A RE-DEFINITION OF THE FERN-GENUS TAENITIS WILLD.

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The present paper includes a new definition of the genus Taenitis, the addition of five species to it (one of them new), a key to the known species, a description of each with citation of synonyms and of the more important previous literature.

The genus was established for the very widely distributed and variable species *T. blechnoides*, which is one of the commonest terrestrial ferns of forest throughout Malesia. This species comprises a complex of forms, but the forms differ by such slight and subtle characters that they are not easily distinguished from dried specimens, and I have not attempted to distinguish them. The common character of all forms of the species is the presence of a longitudinal band of sporangia midway between the midrib and margin of each pinna, and the genus has hitherto been confined to species which have this character, the only variability in soral form being that the band of sporangia is sometimes not quite continuous.

There are, however, other species which agree with *T. blechnoides* in their bristly rhizomes, in the characteristic venation of narrow, oblique, subequal areoles lacking included free veinlets, and in spores, but which differ in having the sporangia disposed either (a) in a submarginal groove, or (b) in a series of small groups which may be variously dispersed over the lamina, or (c) in narrow lines along some or all of the veins, or (d) completely covering the lower surface of specialized very narrow pinnae.

In the past one species with distribution (a) was called *Schizoloma*, another *Lindsaea* (I here add a third); species with disposition (b) were called *Polypodium*; species with disposition (c) were called *Gymnogramme, Hemionitis*, or *Syngramma*; and with disposition (d) *Acrostichum* or *Platytaenia*. I now place them all in *Taenitis*. The very remarkable species *T. hosei* (Bak.) Holttum is exactly intermediate between *T. blechnoides* and species with soral form (c).

In recent years cytological studies of some species have been undertaken. Some of these are still pending, and therefore I do not report upon them, but I can summarize the situation as follows: plants with the sorus-form of *T. blechnoides* either have n = 44 or a number related to this, but the rest have numbers which are not related to 44. However, it is quite clear that those species which differ from *T. blechnoides* in their base number (some of which have usually been placed in *Syngramma*) are also different from species of *Syngramma* which have been investigated and have a base number 29.

The genus *Syngramma* agrees closely with *Taenitis* in its bristly rhizome but differs constantly in venation and consequently in the disposition of sporangia. The veins in *Syngramma* run close together obliquely to the margin, or almost to the margin, before they anastomose, and there are at most two series of very small submarginal areoles (which are not soriferous). The sporangia are in thin lines along the close parallel veins; paraphyses are present or absent (always present in *Taenitis*). Copeland proposed a genus *Crasedodictyum* for a species differing from *Syngramma* as follows: frond pedately branched and paraphyses lacking. But there is a pedately branched species in Malaya (it
needs a new name) which has paraphyses; therefore I cannot think the genus Craspedodictyum well-founded, and unite it to Syngramma. It should be emphasised that species of the genera Taenitis and Syngramma (as here recognized) are sharply distinguishable from vegetative characters.

The three species of Taenitis which have apparently marginal sori all have an arrangement superficially similar to that in most species of Vittaria (as noted by Fée when he established a new genus for Schizoloma cordatum Gaud.). One of these species (T. vittiaroides) has sterile fronds indistinguishable from those of T. blechnoides, but the others have more specialized frond-forms. They were placed in the genera Schizoloma and Lindsaea because they were thought to have indusia as in those genera; but in fact they have no true indusia, their sori (as in Vittaria) lying in submarginal grooves in the lamina. In Vittaria there are all conditions between quite superficial sori and sori in well-developed marginal grooves. It is interesting to note that in the genus Antrophyum, closely related to Vittaria, the arrangement of sori is closely similar to that of Taenitis pinnata and T. lanceolata. It is also noteworthy that species of Vittaria and Antrophyum differ from each other by the peculiar form of their paraphyses, as do the species of Taenitis. In both cases young sporangia are protected by a considerable mass of paraphyses which first develop (and cause trouble to the cytologist).

