. Zeit. (Berlin) 6 (1848) 261.

Phegopteris philippinensis auct.: Mettt., Farngatt. IV (1858) 26, for var. 2 only.

Heterogonium taysmannianum auct.: Holtttum, Reinwardtia 1 (1950) 29, for Cuming 302 only.

Heterogonium gurupahense auct.: Holtttum, Reinwardtia 3 (1955) 271, for pl. ex Malaya et Thailand only.

Süpe to c. 50 cm long, dark, above base minutely hairy on abaxial surface, basal scales thin, to c. 10 × 1.5 mm; fronds slightly dimorphous, those with broadest pinnae always sterile; lamina commonly 30–35 cm long (to 45 cm); pinnae 10–15 pairs, sessile or nearly so; suprabasal pinnae of fertile fronds to 12 × 2.5 cm, lobed to 1–2 mm from the costa, basal acroscopic lobes sometimes elongate and crenate, other lobes obtuse with ± sinuous margins, of sterile fronds to 15 × 3.5 cm, lobes often entire or nearly so; basal basiscopic lobes of basal pinnae always much shorter than acroscopic ones, middle lobes on basiscopic side longer than acroscopic ones, the largest 3.5 cm long and crenate-lobate with pinnate veins in the lobes, middle acroscopic lobes often crenate-lobate on fertile fronds; veins mostly forked except distal ones; lower surface variably hairy on costae, veins and between veins, costal hairs on sterile fronds often more than 1 mm long, fertile fronds always less hairy, sometimes almost glabrous; upper surface of sterile fronds in most cases ± copiously short-hairy between veins with ± abundant long thick hairs also, fertile fronds less hairy than sterile, not always with some thick hairs between veins; sterile fronds of lowland plants sometimes bearing thick hairs only between veins; sori terminal on veins, usually on acroscopic branches of forked veins; indusia brown, thin, glabrous, soon shrivelling, or lacking. – Fig. 19a, b.

Distribution – Thailand, S Burma, Vietnam, Hainan; Malesia: West (most abundant in the Peninsula), Philippines.

Habitat – In forest at c. 0–800 m.

Notes – Philippine specimens are mostly smaller than those of the Malay Peninsula; some quite
small ones are fertile and very hairy, perhaps from exposed places.

The only exindusiate specimens known are the types of Polypodium obscurum Hook. and Phegopteris schizoloma Alderw. I see no clear distinction, other than lack of indusia, between these and the range of indusiate specimens as above described.

There was much confusion in the synonymies of various authors, due to various causes discussed by Holtum in 1975 under H. obscurum. The chief were Hooker's mixture of drawings from different specimens under Stenosemia aurita (1842), the citation of Phegopteris obscura Fée as a basionym though a nomen nudum, and the fact that no author besides Hooker saw specimens of Cuming 302. Basal pinnae on the specimens of Cuming 302 from Herb. Hooker at Kew are nearly all defective, and those of the sterile frond in the photograph reproduced as fig. 1 by Holtum in 1975 are lacking.


Stipe and rachis castaneous, minutely hairy on abaxial surface, basal scales to 15 mm long, hardly 1 mm wide; fronds slightly dimorphous, the lobes of fertile pinnae narrower and more widely spaced than those on sterile fronds; lamina to 75 cm long; pinnae to c. 20 pairs, to 20 cm long, lobed almost to the costa; basal pinnae to 7 cm wide in the middle, the longest basiscopic lobes 6 cm long, very deeply lobulate; suprabasal pinnae to 4 cm wide, costules 6–8 mm apart (most widely in sterile fronds), fertile lobes 3–4 mm wide, crenate, sterile ones to 6 mm wide, crenate-lobate; veins in lobes almost all once forked (paucipinnate in largest lobules of basal pinnae-lobes); lower surface of costa of sterile fronds bearing dense short pale hairs, upper surface between veins bearing many short slender hairs and some long thick pale ones, surfaces of fertile pinnae similar but bearing very few thick hairs between veins on the upper surface; sori subterminal on the acrosiscoic branches of forked veins; indusia thin, light brown.


Habitat — In forest at 250–800 m, the type ‘on well-drained slopes of stiff loam mixed with limestone chips’, a specimen from Los Negros island ‘at base of limestone cliff’.


Similar to H. rufescens in size and form of fronds; differing: stipe and rachis very dark and glossy on the abaxial surface; lobes of both sterile and fertile pinnae at most crenate; lower surfaces of costae of sterile pinnae bearing sparse slender rufous hairs 1 mm long, upper surface lacking short hairs between veins. — Fig. 19e.

Distribution — Malesia: Celebes, Moluccas (Morotai, Ceram, Aru Is.).

Habitat — In forest, 0–1000 m; on ravine slopes in limestone area (Ceram).


Closely similar to H. sagenioides in frond-form, venation and pubescence but possibly less distinctly dimorphous, differing in the distinctly lobulate lobes of all pinnae, those on the basiscopic side of basal fertile pinnae most deeply so with veins pinnate in each lobule; lobes of suprabasal pinnae lobulate up to halfway towards costules, the lobules mostly falcate, acute.

