THE LINDSAEOID FERNS OF THE OLD WORLD II. A REVISION OF TAPEINIDIUM

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INTRODUCTION

Tapeinidium is the second largest of the Lindsaeoid fern genera. In the present study 17 species are distinguished. Until *Tapeinidium* was recognized as a genus its species were included in *Microlepia*, where it was originally described as an infrageneric division, or in *Davallia*. Fée (1852), then Diels (1902), treated it as a genus, but under the incorrectly interpreted name *Wibelia* Bernhardi, which is actually a synonym of *Davallia* (see Copeland, 1947).

The species described so far have mainly been distinguished by their leaf architecture, especially the degree of dissection; see, e.g., van Alderwerelt van Rosenburgh (1909). In my opinion this is at best one of several useful characters. At least equally important is the structure of the petiole and the other axes of the lamina, a character that proved to be very valuable for diagnostic purposes in the neotropical *Lindsaea* species (Kramer, 1957a) but is much less serviceable in the paleotropical ones. In some cases the rhizome scales are also distinctive. These characters have been grossly neglected in the past, and the species distinguished by most authors are generally far too widely circumscribed. Diels (l.c.), for example, listed three species at a time when more than twice as many were known. Accordingly there proved to be a surprisingly large number of undescribed species, viz. 8 out of the 17 recognized here, some of them represented by numerous specimens in many herbaria and collected long ago but never recognized, e.g., *T. novo-guineense* and *T. melanesicum*. This contrasts sharply with the situation in *Lindsaea* in the same region where the number of new species is comparatively very small and relatively many more species have to be placed in synonymy.

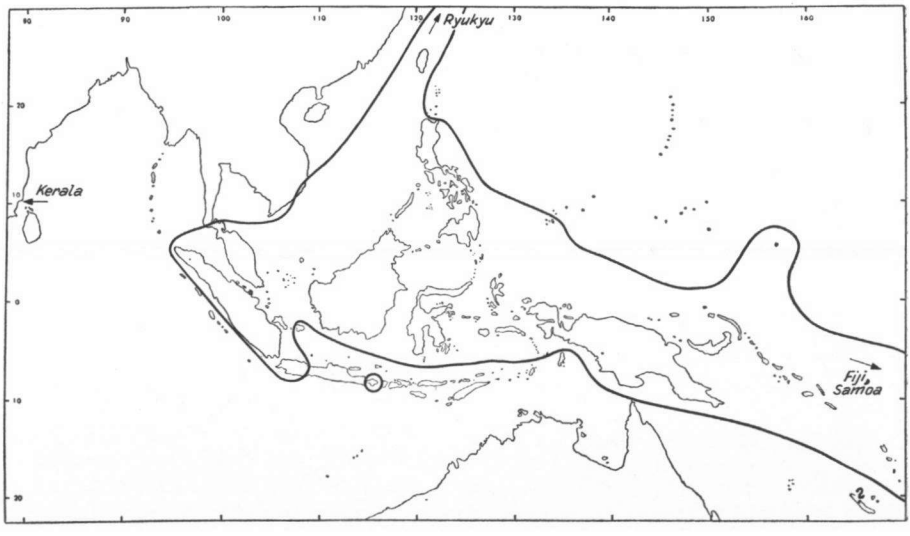
GENERAL TAXONOMIC NOTES

Tapeinidium is a very natural and homogeneous fern genus, and it seems unnecessary to divide it into subgenera or sections. In my former paper (Kramer, 1957a) I stated that it is difficult to separate from *Sphenomeris*. At present it seems that this is only true in the sense that it is difficult to express the difference in simple words, in a key. During the preparation of the present paper there never was any doubt whether a species belonged to one or the other genus. In *Sphenomeris* the leaf pattern of the ultimate divisions is essentially cuneate-dichotomous, with the sori apical on the pinnules (segments); *Tapeinidium*, on the other hand, has a pinnate leaf architecture with the sori on lateral lobes. There are very few exceptions to this rule; in *T. tenue* apical sori usually occur beside lateral ones, and for this and other reasons it may well be the most primitive species in the genus. The spores of *Tapeinidium* are consistently monolete; in *Sphenomeris*

both monolete and trilete ones occur. The rhizome scales of *Sphenomeris* also tend to be more acicular than those of *Tapeinidium*, but the distinction is not very sharp. Much closer to *Tapeinidium* is the genus *Xyropteris*, a fact not recognized when it was first described (Kramer, 1957b). Fertile leaves of juvenile plants are surprisingly like *Tapeinidium*, and the name *Tapeinidium bartlettii* has been given to such specimens, but the unbroken sori and the auriculate pinnae of adult plants are so different from what is otherwise observed in the genus that *Tapeinidium* becomes a much more homogeneous entity when *Xyropteris* is excluded, although the latter seems to be a relatively recent offshoot of the former.

Tapeinidium is distributed from South India and the Ryukyu Islands to Fiji; it is absent from Ceylon, Australia, New Caledonia (?), and most of the Micronesian islands (map 1). The greatest concentrations of species are in Borneo (5), the Philippine Islands (5), Celebes and the Moluccas (6), and New Guinea (6). In western Malesia the representation is comparatively weak. Narrowly distributed endemics, according to our present state of knowledge, occur chiefly in New Guinea which has 3 species confined to it and one extending to the Moluccas, but they also occur in western Malesia and elsewhere.

Most specimens are from mountain forests, but many have occasionally been reported from lower altitudes, and it seems that few species are actually restricted to higher elevations. *Tapeinidium* seems to be difficult to cultivate; no specimens have been seen that were from extratropical botanical gardens and only one or two from tropical gardens.



Map 1. Range of the genus *Tapeinidium*.