A NEW GENERIC DESCRIPTION


Rhizome creeping, solenostelic but not dorsiventral, young parts protected by very dark glossy bristles. Stipes dark, glossy, the adaxial surface grooved distally, no pale lateral lines present. Fronds simple or simply pinnate or rarely trilobed (in T. trilobata the lateral lobes flabellately divided), if pinnate the terminal lamina similar to the pinnae; pinnae simple, entire, rather narrowly elliptic, usually coriaceous, glabrous; midribs of pinnae slightly grooved above, edges of groove not raised; no main lateral veins; veins forming a network of 2, 3 or more series of narrow, oblique, subequal areoles, without included free veinlets. Fertile fronds often with narrower pinnae (or simple lamina) than sterile; sporangia either confined to a (sometimes discontinuous) longitudinal band between midrib and edge, the band in three species in a submarginal groove, or spreading irregularly along the veins, in two species the fertile pinnae very narrow and covered beneath with sporangia; paraphyses abundant, multicellular, with distal cells in most cases shorter than basal ones, never with a large spherical terminal cell, developing before the sporangia and more or less protecting them in their earlier stages of growth; spores trilete.

Type species: Pteris blechnoides Willd., Phytographia 13 (1794) t. 9, f. 3.


KEY TO THE SPECIES

1. Sori superficial on lower surface of lamina.
2. Sporangia not entirely covering lower surface of fertile pinnae.
3. Fronds of mature plants pinnate (except sterile fronds of no. 4).
4. Sporangia in a single ± continuous band parallel to and on each side of the midrib.
5. Pinnae of largest fronds 1 or 2 pairs, each pinna up to 8 × 1 cm . . . 1. T. marginata
6. All fronds on well-grown plants pinnate.
7. Pinnae often few, usually 15—20 cm long, sterile 24—5 cm wide, fertile 1—3 cm; sori ± midway between midrib and edge, rarely interrupted. 2. T. blechnoides
7. Pinnae 6—12 pairs, often under 15 cm long, sterile up to 14 cm wide, fertile less than 1 cm, thin; sori nearer to edge than midrib, often interrupted. 3. T. interrupta
6. Sterile fronds simple, fertile pinnate with 1—3 pairs of very narrow pinnate.
4. T. dimorpha
3. Fronds of mature plants simple (sometimes trifoliate in no. 8).
8. Sporangia spreading along network of veins; lamina of frond commonly up to 25 cm long.
9. Sporangia spreading along almost all veins of network, from costa almost to margin.
6. T. lanceolata
9. Sporangia confined to a median band on each half of the lamina, areas near costa and margin sterile.
7. T. hoselii
8. Sporangia in a continuous band on each side of costa, or in ± distinct sori in a row similarly situated; lamina up to 10 cm long.
10. Lamina of largest fronds c. 8 cm long, 12—20 mm wide.
11. Fronds narrowed to acute apex, midrib distinct almost to apex, sori not reaching apex.
8. T. brooksi
11. Fronds spathulate with rounded apex; the two lateral bands of sporangia joined in an arc across frond just below apex.
9. T. obtusa
10. Lamina of fronds reniform to broadly ovate, not over 1.5 cm long. 10. T. flabellivenia
2. Sporangia quite covering lower surface of very narrow fertile pinnate.
12. Sterile pinnae up to 20 x 3.7 cm, widest at middle, narrowly acuminate; fertile pinnae up to 19 cm long; terminal cell of paraphyses not different from next... 11. T. requiniana
12. Sterile pinnae up to 12 x 3 cm, widest below middle, short-acuminate; fertile pinnae 10—15 cm long; terminal cell of paraphyses larger than next, club-shaped, curved, thick-walled.
12. T. diversifolia
1. Sori in apparently marginal or almost marginal grooves.
13. Simple lamina or pinnae of sterile frond deeply lobed. 13. T. trilobata
13. Simple lamina or pinnae of sterile frond entire.
14. Sterile fronds always simple and ± cordate at base; fertile simple or with 1 or 2 pairs of adnate pinnae. 14. T. cordata
14. Sterile and fertile fronds amply pinnate. 15. T. vittarioides