Distribution — Malesia: Philippines (known only from the type collection).

Habitat — In primary forest on limestone and limestone-derived soils.

Fig. 19. *Heterogonium sagenioides* (Mett.) Holttum. a. Outline of a fertile basal pinna, × 0.6; b. detail of one median acroscopic lobe of a, × 4. — *H. wigmanii* (Racib.) Holttum. c. Two median lobes of a middle pinna, × 4. — *H. pinnatum* (Copel.) Holttum. d. Outline of a sterile basal pinna, × 0.6; e. fertile lobes with sori removed from right lobe to show attachment areas, × 4; f. detail of a basiscopic lobe of d, × 4. — *H. profereoides* (Christ) Copel. g. Fertile lobes of a middle pinna with sori removed from right lobe, × 4 (a, b: *Maisier s.n.*, Penang; c: *Kato 7160*; d–f: *Cuming 237*; g: *Elmer 10807*).
Closely allied to *H. sagenoides*, differing constantly in glabrous lower surface apart from rare short hairs on costules, and the presence of thick hairs on the upper surface confined to short ones near sinuses and very near the margins of lobes; fronds of largest plants differing from those of *H. sagenoides* in broader pinnules which are less deeply lobed, the lobes broader and acute, those of the largest fertile suprabasal pinnules distinctly crenate and subacuminate.

Distribution – *Malesia*: Sumatra (northern; not known south of Sibolangit).

Habitat – At low altitudes in forest.


*Stipe* to 50 cm long, dark, minutely hairy above base, near base bearing scales 8 × 1 mm and longer hairs; sterile lamina not known; *fertile lamina* to 35 cm long; *basal pinnae* to 15 cm long with stalks 10–12 mm, bearing a pair of free pinnules and 2 or 3 pairs adnate; basalar basiscopic pinnule 3.5 × 0.9 cm, deeply lobed, longest basiscopic pinnule 5 cm long, 4 mm wide, lobes on distal part of pinnules much narrower, lobulate, widely spaced and connected by a narrow wing along the costa; *second pair of pinnae* 10 cm or more above basal ones, shaped as distal part of basal pinnule; *veins* not visible on the surface, forming narrow areoles along the costa on distal parts of pinnules, free and forked in pinna-lobes; lower surface of costae and costules bearing sparse short hairs; upper surface of costae densely hairy, of costules less so, a few hairs present near sinuses; sori exindusiate, mostly round, on veins in lobes of pinnules, those on basal veins sometimes elongate.

Distribution – *Malesia*: Borneo (known only from the type locality; with 2 additional collections).

Habitat – On mountain slopes at 150–1000 m, in calcareous area.


*Stipe* to 30 cm long, dark-castaneous, bearing sparse short hairs abaxially; sterile fronds unknown; fertile *lamina* to 35 cm long, bearing 13 pairs of free pinnules; *basal pinnae* 10 cm long with stalks 2–3 mm, 2.5 cm wide in the middle, basal basiscopic lobe 5 mm long, acrosopic 10 mm, longest basiscopic lobe 15 mm long, crenate; *suprabasal pinnae* to 10 × 2.2 cm, near their bases lobed to 1 mm or less from the costa, the lobes well separated, at most slightly crenate distally (apart from the basal acrosopic ones); costules 4.5–5 mm apart; *veins* 6 pairs, forked except the distal ones; lower surface quite glabrous; upper surface of costae densely short-hairy, a few thick hairs present between veins near the margin, especially at sinuses; sori exindusiate, terminal on acrosopic vein-branches.
Distribution – **Malesia**: New Guinea, apart from the type, Biak Island.

Habitat – On limestone (Biak).

Note – Specimens of the type collection were annotated by Zippel, and were probably collected by him; he is known to have collected ferns on limestone in western New Guinea.


Stipe castaneous to very dark, of fertile fronds 40 cm or more long, shorter on sterile, minutely hairy throughout on abaxial surface, basal scales narrow, to more than 10 mm long. *Sterile frond*: lamina to 35 cm long; *pinnae* to c. 12 pairs; middle lobes of basal pinnae little longer on b asis than on acrosopic side, the largest on both sides often ± crenate with some forked veins; suprabasal pinnae to about 12 cm long and 3 cm wide, lobed 3/5–3/4 towards the midrib, the basal lobes of several pinnae narrowed at their bases, their apices ± acute and margins ± crenate; *veins* in other lobes mostly simple; lower surface of costae rather closely hairy, hairs variable in length, short slender hairs also ± abundant on and between veins (few on the type), upper surface of costae densely short-hairy, scattered long thick hairs ± abundant between veins. *Fertile frond: pinnae* to c. 8 cm long, usually less than 1 cm wide, very deeply lobed, lobes commonly 2 mm wide; sorus all along veins, at maturity completely covering lower surface; fronds of intermediate form may occur.