TAPEINIDIUM (Presl) C. Christensen

C. Christensen, Index Filicum (1906) 631. Basionym: *Microlepia* § *Tapeinidium* Presl, Epimel. Bot. (1849) 96. Type species: *Davallia pinnata* Cav. = *Tapeinidium pinnatum* (Cav.) C. Chr.

Wibelia auct. non Bernhardi; Fée, Gen. Fil. (1852) 331; Diels in Engler & Prantl, Nat. Pflanzenfam. I[4] (1902) 216.

Small to medium-sized terrestrial ferns with very short to moderately long-creeping rhizome with at least in the larger species a true solenostele with external and internal endodermis and a medullary strand of sclerenchyma (perhaps lacking in one or two of the smallest species); scales long and narrow, glabrous and non-clathrate. Lamina of a pinnate type up to the last divisions, these never dichotomously divaricate. Sori uninerval or occasionally binerval (very rarely trinerval), never continuous, terminal on the veins, mostly submarginal. Indusium rigid, attached at the base and at least the greater part of the sides. Pluricellular uniseriate filiform paraphyses present in some (probably all) species. Spores monolete, ellipsoidal or almost bean-shaped. Gametophyte unknown.

Remarks. Extensive descriptions of species that are not new will be provided in the regional treatments where they are included and where also some illustrations will be given.

The length of a sorus is measured at right angles to its vein, the width parallel to its vein. This may seem paradoxical, but it makes the use of the terms consistent with the much larger genus *Lindsaea*.

KEY TO THE SPECIES

1. Lamina simply pinnate and with a conform terminal pinna.
   2. Sori submarginal, most often binerval; petiole and rachis abaxially sharply bi-angular; scales to 5 mm long . . . . . **16. T. longipinnulum**
   2. Sori intramarginal, almost always uninerval; petiole and rachis abaxially terete or very obtusely bi-angular, concolorous; pinnae usually obtuse, deeply crenate; scales to 1½ mm long. **17. T. melanesicum**
   2. Sori as in the preceding species; rachis abaxially sharply bi-angular or sulcate, basally dark and pale-margined; pinnae acuminate, very shallowly sinuate; scales to 2½ mm long. **14. T. acuminatum**
1. Lamina more strongly dissected, or, if simply pinnate, the upper pinnae confluent into a pinnatifid leaf-apex or at least the terminal division strongly lobed at its base.
   3. Lamina simply pinnate, or, if more dissected, the primary rachis abaxially sharply carinate; at least a considerable upper portion of the petiole abaxially sharply bi-angular.
      4. Petiole, at least in the upper part, and rachis dark, pale-angled; lamina pinnate + pinnatifid or bipinnate.
         5. Larger pinnae of full-grown plants 20—25 mm wide at the widest point; texture subcoriaceous; margin often reflexed in dry leaves; lobes of larger pinnae sinuate, the sori not on lobes. **8. T. gracile**
         5. Larger pinnae of full-grown plants 10—12 mm wide at the widest point; texture herbaceous; margin not reflexed; lobes of larger pinnatifid or basally subpinnate pinnae lobed, each sorus on a lobe: smaller forms of . . . . . **1. T. tenue**
      4. Petiole pale, or, if occasionally darker, the rachis not also dark and pale-carinate; or lamina simply pinnate.
         6. Lamina to 12 cm long; petiole slender, less than 1 mm thick. . . . **10. T. oligophlebium**
         6. Lamina larger; petiole stouter.
            7. Petiole abaxially obtusely bi-angular, dark and dull, ± pale-angled; rachis abaxially mostly narrowed-rounded; sori submarginal, on saw-teeth; lamina simply pinnate. **13. T. prionoides**
            7. Petiole sharply bi-angular at least near the apex, nearly always pale; rachis abaxially carinate or bi-angular; sori intramarginal; lamina variously dissected.
               8. Lamina pinnate + pinnatifid or more incised *) . . . . . **11. T. luzonicum**
               8. Lamina simply pinnate or in large leaves the basal pinnae with very few basal lobes *).

*) For intermediates see 12a.

9. Rachis abaxially sharply carinate; sori laminal or on short, obtuse lobes. **12. T. pinnatum**

9. Rachis abaxially bi-angular; sori intramarginal, on saw-teeth **15. T. carolinense**

3. Lamina at least pinnate + pinnatifid; primary rachis abaxially terete or bi-angular, or, if obtusely carinate, the petiole abaxially not or only at the apex sharply bi-angular.

10. Primary rachis atropurpureous; secondary rachises (except sometimes the basal ones) abruptly pale; pinnae pinnatifid, with crenate segments, only the basal pinnae occasionally with some pinnatifid basiscopic pinnules; most sori with their greatest extension at right angles to their vein. **9. T. calomelanos**

10. Primary rachis at least at base dark; secondary rachises pale; pinnae pinnate + pinnatifid or subbipinnate; sori with their greatest extension parallel to their vein. . . **5. T. stenocarpum**

10. Primary rachis pale, or, if dark, the secondary rachises not abruptly pale; lamina often more incised.

11. All axes, except the primary, green-margined to base or almost so, i.e., lamina only once fully pinnate, then pinnatifid; secondary axes abaxially rounded. . . **2. T. buniifolium**

11. Lamina mostly fully bipinnate; secondary rachises, if marginate, abaxially carinate.

12. Secondary rachises abaxially black, with two pale lateral or one median pale ridge; lamina bipinnate or almost so, with superficially crenato-lobate pinnules; pinnae not enlarged at base . . . . . **7. T. atratum**

12. Secondary rachises abaxially various but not black with pale ridges; lamina often bipinnate + pinnatifid.

13. Primary rachis and indusia black; ultimate lobes abaxially with very broad and prominent veins occupying $\frac{1}{4}$—$\frac{1}{3}$ of their width. . . . . **6. T. obtusatum**

13. Primary rachis and indusia pale to dark brown; ultimate lobes with immersed, or, if slightly prominent, relatively much narrower veins.