Fronds simple or paucipinnate; stipe of simple fronds up to 12 cm long, lamina up to 14 x 1.5 cm, broadly cuneate at base, narrowed to apex, rigid; stipe of pinnate fronds 10—18 cm long; pinnae 1—2-jugulate, 4.5—8 cm long, 8—10 mm wide, veins obscure; sori linear, near to and parallel with margin, paraphyses as in T. blechnoides; simple fronds often fertile.
Type specimen: Ernst 701, Sumatra, Padang Highlands, Harau Gorge (Z; dupl. at K).
Meijer 7529, same locality (K, L).
Distribution: only known from type locality, at foot of a sandstone cliff where a small waterfall maintains a wet place, in an exposed position.

Fronds of young plants simple, of mature plants pinnate; pinnae very variable in
number, width, and texture, usually 1—5 pairs, commonly 15—20 cm long; sterile pinnae commonly 2.5—5 cm wide, fertile 1—3 cm; sori usually medial, sometimes nearer to edge than to midrib; simple fronds rarely fertile; basal cells of paraphyses elongate, distal part formed of 10—12 very short cells.

**Type specimen:** *D. Klein*, S. India (B, Herb. Willd.).

**Distribution:** Ceylon & S. India, S. Burma, Thailand, Vietnam, Hainan, throughout Malesia to Fiji, Caroline Islands.

Contrary to the statement made on p. 585 of my book of 1954, the sorus in this species does have continuous vascular tissue beneath, and this soral vein does modify the series of oblique areoles. In a Bornean specimen which has unusually thick pinnae (*Chew, Corner & Stainton 590*, Kinabalu) there is a layer of transfusion-tracheids between the sorus and the vein, the surface below the sorus being slightly raised above the general level of the surface of the lamina; this transfusion tissue is apparently not present in fronds which are thinner (it is not shown by Leonard in an account of the anatomy of *Taenitis* in Sc. Proc. R. Dublin Soc., n.s. 15, 1918, 260—261). Another Bornean specimen with very rigid fronds has unusually narrow pinnae (*Richards 1643*, Mt Dulit), sterile 1 cm wide, fertile 6 mm. How far thickness and width of pinnae may be influenced by environment is not known, and could only be decided by experiment. Though the plants are common in nature, they are not easy to cultivate. One from Malaya has been maintained in cultivation at Kew and has been cytologically investigated (Manton 1958), showing n = 44 (originally published as an approximate count, later confirmed as an exact one). Doubtless other cytological forms exist.


Stipe up to 40 cm long, lamina up to 35 cm with 6—12 pairs of pinnae; pinnae nearly all fertile, c. 8—14 × 0.6—1.2 cm, rather thin; sori usually nearer edge than midrib, sometimes very near edge, often ± interrupted, c. 1 mm wide; paraphyses as in *T. blechnoides*.

**Type specimen:** *Wallich*, without locality, probably from Singapore (GL).

**Distribution:** southern half of the Malay Peninsula, Sarawak; usually in rather wet lowland forest.

Though all fronds are usually fertile, a specimen from Sarawak has a sterile frond with 8 pairs of pinnae, up to 1.5 cm wide, wider than the pinna of a fertile frond on the same plant.


Sterile frond always simple, lamina up to 40 × 4.5 cm, stipes usually 10—20 cm; fertile fronds long-stalked, usually with 1—4 pairs of pinnae which are 20—30 cm long, 8—10 mm wide.

**Type specimen:** *Holttum 17399*, G. Muntahak, Johore (SING).

**Distribution:** Malay Peninsula (Johore, Selangor, Pahang) in mid-mountain forest.

Brack. in Wilkes, U.S. Expl. Exped. 16 (1854) 66, t. 8, non Cav. — Dictyogramme elongata (Brack.) Moore, Ind. Fil. (1857) lx. — Dictyogramme pinnata (J. Sm.) Moore, Ind. Fil. (1861) 317. — Gymnogramme pinnata (J. Sm.) Hook., Spec. Fil. 5 (1864) 151; Bak., J. Bot. 17 (1879) 299. — Grammitis pinnata (J. Sm.) F. v. Muell., Fragm. Phyt. Austr. 6 (1868) 124. — Trichogramme pinnata (J. Sm.) Kuhn, Chaetopt. (1882) 328. — Fig. 6.