Distribution – **Malesia**: Borneo, S Sumatra.

Habitat – In lowland forest.


Differs from *H. pinnatum* as follows: both sterile and fertile fronds have up to 3 pairs of stalked or sessile pinnae and to 3 pairs adnate, and in both there is irregularity in the formation of costal areoles which in part or whole of a pinna may be lacking, especially in the narrower fertile pinnae; *lamina* of fertile fronds to 30 cm long with a scaly bud present sometimes at the base of an upper pinna (in *H. pinnatum* such buds only occur on sterile fronds); suprabasal fertile pinnae 10–15 mm wide, lobed to 1–2 mm from the costa, lobes to 2.5 mm wide; *sori* at first round and clearly separate, terminal on veins, indusiate; indusia thin, soon shriveling.

Distribution – Peninsular Thailand; **Malesia**: N Sumatra, Malay Peninsula.

Habitat – All records from limestone, or limestone areas.

Note – This species always grows in association with *H. pinnatum* and may be of hybrid origin, possibly *H. pinnatum × H. sagenioides*, in which case it would be a triploid. Experimental evidence is desirable. The type is smaller than the Peninsular specimens from which the above description is drawn but otherwise agrees with them.


Stenosema aurita auct.: J. Sm. in Hook., Gen. Fil. (1842) t. 94, for Cuming 295, 321 and figs. 1–4 only.

Lastrea spectabilis auct.: J. Sm., J. Bot. 3 (1841) 412, for Cuming 154 only.

Fronds dimorphous. Sterile frond: stipe to at least 35 cm long, not very dark, minutely hairy throughout, basal scales to c. 12 × 1.5 mm; lamina to at least 50 cm long; free pinnae to 10 pairs and 2 or 3 pairs adnate, lower pinnae distinctly stalked; largest suprabasal pinnae 17 × 3.5 cm, near their bases lobed 3/4 towards costa, less deeply distally; costules to 8 mm apart; lobes entire, obtuse; veins anastomosing in 1 row of costal areoles with few additional areoles below sinuses, costular areoles rare; basal pinnae to 5 cm wide, lobed almost to the costa at their bases, lobes all entire, costular areoles lacking or 1 or 2 in longest lobes; lower surface of costae bearing sparse slender hairs to 1 mm long; upper surface of costae bearing dense thicker hairs of variable length, to more than 1 mm, thick hairs scattered all over upper surface between veins; buds lacking on upper surface of costae. Fertile frond: stipe to 60 cm long; lamina to 50 cm long; suprabasal pinnae to 14 × 2.5 cm, lobed to c. 2 mm from costa or more deeply near their bases, basal lobes sometimes ± elongate and rarely crenate; costal areoles present in widest pinnae, usually lacking distally and sometimes almost wholly lacking; costular areoles rare; veins in lobes often forked; basal pinnae wider, their middle lobes rarely crenate; hairs on both surfaces of costae short, no hairs present between veins on upper surface; sori exindusiata, spreading along basal half or more of veins, on both branches of forked veins.

Distribution — Malesia: Philippines (Luzon, Mindoro, Leyte, Samar), Central Celebes, doubtfully in Borneo.

Habitat — In forest at altitudes to 700 m.


Caudex erect, to at least 15 cm tall; fronds variably a little dimorphous; stipe to at least 50 cm long, not very dark, minutely hairy; basal scales firm, to almost 2 mm wide, scales above base early caducous; lamina to at least 80 cm long; pinnae to at least 12 pairs, lobed apical lamina relatively short; suprabasal pinnae to 23 × 5 cm, those fully fertile more deeply lobed and with more widely separated lobes than those with few sori (wholly sterile pinnae rare); costules on largest fronds 10–12 mm apart; lobes entire, obtuse, or the more fully fertile ones ± attenuate with sinuous margins; basal pinnae very deeply lobed near their bases, the basal pair of lobes sometimes almost free; veins forming costal areoles and many additional ones below sinuses between lobes, in the lobes many pairs of costular areoles and usually some between these and the margin; lower surface of costae glabrescent, upper surface densely covered with short hairs, a few hairs present near sinuses between lobes on upper surface; scaly buds often present on upper surface of costae near their bases; sori exindusiata, in one row on each side of costules, also very irregularly between costae and sinuses between lobes, variously elongate along veins, almost all on connected veins, a few on free veins near apices of lobes. — Fig. 19g.

Distribution — Malesia: Borneo (Sabah, Sarawak), Philippines (Mindanao, Mindoro), New Guinea.

Habitat – In lowland forest and to 1000 m; in the G. Mulu National Park, Sarawak, often in limestone areas.