14. Indusia about twice as broad as long, 0.3 mm long; margin bordering the apical sorus of the segment usually denticulate; texture herbaceous. **1. T. tenue**

14. Indusia longer, or, if only $\frac{1}{3}$ mm long, ± isodiametric or longer than broad; margin bordering the apical sorus entire, or no apical sorus; texture firmer.

15. Larger segments pinnatifid, each lobe with a sorus overtopped by part of the lobe . . . . . **3. T. amboynense**

15. Larger segments (except for the basal pinnae) crenate, each lobe with a terminal or subterminal sorus.

16. Secondary rachises abaxially terete in a considerable basal portion; basiscopic pinnules of basal pinnae usually enlarged and more dissected than the others . . . . . **4. T. novoguineense**

16. At least the larger secondary rachises abaxially carinate; basiscopic pinnules of basal pinnae rarely enlarged and more dissected. **11. T. luzonicum**

1. Tapeinidium tenue (Brackenridge) Copeland, B.P. Bishop Mus. Bull. 59 (1929) 69. — Basionym: *Microlepia tenuis* Brackenridge, U. S. Expl. Exped. (1854) 236. Type: Sandalwood Bay, Fiji (Vanua Levu?), *U. S. Explor. Exped. 3* (US).

Davallia denhami Hooker, 2nd Cent. Ferns (1860) pl. 47. — *Microlepia denhami* (Hooker) Moore, Ind. Fil. (1861) 292. — *Lindsaea denhami* (Hooker) Mettenius *ex* Kuhn, Verh. Zool. Bot. Ges. 19 (1869) 573. — *Wibelia denhami* (Hooker) Kuhn, Chaetopt. (1882) 346. — *Tapeinidium denhami* (Hooker) C. Christensen, Ind. Fil. (1906) 631. — Type: *Milne 116*, Viti Levu, Fiji (K).

Tapeinidium tenuius Copeland, Philip. J. Sc. 60 (1936) 110, pl. 17. — Type: *Brass 3025*, San Cristóval, Solomon Is (MICH).

The relatively narrow scales, only up to 4 cells wide and the greater part uni- or biseriate, the denticulate lobes, and the sori that are often terminal as well as lateral.

together with the thin texture, characterize this species rather well. In the type the teeth of the lobes are almost, the terminal sori quite lacking, but otherwise it matches the other specimens well. In size and degree of dissection it is quite variable; except for the two types the Fijian specimens are smaller and less incised than the plants from the western part of the range.

Distribution: Seen from: Admiralty Is (Manus), Bismarck Archipelago (New Hannover, New Ireland), Solomon Is (San Cristóval, Santa Ysabel, Guadalcanal), New Hebrides (Aneityum, Banks I.), Fiji (Viti Levu, Vanua Levu, Ovalau). Specimens labelled 'New Caledonia' and 'Isle of Pines' are probably from the New Hebrides (Kramer, 1967).

2. Tapeinidium buniifolium Kramer, *spec. nov.* — *T. moluccanum auct. non* (Blume) C. Chr.; Wagner & Grether, Univ. Calif. Publ. Bot. 23 (1948) 36. — Type: *Grether & Wagner 4188*, Manus, Admiralty Is, Tjajiak Mts, Mt Dremsl region, in mountainside woods, *c.* 2000 ft. (MICH; isotype US).

Rhizomatis partes perbreves solum adsunt; squamae rubro-fuscae, pro parte majore aciculares, uni- vel biseriatae, basi paullo latiores. Petioli abaxialiter, ut videtur, basi subteretes, supra obtuse biangulares. Lamina probabiliter deltoidea, pinnata et quadripinnatifida vel basi subbipinnata et tripinnatifida; apex laminae deest, probabiliter pinnatifidus. Pinnae primariae minime 4 pro latere, majores oblongae, breviter petiolulatae, pinnis secundariis majoribus pro latere circ. 12—15. Rhachis primaria straminea ad brunnea, abaxialiter, ut videtur, biangularis; rhachides ceterae abaxialiter stramineae, teretes, anguste viridi-marginatae ad basim vel basales fere ad basim. Segmenta lanceolata vel linearia, chartacea, basi profunde pinnatifida, apice dentato-lobata. Lobi ultimi majores lanceolato-ligulati, ad 4 × 1¾ mm, subacuti, saepe subfalcato-adscendentes, asymmetrici, margine anteriore, ubi sorus, gibboso; lobi minores triangulares, soro subterminali. Venae simplices vel in lobis majoribus furcatae. Sori uninervii; indusium brunnescens, marsupiiforme, basim versus angustatum, longitudine et latitudine ± aequis.

Remarks. Only known from the type collection, as cited above. The most finely dissected species, except for the larger forms of *T. tenue*, from which it differs, i.a., by all axes being marginate to the base or almost so.

3. Tapeinidium amboynense (Hooker) C. Christensen, Index Filicum (1906) 631. — Basionym: *Davallia amboynensis* Hooker, Spec. Fil. I (1846) 178, t. 56 C. — *Lindsaea amboynensis* (Hooker) Mett. *ex* Kuhn, Ann. Lugd. Bat. 4 (1869) 279. — *Wibelia amboynensis* (Hooker) Kuhn, Chaetopt. (1882) 346. — Lectotype: *A. Smith s.n.*, Ambon (Amboyna), 'from P. B. Webb' (K).