var. pinnata. — Fronds pinnate, pinnae commonly 2—4 pairs, rarely up to 7; sterile fronds about as in T. blechnoides but pinnae always rather thin and with edges distinctly crisped when dry; fertile pinnae not or little narrower than sterile, sporangia scattered thinly along the veins almost from midrib to margin in irregular oblique lines up to 7 mm long, rarely on all sides of an areole in the venation; distal cells of paraphyses not much shorter than basal ones.

Type specimen: Barclay s.n., 1839, Island of Jobia (= Japen), West New Guinea (K).


var. brachysora (Bak.) Holttum, comb. nov. — Gymnogramme pinnata var. brachysora Bak., l.c. 1879. — Sori 3—4 mm long, oblong, rarely round or linear, scattered rather irregularly or sometimes in a median band only.

Fiji: Milne 322; Horne 737 (K).

var. polypodioides (Bak.) Holttum, comb. nov. — Gymnogramme pinnata var. polypodioides Bak., l.c. 1879. — Sori round or broadly elliptic in outline, scattered throughout lamina. — Fig. 4.

Fiji: Horne 605 (K).

The typical form of this species is fairly uniform throughout its range in distribution of sporangia, but two collections from Papua (Carr 12663, 12144, Koitaki) have the sori confined to a median band, thus approaching T. hosei of Sarawak (which has only simple fronds). I found plants near Cairns in N. Queensland with two pairs of pinnae; spores from this gathering germinated at Kew and two generations of plants have been raised, sometimes producing sori on their largest simple fronds but always producing pinnate fronds later.

There are several specimens from Fiji at Kew, representing Baker's two varieties, and from these it seems doubtful whether the two are really distinct. It does seem however that together they are distinct from the normal form of the species, and if field study in Fiji confirms this, it might be best to rank them together as a distinct species.

6. Taenitis lanceolata (Diels) Holttum, comb. nov. — Syngramma lanceolata Diels in E. & P., Nat. Pfl. Fam. 1, Abt. 4 (1899) 257, new name for Hemionitis lanceolata Hook., 2nd Cent. Ferns (1861) t. 55, non Linn. — S. hookeri C. Chr., Ind. Fil. (1905) 346, (1906) 629; Copel., Bishop Mus. Bull. 59 (1929) 75. — Fig. 2.

Fronds simple, fertile and sterile isomorphous or sterile somewhat broader; stipe dark brown, glossy, 8—15 cm long; lamina up to c. 25 × 4 cm (fertile), sterile fronds up to 3½ cm wide, widest below middle, tapering gradually to apex, thinly coriaceous when dry; veins forming about three irregular series of oblique areoles; sporangia borne all along all the veins almost to the margin; paraphyses of 5 or 6 cells, distal one longer than wide; spores trilete, pale, inner faces verruculose, outer face with raised reticulum.

Type specimen: Milne s.n., Fiji (K).

Specimens collected on the Royal Society Expedition to the Solomons (1965) are: 4044, Guadalcanal; 4272, San Cristobal, 2400 ft in mossy forest; 4450, Kolombangara, 2800 ft, on ridge top.


Stipe of sterile frond 15—20 cm, of fertile up to 25 cm, dark, glossy; fronds simple; sterile lamina 27 × 5.5 cm, fertile 31 × 4.3 cm, widest below middle, tapering gradually to apex; venation of fertile frond anastomosing from near costa, of sterile mainly in outer half; sporangia distributed along all veins in a median band 8—9 mm wide on each half of fertile frond (leaving a sterile strip 4 mm wide on each side of costa and a marginal sterile band up to 8 mm wide); paraphyses of 10—12 cells, all rather short, distal one swollen.

Only known from the original collection, G. F. Hose 18, Mt Matang, Sarawak, 1500 ft (K).