Note – The above description is based on the largest plants from G. Mulu, but much smaller plants with pinnae 10 cm long may be fertile, especially on limestone. One collection from Mt Kinabalu has narrower fertile pinnae, little different from those of *H. aspidioides* but with sori almost all on connected veins. The larger specimens are intermediate between *H. aspidioides* and *H. giganticum*. They need experimental treatment to arrive at a better understanding of this relationship. The presence of scaly buds on the upper surface of costa are notable.


carpa* (Hook.) Bedd., Handb. Ferns Brit. India, Suppl. (1902) 48; Alderw., Malayan Ferns (1908) 172. – *Tectaria megalocarpa* (Hook.) C. Chr., Index Filic. Suppl. 3 (1934) 182. – Type: *T. Lobb s.n.*, Java (K).

*Nephrodium oligodictyon* Baker, Ann. Bot. (London) 5 (1891) 328. – Type: Hutton, Malay Is. ex Herb. Veitch (K); probably from Java.


*Tectaria calcicola* Copel., Brittonia 1 (1931) 72, pl. 1. – Type: *Clemens 20745*, Sarawak, Bidi cave (UC; iso K, NY).

Fronds of largest plants differing from largest fronds of *H. profereoides* as follows: *apical lamina* commonly 20 cm long, deeply many-lobed, grading to adnate pinnae; pinnae rarely more than six pairs, sometimes all slightly adnate except the basal ones, lacking buds on upper surface of costa, largest to 28 × 6 cm, lobed near their bases to 3 mm from costa (sterile ones less deeply), lobes of the largest sometimes slightly crenate; *basal pinnae* short-stalked, distinctly shorter than those next above them, middle basiscopic lobes of largest sometimes much elongate and lobulate; *sori* sometimes almost circular, usually ± elliptical and attached by a short linear receptacle, indusiate or not, the indusium (if present) persistent but not covering the whole sorus.

Distribution – *Malesia*: Western, Moluccas.

Habitat – In forest, to 1000 m or more, on stream banks and on steep slopes in ravines, apparently sometimes on limestone.

Note – I see no distinction in other characters between fronds with indusiate and exindusiate sori. I have seen distinctly crenate lobes of suprabasal pinnae only in Blume’s type collection. One collection from limestone in Sarawak (Paul & Erwin S 27482) has somewhat elongate indusiate sori, several pairs of stalked pinnae and a bud on the upper surface of the costa of one of them; it is perhaps a hybrid. Of six known collections from the Malay Peninsula only one is indusiate. A widely distributed species but nowhere abundant.

Suprabasal pinnae to 9 cm apart, to 32 cm long and 9 cm wide, lobed to 5–6 mm from costa; costules c. 1.7 cm apart along costa; lobes crenate, narrowed in distal 2 cm to an almost acute tip, c. 10 mm wide, the sinuses between them broadly rounded; veins forming narrow areoles along costae with one series of small additional areoles below sinuses, also a regular series of costular areoles connecting the veins which run from costules to the marginal crenatures, the veinlets from such veins also sometimes anastomosing; upper surface of costae and costules closely short-hairy, surfaces otherwise glabrous; sori small, round or nearly so, exindusiate, on veinlets on each side of the small veins which run from costules to crenatures.

Distribution — Malesia: Sumatra (West, 2 coll.).

Habitat — In forest, the type at 1200 m.

Note — The type consists of 3 suprabasal pinnae only. The second collection, Alston 14315, above Indrapura, is a smaller specimen.


Stipe to at least 50 cm long, dark and glossy above the base, scales on basal part to 10 × 1 mm; fronds very dimorphous. Sterile frond: lamina to 70 cm or more long; suprabasal pinnae to 21 × 4 cm, lobed to 2–2.5 mm from the costa, lobes well spaced, mostly entire (rarely slightly crenate), narrowed distally; basal veins in lobes usually free, but sometimes forming areoles along costae; veins above the base forked once or twice, often forming areoles along costules; erect hairs 0.1 mm long abundant on lower surface of costae. Fertile frond: pinnae to 2 cm wide, lobed to less than 1 mm from the costa, lobes 2 mm wide, widely separate; veins forming one narrow areole on each side of costules; sporangia densely arranged along all veins.

Distribution — Malesia: Lesser Sunda Islands (Sumba, Flores, Babar).

Habitat — A specimen from Babar grew on coral rock, in shade; no information with type.


Fronds strongly dimorphous. Sterile frond: stipe dark purplish brown, commonly 15–30 cm long, minutely hairy, later glabrescent on the abaxial surface (persistent longer hairs near apex), basal scales c. 8 mm long, less than 1 mm wide; lamina 15–20(–30) cm long, on young plants deltoid, on older plants elongate; basal pinnae with stalks 2 mm long, above them 1–3 pairs of ± adnate pinnae often with buds at their bases; basal pinnae to c. 12 × 4 cm, lobed to 5–7 mm from the costa, lobes broad, obtuse, entire; suprabasal pinnae lobed less than halfway to costa, upper ones much less deeply; apical lamina deltoid, deeply lobed, lobes entire; veins forming areoles along costae of pinnae and a few along costules in lobes of larger pinnae; lower surface variably short-hairy on costae, otherwise almost glabrous; upper surface densely hairy on costae with a few short thick hairs near sinuses.