Davallia stenoloba Baker in Beccari, Malesia III (1886) 35. — *Tapeinidium moluccanum* (Blume) C. Chr. var. *stenolobum* (Baker) C. Chr., Index Filicum Suppl. III (1934) 176. — *Tapeinidium stenolobum* (Baker) Wagner & Grether, Univ. Calif. Publ. Bot. 23 (1948) 36. — Type: *Beccari s.n.*, Mt Salhutu, Ambon, 1000 m (FI, fragm. K).

Tapeinidium moluccanum C. Chr., Index Filicum Suppl. III (1934) 176, and of nearly all later authors; not *Davallia moluccana* Blume, Enum. (1828) 237 (= *Saccoloma* spec.).

Tapeinidium amplum Copeland, Occ. Papers Bishop Mus. 15 (1939) 82, f. 3. — Type: *Takamatsu 1572*, Garasumao, Palau Is. (MICH; isotypes BISH, K, US).

Distribution: Seen from Celebes, the Moluccas (Talaud, Morotai, Halmahera, Ternate, Ambon, Ceram), the Kei Is, Waigeo, Biak, Western New Guinea, and the Palau Is. A specimen in BO labelled 'Borneo *Nieuwenhuis? 166*' is probably from elsewhere.

Remarks. The type of *Davallia moluccana* Blume at L was examined by the writer;

it is a *Saccoloma*, not a *Tapeinidium*, though in habit very similar to *T. amboynense*. *Ithycaulon*, based on *D. moluccana*, is therefore a synonym of *Saccoloma*, not of *Tapeinidium*, as was recently stated.

Related to *T. stenocarpum*, *T. tenue*, and *T. luzonicum*; the character stated in the key under heading 15 indentifies this species quite readily.

4. Tapeinidium novoguineense Kramer, *spec. nov.* — Type: *Schlechter 14319*, Torricelli Mts, Territory of New Guinea, 700 m (B, 2 sheets; isotypes BM, BO, K, P).

Rhizoma breviter vel pro genere longius repens, squamis brunneis, pro parte majore pluriseriatis, ad 3 mm longis vestitum. Petiolus stramineus vel obscurior, abaxialiter teres. Lamina bipinnata, vel bipinnata et pinnatifida, basi nonnumquam tripinnata, elongato-triangularis vel subquinquangularis-triangularis, rarius oblonga; rhachis primaria straminea vel pallide brunnea, abaxialiter teres vel angustato-teretiuscula, ad apicem tantum carinata. Pinnae majores 15—35 pro latere, basi latere anteriore latiores, pinnatae, 12—16 cm longae, pinnulis ca. 20—30 pro latere; pinnulae posteriores basales pinnarum basalium plerumque valde protractae, magis incisae. Rhachides secundariae (et ceterae) stramineae, abaxialiter infra teretes, supra carinatae. Pinnulae ultimae liberae circ. 20—30 pro latere, subcoriaceae vel coriaceae, nonnumquam statu sicco revolutae, lanceolatae, obtusae vel subacutae, majores vulgo 3—4 cm longae, 3—4 mm latae, crenatae vel pinnatifidae. Venae in lobis simplices vel in majoribus furcatae, subprominulae. Pinnae et pinnulae superiores abbreviatae, confluentes. Sori singuli in lobis vel rarius bini vel ultra, uninervii; indusium marsupiiforme ad subtriangulare, marginem non attingens, a marginibus lateralibus et apicalis lobi aequidistans.

Distribution: Japen, Western New Guinea, Papua, and the Territory of New Guinea.

Remarks: This is a widespread species in New Guinea, on labels often said to be locally common. I have seen almost 50 different collections, and a few doubtful ones. The sheets were usually labelled '*T. moluccanum*'. It seems very close to *T. stenocarpum* which may be only a form of it; this is difficult to judge as I have seen only two collections of the latter. But the obtusely bi-angular petiole and rachis with paler edges, the linear ultimate and penultimate segments, and the narrower sori of *T. stenocarpum* seem to be distinctive enough. *T. amboynense* is undoubtedly also very closely related.

5. Tapeinidium stenocarpum van Alderwerelt van Rosenburgh, Nova Guinea 14 (1924) 52. — Type: *Lam 1442*, W. New Guinea, mountain ridge near Idenburg R., terrestrial in swampy Vaccinium forest, alt. 1420 m (BO; isotypes K, L, SING, U; fragm. US).

Remarks. Except for *T. tenue* and *T. buniifolium* this is the most finely dissected species. It seems to be closest to *T. novoguineense*; for the differences see the key and the note under the last-named species.

Apart from the type only one collection seen: *Brass 12102* (GH, MICH), also from W. New Guinea.

6. Tapeinidium obtusatum van Alderwerelt van Rosenburgh, Nova Guinea 14 (1924) 52. — Type: *Lam 1857*, W. New Guinea, mountain ridge near Doormantop, terrestrial in forest, alt. 2500 m (BO; isotypes L, SING, U).

Remarks. This distinctive species, only known by its type collection, is readily identified by the characters described in the key. It is the most coriaceous one of the finely dissected species. Its affinity is uncertain.

7. Tapeinidium atratum Kramer, *spec. nov.* — Type: *Lam 1556*, W. New Guinea, mountain ridge near Doormantop, 1420 m (BO, 2 sheets; isotypes L, SING, U).