Fronds simple or trifoliate; stipe of simple frond up to 7 cm, lamina up to 8 × 1.2 cm, widest near base, gradually narrowed distally, apex acute; sori about mid-way between costa and edge, not reaching apex, sometimes broken, paraphyses as in *T. blechnoides*; trifoliate fronds with lateral pinnae smaller than terminal, sometimes with rounded ends.

*Type specimen*: Brooks 3, Bongo Range, Sarawak (BM; MICH?).

*Distribution*: Sarawak (few collections).

Christensen considered that this species should be united with *T. obtusa*, and he may have been right; further collections of both are needed. Copeland only described simple fronds, but there are two trifoliate fronds in the type collection at BM.


Fronds simple, up to 6 cm long and 1.8 cm wide at base, spathulate, very rigid, midrib not reaching broadly rounded apex; sori almost continuous (except on fronds of young plants) and running in an arc across the frond just below apex; paraphyses as in *T. blechnoides*.

*Type specimen*: T. Lobb s.n., Sarawak (K).

*Distribution*: Sarawak (few collections).


Fronds reniform to broadly ovate, largest 1.5 cm long; edges more or less distinctly toothed; sori several, almost round, in an arc across apex of frond, paraphyses as in *T. blechnoides*.

*Type specimen*: Beccari, Banting, Sarawak (FI, K).
Distribution: Sarawak, N. Borneo, in crevices of sandstone rock (four collections; none recent).


Stipe of sterile frond 40—50 cm long, of fertile frond up to 70 cm; sterile frond with 3—6 pairs of pinnae, pinnae 15—20 × 2.3—3.7 cm, widest about middle, narrowly acuminated; apical pinna often united at base to a lateral one; fertile pinnae up to 6 pairs, largest seen 19 cm long, 2½—3½ mm wide, covered beneath with sporangia; all cells of paraphyses thin-walled, apical one not of distinctive shape.

Type specimen: Gaudichaud, Rawak (Lawak) Island, N.W. New Guinea (P).

Specimens seen: T. G. Walker 10279, 10280, 10281, New Britain, near Fulleborn Harbour, Kandrian Subdist., in dense undergrowth in forest 10—20 yards from the sea (BM).

Walker's specimens agree exactly with Gaudichaud's figure. Specimens previously at BM and K which were named T. requiniana prove to be distinct and are here described as a new species, T. diversifolia. Copeland states that T. requiniana and T. blechnoides intergrade, but I have seen no evidence of this.

12. Taenitis diversifolia Holttum, sp. nov.

Rhizoma breve repens, apice setis atris nitidis 2 mm longis vestitum. Stipes stramineus vel ± rufo-suffusus, frondis sterilis 25 cm longus, fertilis ad 45 cm. Lamina sterilis c. 15 cm longa, 20 cm lata, pinnata; pinnae vulgo 3-jugatae, contiguae, tenues, late patentes, inferiores breviter stipitulatae, omnes asymmetricae; pinnae infimae maximae, 10—12 × 2.5—3.0 cm, anguste ovatae, basi basiscopice multo exciseae, apice breviter acuminatae, marginibus incrassatis et crispatis; venae in siccó supra manifestae. Lamina fertilis more sterilis pinnata sed pinnae oblique; pinnae maximae 10—15 cm longae, 4 mm latae, infimae stipitulis 3—4 mm longis praeditae, superiores basi decurrentes; venae obscurae, areolis paucis; pagina inferior omnino sporangiis obtecta; paraphyses tenues, cellula suprema clavata rigida brunnea, cellulis ceteris hyalinis cum parietibus tenuibus.

Type specimen: Royal Society Expedition to the Solomon Islands (RSS) 4360, Kolombangara I., terrestrial in forest on low ridge-top near river, 30 m alt., locally frequent (K).

Solomon Islands. RSS 4516, Santa Ysabel, occasional by small stream in forest just behind beach; RSS 4552, E. San Jorge, 1½ km inland, occasional in more open parts of forest; RSS 4881, Small Malaita, 30 m; Comins s.n., Oct. 1890, San Cristobal (K); Waterhouse 79, New Georgia (K).