Fertile frond: stipe to at least 45 cm long; lamina to c. 15 cm long, its parts as in sterile fronds but pinnae lobed to a very narrow wing along costae, lobes less than 2 mm wide and well-spaced, covered beneath by sporangia which project beyond the margin. — Fig. 19d–f.

Distribution — S Thailand; Malesia: Sumatra, Malay Peninsula, Borneo, Philippines.

Habitat — On limestone in shade, often abundant, also rarely on other rocks in Malay, more frequently in Luzon; in alluvial forest in limestone area of G. Mulu, Sarawak.

Cytology — The chromosome number 80–82 was recorded by Manton in Holttum (1955), now been corrected by T.G. Walker (in litt.) to n = 80.

Note — One specimen from Gopeng (Perak) has basal pinnae of Tectaria form on one frond.
Cyclopetlis


Caudex short, erect, its scales narrow, entire or with marginal teeth formed by outgrowths from single cells; fronds simply pinnate; rachis rounded on both surfaces in living plants, the lower surface bearing small scales and short erect multicellular hairs, upper surface almost glabrous; pinnae sessile, articulate to the rachis, subentire, their bases cordate at least on the basiscopic side (hastate on one species); unicellular glands lacking; veins free, arising from the costae of pinnae in paucipinnate groups, the lower veinlets not nearly reaching the margin; sori dorsal on lateral veinlets, in one to several irregular rows parallel to the costa; indusia peltate. — Fig. 20.

Distribution — Malesia and SE Asia (c. 6 species); widely in tropical America (1 species).

Habitat — Forest plants of low altitudes; all records indicate a rocky habitat, some species on limestone.

Cytology — Base chromosome number 41 (C. semicordata only). The only recorded cytological observation is of the West Indian species, which is diploid.

Taxonomy — This small genus is not nearly allied to any other in the Tectaria group. The plants grow on rocks, where their roots would be more quickly affected by periods of dry weather than those of plants rooted in the soil; the small simple and articulate nature of their pinnae are well adapted to this habitat. But the reduction of lower pinnae and lack of any distinctive character in them are peculiar in this group of genera. The nature of the marginal teeth (where such exist) on scales of the caudex and stipes is also (so far as my observation goes) peculiar. The nature and distribution of hairs on the rachis resemble those in Pteridrys.

The distribution of Cyclopetlis is peculiar, also the fact that although quite widely distributed in the American tropics it is there very uniform, whereas in Malesia there are certainly several species, though they were not clearly distinguished by the earlier authors, the result being a complex synonymy.

The West Indian species was the first known and is therefore the type; it was included in Polystichum by earlier authors on account of its peltate indusia. In 1846 John Smith had a plant in cultivation at Kew and for the first time recognized the distinctness of the genus, but he did not clearly distinguish between the West Indian species and Philippine ones of which he had specimens collected by Cuming.
KEY TO THE SPECIES

1. Bases of pinnae, at least on their acroscopic side, cordate ................. 2
   b. Bases of pinnae hastate, their basal auricles acuminated ........... 5. C. mirabilis
2a. Pinnae of mature plants 10 cm or more long .................................. 3
   b. Pinnae of mature plants c. 3.5 cm long ................................. 4. C. rigida
3a. Few pairs of lower pinnae slightly reduced and more widely spaced; scales bearing marginal teeth ........................................ 1. C. crenata
   b. Many pairs of lower pinnae gradually much reduced; scales lacking marginal teeth 4
4a. Sori exindusiate; acroscopic bases of middle pinnae not cordate 2. C. novoguineensis
   b. Sori indusiate; acroscopic bases of middle pinnae cordate ........ 3. C. presliana

1. Cyclopeltis crenata (Fée) C.Chr., Index Filic. Suppl. 3 (1934) 64. — Hemicardion crenatum Fée, Mém. Foug. 5. Gen. Filic. (1852) 283, t. 22a, f. 1. — Aspidium semicordatum Sw. var. crenatum Hook., Sp. Fil. 4 (1862) 17.
   — Cyclopeltis semicordata var. crenata Alderw., Malayan Ferns (1908) 163. — Type: Gaudichaud s.n., Tourane (RB, not seen; iso K).
Aspidium semicordatum var. truncatum Hook., Sp. Fil. 4 (1862) 17. — Type: Parish s.n., Moulmein (K).
Polystichum semicordatum auct. non (Sw.) Moore: Bedd., Ferns Brit. India (1865) t. 35; Handb. Ferns Brit. India (1883) 201, for Asian and Malayan specimens only.