Rhizoma pro genere longius repens, squamis anguste triangularibus, apice aciculari longo, ad 2 mm longis obtectum. Petiolus atratus, abaxialiter supra acute biangularis, costis haud pallidioribus, infra sensim teretiusculus. Lamina bipinnata, pinnis pro latere circ. 15—20, remotis, adscendentibus, anguste deltoideis, breviter acuminatis, pinnatis, supra pinnatifidis; rhachis primaria atrata, abaxialiter acute biangularis, supra costis pallidioribus. Rhachides secundariae obscurae, abaxialiter costis pallidis duabus, lateralibus, vel singulis, medialibus. Pinnae superiores abbreviatae, confluentes? Pinnulae rigide coriaceae, statu sicco fuscae, ad 35 pro latere, angustissime lanceolatae, ad 17 × 4 mm, pinnatilobatae, lobis pro latere circ. 9, late rotundatis, ad 1 × 1 mm, apice obtusae, basi cuneatae, decurrentes. Costae pallidae, abaxialiter prominulae, obtusae. Venae immersae, simplices vel unifurcatae. Sori singuli, rarissime bini vel terni in lobis, uninervii, prope marginem anteriorem, paulum sed manifeste sub apice; indusium atratum, marsupiiforme.

Remarks. The regularly pinnate lamina with only shortly acuminate pinnae and especially the dark colour of the axes and indusia, with the secondary rachises abaxially pale-margined, are distinctive for this species which is only known by its type collection.

8. Tapeinidium gracile (Blume) van Alderwerelt van Rosenburgh, Malayan Ferns (1909) 315. — Basionym: *Davallia gracilis* Blume, Enum. (1828) 233. — *Microlepia gracilis* (Blume) J. Smith, London Jo. Bot. 1 (1842) 427. — *Davallia pinnata* Cav. var. *gracilis* (Blume) Baker, Syn. Fil. 1st ed. (1867) 98, *comb. valid.* ? — *Wibelia gracilis* (Blume) Christ, Ann. Jard. Buitenz. II, 5 (1905) 134. — Type: *Blume 1731* or *s.n.* from Java (L).

Distribution: Indo-China (one coll. from Nhatrang, Annam), West Java, Bali, Borneo (one coll. each from Brunei and Sarawak), Celebes, Ceram, and the Philippine Is (Luzon, Negros, Mindanao, Sulu Archip., Leyte, and Mindoro). The species seems to be most common in Java and Luzon. Its absence from Sumatra and the Malay Peninsula is rather surprising.

Remarks. Rather easily recognized by the pinnate + pinnatifid lamina and dark, abaxially pale-margined axes, the bi-angular petiole, and the carinate primary rachis. It may be that the correct name for this species is *Tapeinidium lineare* (Cav.) C. Chr.; I have not seen the type of *Dicksonia linaeris* Cav. On a photograph kindly sent from Madrid by Dr E. Paunero the specimen looks most like *T. 'biserratum'*, but the character of the axes which I regard as crucial is not visible.

9. Tapeinidium calomelanos Kramer, *spec. nov.* — Type: *Korthals s.n.* from G. Sakoembang, S.E. Borneo (L, 2 sheets).

Rhizoma breviter vel (pro genere) longius repens, squamis badiis elongato-triangularibus longe acuminatis ad 2 mm longis vestitum. Petioli pullo-atropurpurei, abaxialiter teretes. Lamina pinnata et profunde pinnatifida vel basi bipinnata (et pinnatifida), elongato-triangularis vel oblonga vel subquinquangularis, 10—35 cm longa, subcoriacea vel coriacea. Rhachis primaria atropurpurea vel rarius obscure badia, abaxialiter teres. Rhachides secundariae (et ceterae) abrupte pallidae (interdum praeter basales), abaxialiter omnino teretes. Pinnae majores 12—20 pro latere, lanceolatae, inferiores vulgo triangulares, subsessiles, acuminatae, profunde pinnatifidae vel basi interdum pinnatae et tunc pinnulae majores basiscopicae interdum pinnatifidae, ceterae pinnatilobatae; segmenta (pinnulae) majores ad 18 pro latere, adscendentia, lanceolata, serrata vel crenata, basi inaequaliter cuneata, obtusa vel subacuta, ad apicem mox decrescentia. Pinnae ad apicem laminae confluentes. Venae simplices vel in lobis majoribus furcatae, immersae vel

paulum prominulae. Sori uninervii, singuli in lobis; indusium obscurum, vulgo longius quam latum, marginem non attingens.

Distribution: Sumatra (locality perhaps incorrect), Borneo (beside the type *Korthals s.n.* without locality, B, BM, L), Celebes (*Elbert 3113*, BO, K, L, SING), and Luzon (*Alcasid & Edaño 5083* and *Merrill 933*, both MICH).

Remarks. I have long hesitated before describing this as new; it is known from a few scattered, mostly rather old collections. Its leaf architecture is rather like that of certain forms of *T. luzonicum*, but the axes are entirely different. The dark, abaxially terete primary and the abruptly pale secondary axes are unique in the genus. The Philippine collections are smaller than the other ones.

10. Tapeinidium oligophlebium (Baker) C. Christensen, Index Filicum (1906) 631. — Basionym: *Davallia oligophlebia* Baker, Jo. Bot. 26 (1888) 323. — *Wibelia oligophlebia* (Baker) Christ, Ann. Jard. Buitenz. II, 5 (1905) 134. — Type: *Ch. Hose 220*, Sarawak, Laupi (K).

Protolindsaya brooksii Copeland, Philip. J. Sc. 5, Bot. (1910) 283. — *Tapeinidium brooksii* (Copel.) C. Chr., Index Filicum Suppl. III (1934) 176. — Type: *Brooks 47*, Sarawak, Gunong Bengkaim (SAR, holotype?; isotype BM, 2 sheets; specimens with the same number but different dates in BM, K, and P).

This small species looks suspiciously like a depauperate but fertile form of another species, e.g., *T. luzonicum*. But the almost 20 collections I have seen are all from Borneo (Sarawak, except one which is from Kalimantan), whereas *T. luzonicum* occurs throughout western and central Malesia. This leads to the conclusion that it is a taxon that deserves recognition, although it may not be a distinct species.