Banks Island. Veitch s.n. (K).
New Hebrides. Woods 60, Anteilum (K).


Sterile fronds on slender stipes 10—15 cm long, lamina trilobed, up to 6 × 2.5 cm; apical lobe deeply and obliquely pinnatifid, its divisions simple, 2—3 mm wide with rounded apices, or wider and bilobed; lateral lobes flabellate, deeply divided into 2 or 3
divergent segments which may be again bi- or tri-lobed; texture very firm, veins in each of the secondary lobes twice or more dichotomous, uniting close to apices of ultimate lobes. Fertile fronds simple or with very short basal lobes, edges entire or sinuose; simple frond or terminal lamina up to 3.5 cm long, 5 mm wide, with a continuous sorus close to its edge protected by a thick false indusium; paraphyses slender, about as in T. cordata.

**Type specimen:** C. Hose s.n., 1890, Niah, Sarawak (K).

**Distribution:** Sarawak (three collections, apparently from limestone).

The fertile frond is very like that of T. cordata, and Charles Hose found both species on limestone at Mulu; but I think the two species are distinct.


Sterile fronds: stipe 4—7 cm, lamina very rigid, broadly ovate to ovate-acute, base ± cordate, 4—12 cm long, 2$\frac{1}{2}$—4$\frac{1}{2}$ cm wide. Fertile fronds: stipe 7—15 cm, lamina simple, 7—14 cm long, 5—12 mm wide, base rounded, tapering to the acute or narrowly rounded apex, or trilobed with apical lobe longer than laterals; sori in an apparently marginal groove, almost from base to apex, both edges of groove cartilaginous; elongate receptacle of sorus joining ends of all veins and distinctly intra-marginal with no free veins beyond it; paraphyses slender, their distal cells not shorter than basal ones.

**Type specimen:** Gaudichaud, Rawak I. (= Lawak), W. New Guinea (P, dupl. at K), 'sur les rochers calcaires nues quiavoisinent le rivage'.

**Distribution:** Borneo, Celebes, the Philippines (Bohol, Samar), W. New Guinea; apparently always on limestone.

This species has been reported as occurring in the Malay Peninsula. The only evidence for this is Hooker's writing, on the only sheet in his herbarium bearing specimens of this species. This writing is evidently a later addition, as Hooker only referred (in Spec. Fil. vol. 1, 1846) to specimens collected by Hinds near New Guinea when publishing his description and illustration (a composite one, from different fronds now on the sheet). One frond, not illustrated, overlaps another, and must have been added later, and it appears that Hooker's words 'Malacca, an L. cordata' refer to this. No other record of a specimen from Malaya exists, and there is no record of a collector's name; without further evidence I do not think that Malaya should be included in the known distribution of the species. The first collection from Borneo was by Charles Hose in 1890.

### 15. Taenitis vittarioides Holttum, Kew Bull. 20 (1966) 460. — Fig. 5.

Stipe 40—50 cm long, frond pinnate; pinnae 3—7 pairs, 18—24 cm long, sterile ones 3 cm wide, fertile 1.2—1.7 cm wide; sori like those of T. cordata, submarginal, in a groove; paraphyses as in T. blechnoides.

**Type specimen:** Korthals s.n., West Sumatra (L, dupl. at K).

Only known from the type collection. The sterile fronds could not be distinguished from T. blechnoides, and the two species must be very closely related. It appears as if T. vittarioides is a local mutation; and as no other similar specimens have been found in Sumatra since Korthals (about 1834—35) the species cannot be widespread. A remarkable
fact is that the only other collection which resembles the type of *T. vittaroides* is one from Ceram (*Buvalda 6016*, Mt Tunbean, 300 m, in primary forest with *Agathis*). The Ceram specimens have sori exactly as in *T. vittaroides*, but are considerably smaller than those from Sumatra, and their pinnae have a much thicker lamina. Can they represent an independent mutation similar to that which produced the Sumatran plants? One would like to subject such plants to experimental treatment.