Scales on caudex to more than 15 mm long, less than 1 mm wide, bearing (at least distally) many short teeth formed by outgrowths from marginal cells (in some Bornean specimens very short); stipe 15–40 cm long, scaly throughout when young; lamina to 60 cm or more long; pinnae commonly to 20 pairs, distal ones gradually smaller and falcate, lamina-apex pinna-like, a few pairs lower pinnae more widely spaced and slightly reduced; middle pinnae almost at right angles to the rachis, largest sterile ones 13 × 2 cm, almost contiguous, fertile ones often narrower and more widely spaced, base truncate to subcordate on acroscopic side, rounded to deeply cordate on basiscopic side, margins ± crisped when living, entire or ± crenate, apex short-acuminate; upper surface of rachis and costae glabrous or a few hairs present near bases of costae of lower pinnae; lower surface of rachis bearing many narrow scales and also short erect hairs, more slender hairs present on costae; sori dorsal on veinlets, or sometimes terminal on the basal acroscopic one of each group, usually in 3 irregular rows on each side of the costa; indusia small, not covering sorus at maturity, shrivelling later. — Fig. 20a–c.

Distribution — Southern Burma, Thailand and Vietnam; Hainan; in Malesia: western Malesia and Philippines.

Habitat — In forest on rocks, usually but not always on limestone.

Hybrids — Mr M.G. Price, who has made extensive field studies of ferns on Mt Makiling, Luzon, writes that though both C. crenata and C. presliana grow in the forest on that mountain, he observed no hybrids, but that Weber 1547 and Ramos BS 13829, both from Cagayan Province, Luzon, are probable hybrids. Weber 1547 is represented at Kew; it is intermediate in frond-form between the two species and its scales have some teeth.


*Stipe* 4–20 cm long, bearing scales throughout; basal scales to more than 15 mm long, less than 1 mm wide, thin, not toothed; *lamina* to 100 cm long; rachis very copiously short-hairy on the lower surface with some very narrow scales; *pinnae* many pairs, distal and lower ones gradually smaller; middle pinnae to c. 14 × 1.5 cm, acroscopic base truncate with a ± distinct acute auricle, basiscopic base strongly cordate, margins entire or irregularly undulate, apex of pinnae of larger fronds narrowly acuminate, short-acuminate on small fronds; *basal pinnae* c. 1 cm long and wide with cordate acroscopic base; *sori* exindusiate, in 1 or 2 irregular rows parallel to the costa, the inner row terminal on basal acroscopic veinlets, the outer row mostly not terminal on next veinlets.

*Distribution* — *Malesia*: Eastern New Guinea, Bismarck Archipelago; Solomon Islands.

*Habitat* — Forest ferns on limestone soils, often on a steep slope, or on rocks or stream banks.


Aspidium semicordatum Sw. var. subdimorphum Christ in Warb., Monsunia 1 (1900) 76. — Type: Warburg 16587, Celebes (B).


Scales on caudex to 15 × 1.5 mm, rather firm, entire; stipe 3–15 cm long, with rachis bearing narrower scales on abaxial surface; lamina to 100 cm long; pinnae very numerous, many lower pairs gradually reduced, the lowest sometimes only 1 cm long, upper pinnae also gradually reduced and grading to the frond-apex; middle pinnae commonly 10 × 1.5 cm, largest seen 13 × 1.8 cm, base variably cordate on acroscopic side, strongly so on basiscopic side; margins of larger pinnae distally irregularly sinuate to crenate; apex of pinnae on small fronds obtuse, on larger fronds gradually attenuate; lower surface of rachis densely covered with short erect hairs (residual narrow scales also present); lower surface of costae lacking hairs but sometimes bearing small scales; upper surface glabrous; sori mostly at apices of veinlets, in larger pinnae in 2 rather irregular rows nearer to margin than to costa, the inner row on basal acroscopic veinlets; indusia covering mature sori. — Fig. 20.d.

Distribution — Malesia: Borneo, Philippines, Celebes, Moluccas (Ambon, Ceram), New Guinea.

Habitat — On limestone, in shade.

Note — In 1841 John Smith gave the name Las-trea presliana to a Cuming Philippine specimen which he recognized as distinct from the West Indian Aspidium semicordatum Sw., though Presl had previously ascribed a Haenke Philippine collection to the latter. Smith referred to Presl’s description and also described a difference in venation between the species. Though the latter difference does not hold, Smith’s name and his cited type are now accepted. In 1852 Fée published the first good description of the Philippine species, based on the same Cuming collection; Morton (1967) preferred to accept Fée’s name on account of the error in John Smith’s description.


Stipe very short, its basal scales c. 5 mm long, narrow, dentate distally; lamina to 40 cm long; pinnae rigid, almost entire, narrowed both to base and apex, apex obtuse, base cuneate on the acroscopic side, middle ones 3.5 × 1 cm, lower ones decrescent, lowest 10–15 mm long; veins distinct on upper surface, not on lower; abaxial surface of rachis bearing many very narrow scales and very short hairs, costa also scaly beneath; sori in one row on each side of costae, indusiate; indusia firm, covering mature sori.

Distribution — Malesia: New Guinea (known only from the type collection).

Habitat — On rock-wall in forest.

Notes — Cyclopeltis rigida agrees in scales with C. crenata but differs in its much smaller rigid pinnae, the lower ones gradually reduced.