The type of *Protolindsaya brooksii* has almost linear laminas with very short pinnules, but two collections by *Richards* (*2024*, K, SING, U, US, and *1747*, K) connect it with typical *T. oligophlebium*.

11. Tapeinidium luzonicum (Hooker) Kramer, *comb. nov.* — Basionym: *Davallia luzonica* Hooker, Spec. Fil. I (1846) 174, t. 60 B, f. 2, 3, 5. — *Wibelia bipinnata* Fée, Gen. Fil. (1852) 331, *nom. superfl.* — Type: *Cuming 139* (K ?; isotypes B, L).

Lindsaea pinnata (Cav.) Mett. *ex* Kuhn var. *bipinnata* Mett. *ex* Kuhn, Ann. Mus. Lugd. Bat. 4 (1869) 279. — Lectotype: *Zollinger 1305*, Java (HBG, L, isotypes).

Davallia philippinensis Harrington, J. Linn. Soc. Lond. 16 (1877) 27. — *Microlepia philippinensis* (Harrington) Copeland, Polypod. Philipp. (1905) 56. — *Tapeinidium philippinense* (Harrington) C. Chr., Index Filicum Suppl. III (1934) 176. — Type: *Steere s.n.* Luzon, Mt Mahayhay (K).

Davallia hosei Baker, J. Bot. 26 (1888) 323. — Type: *Ch. Hose 219*, Sarawak, Lambur (K).

Tapeinidium sumatranum van Alderwerelt van Rosenburgh, Bull. Jard. Bot. Buitenz. III. 2 (1920) 174. — Type: *Brooks 332/S*, Sumatra, Benkulen (BO, fragm.).

Tapeinidium biserratum sensu Holttum, Rev. Flora Malaya II (1954) 339, and of other authors; not *Davallia biserrata* Blume.

Distribution: Thailand (1 coll.), Malaya (Pahang, Kelantan, Trengganu, Perak, Johore), Natuna Is, Lingga Is, Banka, Sumatra, West Java (few coll.), Borneo (Sabah, Brunei, Sarawak, Kalimantan), Celebes, and the Philippine Is (Luzon, Mindanao, and Polillo).

Remarks. This widespread species is readily identified by the pale petiole which is abaxially bi-angular at least in the upper part, the pale, abaxially sharply carinate primary and secondary rachises and costa, and by the at least pinnate + deeply pinnatifid lamina.

It may only be a deeply incised form of *T. pinnatum*, and there are some intermediates (see under '*T. biserratum*', after the following species), but, as already noted by Holttum (l.c., p. 340), typical specimens of *T. luzonicum* and of *T. pinnatum* are so overwhelmingly more numerous than intermediates that I prefer to treat them as distinct.

The above applies to var. *luzonicum*. Although it seems dangerous to describe varieties in a genus where many species are distinguished by rather slight differences only, the following two forms which are distinct from the bulk of the specimens of *T. luzonicum* differ by such superficial characters that I prefer to call them varieties; they are also geographically much more restricted.

a. var. **leptophyllum** Kramer, *var. nov.* — Type: *Elmer 14103*, Mindanao, Mt Urdaneta (L; isotypes BO, HBG, MICH).

Differt a varietate *luzonica* petiolis gracilioribus, basi laminae maxime 1 mm crassis, saepe brunneis; lamina graciliore, basi subtripinnata, habitu eam Pityrogrammae calomelaneos simulante, segmentis ultimis liberis minoribus, anguste lanceolatis, plurimis non ultra 1 cm longis, 1—2 mm latis; venis magis conspicuis, in lobis saepe simplicibus; soris singulis vel binis in lobis saepe regulariter rotundatis; indusiis ca. 0.3 × 0.3 mm.

PHILIPPINES. Negros: *Whitford 1498* (MICH); *Edaño 21429* (MICH), id. *5952* (GH, juvenile, doubtful). — Mindanao: *Loher 1117* (K, US); *Mendoza & Convocar 8711* (MICH, SING); *Warburg 14157* (B); *Elmer 14103* (type, L, BO, HBG, MICH). — Camaguin: *Ramos 14878* (B, BO, K, L, SING, US). — Panay: *Ramos & Edaño 30666* (B, BM, BO, L, US). — Leyte: *Wenzel 551* (GH), *777* (MICH). — Luzon: *Micholitz s.n.* (GH, K); *Vidal s.n.* (K); *Weiss 4107* (L); *Elmer 17852* (K, *p.p. mai.*).

Remarks. This variety is not unlike *T. tenue* but differs in some important characters like the non-dentate soriferous lobes and the structure of the rachis. The differences from typical *T. luzonicum* are quantitative rather than qualitative and it seems therefore better to treat it as a variety.

b. var. **thelypteridoides** Kramer, *var. nov.* — Type: *W. M. A. Brooke 8190*, Sarawak, Mt Santubong, 2000 ft, on damp rock in forest (L; isotypes SING, US).

Recedit a varietate *luzonica* lamina solum pinnata + pinnatifida vel pinnatilobata, pinnis regulariter incisis, infimis maxime ad ⅔, lobis oblongo-ligulatis, leviter serrato-crenatis; textura chartacea; venis manifestis; soris saepe magis inframarginalibus. Habitu speciei Thelypteridis, e.g., Th. dentatae, sat similis.

BORNEO. Sarawak: *W. M. A. Brooke 8190* (type). North Borneo: *W. Meijer 560* (BO, L), *562* (BO, K, L); id. *SAN 23293* (K, L).

Remarks. This may be a species in its own right, but a few specimens almost bridge the gap between it and var. *luzonicum* which makes treatment as a variety preferable.

12. Tapeinidium pinnatum (Cav.) C. Christensen, Index Filicum (1906) 631. — Basionym: *Davallia pinnata* Cavanilles, Descr. (1802) 277 (*non* Mett. *ex* Kuhn, 1869). — *Saccoloma pinnatum* (Cav.) Presl, Tent. Pteridogr. (1836) 126. — *Microlepia pinnata* (Cav.) J. Smith, Hooker's Jo. Bot. 3 (1841) 416. — *Wibelia pinnata* (Cav.) Bernhardi *ex* Fée, Gen. Fil. (1852) 331, t. 27 bis B. — *Lindsaea pinnata* (Cav.) Mett. *ex* Kuhn, Ann. Lugd. Bat. 4 (1869) 279. — Type: *L. Née s.n.*, Philippine Is (also incorr. cited 'Chile') (MA, not seen; photogr. U).

Davallia flagellifera Hooker & Greville, Ic. Fil. (1831) t. 183, *ex char.* — Type: *Wallich s.n.*, Pulu Penang, not seen.

Davallia serrata Roxburgh *ex* Griffith, Calc. Jo. 4 (1844) 514 (*non* Willdenow, 1810), *ex char.* — Type: *Roxburgh s.n.*, Prince of Wales' Island (Pulu Penang), not seen.

Wibelia javae Fée, Gen. Fil. (1852) 331, *ex char.* — Type: *Kollmann* s.n., Java, not seen.

Davallia firmula Baker, Ann. Bot. 8 (1894) 123. — *Microlepia firmula* (Baker) C. Chr., Index Filicum (1906) 426. — *Tapeinidium firmulum* (Baker) C. Chr., Index Filicum Suppl. III (1934) 176. — Type: *W. Hancock 72*, Sumatra, Barisan Range, near Luva (?) (K).

Distribution: S. India (Kerala, one coll.), the Ryukyus, Taiwan, Thailand, the Malay Peninsula (Pahang, Kelantan, Selangor, Malacca, Negri Sembilan, Johore, Perak, P. Penang), Singapore, the Riau Is, Sumatra, the Lingga Is, Banka, W. Java, Borneo (Sabah, Sarawak, Kalimantan), Celebes, and the Philippine Is (Sulu Archip., Leyte, Basilan, Polillo, Mindanao, Bucas Grande, Palawan, Biliran, Mindoro, Panay, Luzon).

Remarks. This is the most common and widespread species in the genus, distinguished by pale to medium brown, abaxially at least above bi-angular petiole, abaxially sharply carinate rachis, simply pinnate lamina with the upper pinnae confluent into a pinnatifid leaf-apex, serrate or crenate linear pinnae, and laminal sori, i.e., not so close to the margin as to be in the lobes.

12a. Tapeinidium biserratum (Blume) van Alderwerelt van Rosenburgh, Malayan Ferns Suppl. (1917) 509. — Basionym: *Davallia biserrata* Blume, Enum. (1828) 232. — *Microlepia biserrata* (Blume) Presl, Epimel. Botan. (1849) 97. — Type: *Blume s.n.*, Java (L).

Remarks. Blume's type of *Davallia biserrata* agrees with a series of intermediates between *T. luzonicum* and *T. pinnatum*. There are between 25 and 30 of these intermediates, relatively very few in comparison with the large series of typical specimens of both species. They occur throughout their common range: Malaya, Sumatra, West Java, Borneo, and the Philippine Is. Some have the irregular dissection pattern often found in hybrids (Wagner, 1962; Meyer, 1965), e.g. *Scortechini s.n.* (BM) and *Kunstler 2144* (SING), both from Perak. In these and other intermediates I failed to find anything but what seemed to be normally developed spores. There is thus no direct evidence of hybrid origin, and if the two species are so closely related as to have fertile hybrid offspring one wonders what barrier keeps them largely apart. My impression is that *T. biserratum* is a phenotypic, aberrant form of *T. pinnatum*, but apart from a specimen with leaves of the shape of *T. pinnatum* with those of *T. biserratum* on one rhizome (*Micholitz s.n.*, Philippines, K), I have no proof for this. Field studies might help to find a solution for the problem. — See also the note at the end of the present paper.

13. Tapeinidium prionoides Kramer, *spec. nov.* — Type: *Bünnemeijer 1910*, Banka, G. Siang, Sungai Liat (L; isotype BO).

Tapeinidio pinnato simile, differt rhachide abaxialiter haud carinata, saepe angustato-teretiuscula, petiolo obscuro; pinnis serratis, dentibus adscendentibus, basali saepe majore, soris dentes insidentibus, indusio marginem fere attingente.

South China sea Islands. Anambas Is: *Henderson 20445* (BO, SING). — Riau Is: *Bünnemeijer 7886* (BO, L), *7887* (BO, L); *Fox s.n.* (SING); *Schlechter 13635* (B). — Lingga Is: *Bünnemeijer 6632* (BO, L, U). — Banka: *Bünnemeijer 2135* (BO, L), *1910* (type, L, BO).

Remarks. The specimens I saw had been determined as *T. pinnatum*, but the features described in the Latin diagnosis exclude them. The species has a remarkable distribution, occurring on some small islands to the East of Malaya and Sumatra.

14. Tapeinidium acuminatum Kramer, *spec. nov.* — Type: *Escritor 21173*, Philippine Is, Luzon, Isabela Prov., Palanan Bay (L; isotypes BO, BRI, GH, MICH).

Tapeinidio pinnato simile, differt lamina imparipinnata, scilicet pinna terminali conformi; rhachide abaxialiter biangulari, costis duabus lateralibus, pallidis, nec carinata, ut in T. pinnato.