Cyclopeltis rigida has pinnae about the same length as those of C. kingii (Hance) Tagawa from the Caroline Islands, but the latter has thin pinnae differently shaped. The scales of the type of C. kingii are not well preserved but do appear to have marginal teeth distally.


Stipe more than 35 cm long, its scales (not well preserved on the type) bearing some marginal teeth; frond-form as C. crenata, a few pairs lower pinnae slightly reduced; the bases of all pinnae strongly auricled on both sides, the auricles narrowly acuminate, the acroscopic one much shorter and narrower than the basiscopic one; largest pinnae c. 16 × 2 cm; sori as in C. crenata but in four rows.

Distribution — Malesia: Borneo (known from the type only).

Note — For much of the above information I am indebted to Mr M.G. Price who has examined the type. It appears that the type was a chance mutant from C. crenata which probably did not become dispersed and may now be extinct.
LASTREOPSIS


Caudex creeping or suberect, its vascular system a radially symmetrical dictyosteole; stipe grooved on the adaxial surface with linear aerophores along the ridges bordering the groove; scales on caudex and near base of stipe firm, narrow, consisting mainly of narrow cells, not clathrate, scales on rest of frond small and never abundant; frond in almost all species deltoid-pentagonal, the basal pinnae longest and with elongate basal basiscopic branches; lamina always much dissected, the ultimate leaflets always small and ± deeply lobed with asymmetric bases, their margins thickened and decurrent to join the margins of the groove of the pinna-rachis, the prominent costae of the distal parts of pinnae decurrent to form a raised band between the thickened margins of the groove; veins always free; hairs almost always present on both surfaces of axes and often on lamina, always consisting of several cells, in some species acute, remaining stiff when dried, in other species not acute and becoming contorted when dried; unicellular glands sometimes present, ovoid to elongate; sori orbicular, indusiate or not, the indusia in some species bearing glands like those of the lamina; sporangia lacking appendages on the body but usually bearing glands on the stalk; spores winged or with many obtuse protuberances. — Fig. 21.

Distribution — Pantropic; about 35 species, most abundant in Australasia.

Habitat — Forest ferns, mostly of seasonal climates; Malesian species on mountains, mostly at high altitudes.

Cytology — Base chromosome number 41; Malesian species L. rufescens and L. tenera diploid; some Australian species tetraploid.

Taxonomy — In his Index Filicum (1905) Christensen included all species of Lastreopsis, as here delimited, in the genus Dryopteris which he recognized as being a complex, for which he proposed a tentative subdivision on pp. xx–xxii. In attempting a better subdivision, in his Monograph of Dryopteris (1913 and 1920), he limited himself to the species of tropical America. R.C. Ching spent three years (1929–1932) in Europe, studying ferns with Christensen and visiting the major European herbaria to see the types of Chinese species. He attempted to apply the ideas expressed in Christensen’s Monograph to the species of Asia. In so doing he recognized that in Asia there is more than one group of species which accord with Christensen’s definition of Dryopteris subg. Ctenitis. One such group he separated under the name Lastreopsis (1938) noting that the hairs on the frond are not contorted when dried; he included only four species (one of them is here excluded). In a new classification of Leptosporangiata ferns (1940) he raised Dryopteris subg. Parapolystichum (Keyserl.) C. Chr. to generic rank, placing it, without discussion, in the
family *Thelypteridaceae*, evidently because the hairs are different from those in his *Lastreopsis*, though they are quite different from the hairs shown by Christensen to be characteristic of *Thelypteris*. Ching added two species of the Pacific to those of tropical America included by Christensen in his subgenus.

Dr M.D. Tindale published an account of the Australian species of *Lastreopsis* in 1957. Then, looking more widely, she discovered that there are species of *Lastreopsis* in Africa and America and prepared a full monograph of the genus (1965) recognizing 33 species. In so doing she re-defined the genus and concluded that it comprises species with different types of hairs, including those placed in *Parapolystichum* by Ching. With this conclusion I agree. As an indication of past confusion, it is notable that synonyms in 14 different genera are recorded by Tindale.

*Lastreopsis* accords with *Ctenitis* in the presence of glands on various parts of the frond, on indusia and on the stalks of sporangia. It differs from *Ctenitis* in scales, in the shape of axes of the frond in relation to the leaflets they bear (not noticed by Ching) and in the position of linear aerophores on stipe and rachis (mentioned by neither Ching nor Tindale). In scales *Lastreopsis* is nearer to *Tectaria* than to *Ctenitis*.