Remarks. Only known from the type collection; but two collections from North Borneo may also belong to this species. They are, however, more robust and have paler axes; one, *Wood 2007*, Lahad Datu Distr. (K), is incompletely fertile, the other, *W. Meijer SAN 20989*, Ranau Distr. (K), is sterile. These two collections may even represent another, undescribed species. The type and the Wood collection have abortive spores, an indication of hybrid origin, but I am unable to suggest what the parent species may have been.

15. Tapeinidium carolinense Kramer, *spec. nov.* — Type: *Kanehira 1615*, Caroline Is, Ponape (US, 2 sheets).

Tapeinidio pinnato simile, differt rhachide abaxialiter bi-angulari nec carinata, sorisque margine plus approximatis, dentes serriformes insidentibus; squamae rhizomatis 5 mm longae; sporae perbreviter ellipsoidales.

CAROLINES. Ponape: *Finsch 29* (B); *Kanehira 795* (BISH), *1549* (K), *1615* (type, US); *Takamatsu 954* (BISH, BO, MICH, US); *Ledermann 13456* (B, K), *13678* (B, K), *13800a* (B, K); *Stone 5384* (U).

Remarks. In spite of its similarity to *T. pinnatum* this species is easily recognized by the above-mentioned characters. It also shares some features with *T. longipinnulum*. It seems to be fairly common in Ponape; surprisingly I have not seen any specimen from Kusaie.

16. Tapeinidium longipinnulum (Cesati) C. Christensen, Index Filicum Suppl. III (1934) 176. — Basionym: *Davallia longipinnula* Cesati, Rendic. R. Accad. Sci. Fis. e Mat. Napoli 16 (1877) 29; Beccari, Malesia III (1886) 35. — Type: *Beccari s.n.*, New Guinea, Ramoi (FI).

Davallia intramarginalis Cesati, l.c. (1877) 29. — Type: *Beccari s.n.*, New Guinea, 'Mt Arfak a Putat' (FI).

Tapeinidium marginale Copeland, Philipp. J. Sc. 6, Bot. (1911) 82. — Type: *King 283*, New Guinea, Papua (MICH; isotype P).

Remarks. This species is often confused with *T. pinnatum*, but it seems to be much closer to *T. melanesicum*. The conform terminal pinna distinguishes it at once from the first-named species; for the differences with *T. melanesicum* see the key.

T. longipinnulum is apparently not uncommon in New Guinea; I have seen many collections from W. New Guinea and smaller series from the Territory of New Guinea and Papua, furthermore from Woodlark and Rossel Islands off eastern Papua, and three collections from Ceram: *Buwalda 5907* (BO, K, L) and *Kornassi 67* (BO) and *712* (BO, L).

17. Tapeinidium melanesicum Kramer, *spec. nov.* — Type: *Stone 2512*, Solomon Is, Santa Ysabel, Horara Islet, Tatamba Lagoon (U; isotypes BISH, US).

Rhizoma breviter repens, squamis pullo-brunneis, pro parte majore uni-biseriatis, ad 1½ mm longis vestitum. Petiolus brunneus ad purpureo-castaneus, abaxialiter teres vel ad apicem breviter obtuseque biangularis, ecanaliculatus et concolor. Lamina oblonga, simpliciter pinnata, pinnis plerumque 10—15 pro latere et terminali impari conformi; rhachis straminea vel fusca, abaxialiter teres vel obtuse biangularis. Pinnae coriaceae, angustissime lanceolatae, acutae vel breviter acuminatae, 10—25 cm longae, 6—15 mm latae, leviter et regulariter crenatae vel bis crenatae, lobis valde adscendentibus. Costa

abaxialiter prominens, obtusa; venae prominulae, maxime obliquae, uni- vel rarius bifurcatae. Sori singuli vel bini, sub lobis eosque leviter ingredientes vel ad apicem pinnae lobos insedientes, uni- vel rarius binervii. Indusium pallidum vel brunneum, marsupiiforme, marginem non attingens.

Remarks. This species was formerly confused with *T. longipinnulum* or *T. pinnatum*; the differences are stated in the key.

I have seen 28 collections which will be cited in the account of the Lindsaeoid ferns of the smaller Pacific Islands. They are from the Solomon Is (Santa Ysabel, Santa Cruz, San Cristóbal), the New Hebrides, the Santa Cruz Islands (Vanikoro), and Fiji (Viti Levu, Vanua Levu, and Ovalau).

SPECIMENS OF UNCERTAIN IDENTITY

As often in monographic work a number of problematic specimens remain. Noteworthy among these is a series of plants from the Philippine Islands that resemble *T. gracile* in most characters, notably those of the axes, but have much less incised pinnae, not unlike those of *T. 'biserratum'*. They may represent hybrids, but the spores seem to be normally developed. It is not impossible that they belong to an undescribed, endemic Philippine species to which the type of *T. lineare* may also belong. The fact that they share characters of two species makes me refrain from describing them here as a species. Good examples are: *Elmer 18107* (BO, GH, MICH, US) from Luzon, and *Elmer 10912* (BO, L, MICH, US) and *7973* (BO, L) and *Sulit 8732* (MICH, SING), all from Mindanao.

EXCLUDED SPECIES

Tapeinidium bartlettii Copeland, Univ. Calif. Publ. Bot. 14 (1929) 376, pl. 60 = *Xyropteris stortii* (v. A. v. R.) Kramer.

Tapeinidium moluccanum (Blume) C. Chr., Index Filicum Suppl. III (1934) 176 = *Saccoloma sp.* (see under *T. amboynense*).

Tapeinidium moorei (Hooker) Hieronymus, Hedwigia 62 (1920) 13 = *Lindsaea moorei* (Hooker) Fournier. See Kramer 1967, p. 569.

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