**KEY TO THE SPECIES**

1a. Hairs on upper surface of rachis ctenitoid, shrivelled when dried or with obtuse apical cells ........................................ 2

b. Hairs on upper surface of rachis persistently terete with acute apical cells

4. *L. tenera*

2a. Sori exindusiate; scales less than 2 mm long ............ 1. *L. rufescens*

b. Sori indusiate; scales much longer .......................... 3

3a. Frond wholly anadromous ........................................ 2. *L. novoguineensis*

b. Frond catadromous distally .................................... 3. *L. subsparsa*


*Caudex* short-creeping, covered with persistent appressed firm scales little over 1 mm long; *stipe* to 40 cm long, light castaneous, persistently scaly near base only; *lamina* to 45 cm long; basal pinnae to 20 cm long, bearing 1 or 2 pairs of free and 1 or 2 pairs adnate pinnules, the rest deeply lobed, the lobes crenate, basal basiscopic pinnule to 11 cm long with 1 pair of free tertiary leaflets; basal acrosopic pinnule c. 7 cm long; middle pinnae deeply obliquely lobed, the largest with a pair of adnate pinnules; *rachis* bearing ctenitoid hairs 0.3 mm long on abaxial surface, thicker longer hairs on adaxial surface; many ± appressed cylindric yellowish glands on lower surface, on and between veins; *sori* medial on pinna-lobes, on acrosopic branches where veins are forked, exindusiate, some
Fig. 21. Lastreopsis tenera (R. Br.) Tindale. a. Base of a distal pinna, showing basiscopic base of lamina hardly thickened, × 4. — L. rufescens (Blume) Ching. b. Outline of a basal pinna, × 0.5; c. leaflet of a middle pinna, × 2.2; d. upper surface of rachis and its junction with pinna-rachis, × 12; e. upper surface of pinna-rachis of a middle pinna, showing the thickened margins of two pinnules joining the raised margin of the pinna-rachis, × 16 (a: Copeland 2090; b, c: Mousset s.n., Java; d, e: Mousset 376).
cylindric glands present on stalks of sporangia; spores with inter-connected wings or crests. — Fig. 21b–e.

Distribution — Sri Lanka; in Malesia: Java and Lesser Sunda Islands; NE Queensland.

Habitat — On mountains, middle elevations to 2300 m, on shaded slopes.


Caudex suberect, bearing firm scales to 6 × 1.5 mm; stipes to 60 cm long, scaly as caudex at the base, covered throughout with very short hairs; lamina to 35 cm long, very firm; basal pinnae to 25 cm long, bearing 4–5 pairs of free pinnules, the rest connected by a narrow wing along the pinna-rachis; basal basiscopie pinnule to 13 cm long, bearing 1 pair of deeply lobed free tertiary leaflets 2.5 × 0.6 cm and many other pairs connected by a narrow wing; second pair of pinnae also with pinnae basal pinnules; upper pinnae all anadromous at their bases; lower surface of pinna-rachis bearing many glands and very few short hairs, upper surface bearing ctenioid hairs 0.1 mm long; sori medial on veins, covered with very firm glabrous reniform indusia.


Habitat — Widely on mountains at 1800–3000 m altitude.


In size and form of fronds near L. novoguineensis, also in pubescence, but tertiary and other ultimate leaflets at most crenate; indusia small, caducous.

Distribution — Malesia: Java (known only from the type).

Habitat — At 2000 m altitude.


Aspidium gardnerianum Mett., Farnagg. IV (1858) 71. — Type: Gardner 60, Sri Lanka (B; at K Gardner 1110).


Caudex short-creeping with very closely placed stipes; scales thin, to c. 10 × 1 mm, persistent; stipe to 50 cm long, light castaneous, bearing slender terete hairs to 0.5 mm long; lamina to 75 cm long and wide but fronds 20 cm long, sometimes fertile; basal pinnae to 30 cm long (including stalk 3.5 cm), basal basiscopie pinnules to 15 × 8 cm bearing tertiary leaflets to 4 × 1.5 cm lobed almost to their costae, the lobes crenate, the lowest tertiary leaflets free, the rest decurrent or joined by a narrow wing, basal acroscopic pinnules to 10 × 5 cm bearing tertiary leaflets to 2.5 × 1.2 cm; upper pinnae catadromous; rachis bearing terete hairs 0.5 mm long both sides, those on the abaxial side slender, spreading, on adaxial side antrorse, thicker, sometimes longer; lower surface of leaflets bearing short erect hairs on and between veins,
also some almost spherical red glands, upper surface with fewer hairs; sorî at or near ends of veins; indusia small, bearing red spherical glands. – Fig. 21a.

Distribution – S India & Sri Lanka; in Malesia: Sumatra, Bali, Philippines (Luzon, Leyte); Taiwan; Queensland, New Caledonia, Fiji.

Habitat – In Luzon at 250–700 m, in forest.

Note – The margins of decurrent bases of leaflets are hardly thickened in this species.
INDEX TO SCIENTIFIC PLANT NAMES

Suprageneric epithets have been entered under the family name to which they belong preceded by the indication of their rank (subfamily, tribe, etc.). Infrageneric epithets have been entered immediately under the generic name to which they belong, preceded by the indication of their rank (subgenus, section, etc.). Infraspecific epithets have been entered under the specific name to which they belong preceded by the indication of their rank (subspecies, variety, forma, etc.).

Synonyms have been printed in *italics*. Page numbers in **bold type** denote main treatment; an asterisk behind a page number denotes the presence of a figure of the concerned taxon.

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