

Specific Concept in *Humata pectinata* (J. E. Smith) Desv.

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Introduction

The genus *Humata* Cav., of Davalliaceae affinity, is a typically tropical East Asian group of ferns, extending with a few outlying species to Madagascar in the West, Japan in the North and far into the Pacific to the East, but having its centre of distribution in Malesia. Thus, several species of *Humata* occur in Malaya-proper and the reader may be referred to the account of the genus in Holttum's well-known book on the ferns of Malaya (1954).

Holttum remarks on the difficulty of specific delimitation in the genus generally, caused by plasticity and variability, also to be observed, by the way, in other genera of the same relationship, like *Davallia*, *Scyphularia*, etc. In fact, Holttum suggests in the elaborate observations he makes under the specific descriptions that several species described from adjacent regions are doubtfully distinct from the Malayan *Humatae* recognized by him. But in the case of *Humata pectinata* (J. E. Smith) Desv., additional comment is limited to a short note on its ecology.

Still, a long history is attached to the name *Humata pectinata*, also as to how it should be interpreted and it may therefore be interesting to follow the vicissitudes of the specific concept that have been attached to this name.

Historical Account

It was perhaps ironical that J. E. Smith (1793), when first describing *Davallia pectinata*, based his diagnosis on two specimens, collected in localities that could hardly have been farther apart. He had received these plants from Banks and after the diagnosis Smith added:

"Habitat in India Orientali, D. Hurloch 1786, eandem forte in Otaheite legit Nelson. H. Banks."

Alston (1933) commented on these types, still present in the Smith Herbarium now at the Linnean Society in London, in a publication that will be more fully discussed further on. It should be mentioned at this stage that Alston convincingly explained that Hurloch's plant came most probably from the Nicobar Islands, i.e. the most westerly limit of the distributional area of the *Humata pectinata* alliance, whereas the Nelson plant came from the most easterly (Otaheite = Tahiti).

The lamina of the two types are narrow-deltoid, the lowest segments being the largest. However, the basiscopic side of the lowest segments in the Hurloch-collection has only one prominent lobe, whereas the Nelson-collection has several, gradually passing distally into smaller crenations towards the segmental apex.

Gaudichaud (1827) described and illustrated *Nephrodium gaimardianum*, typified by a specimen now at Paris from Lawak (= Rawak) Island near Waigeu off West Irian, collected by his friend Gaimard. This must be considered an entirely independent description: no mention is made of J. E. Smith's publication

and the likeness of *N. gaimardianum* to Smith's plant. The fern Gaudichaud illustrates is slightly narrower, lanceolate, and has one lobe on the lowest pair of segments.

A year later Wallich published his list (1828) and gave the name *Davallia parallela* to the Singapore collection No. 251. Wallich's names are "nomina nuda", but *D. parallela* was validated by Hooker, as shown hereunder.

Wallich's plant is hardly different from Gaudichaud's type of *Nephrodium gaimardianum*, with one small lobe on the lowest pair of segments.

Blume (1828) misconstrued *Davallia pectinata* J. E. Smith and gave that name to a species of *Prosaptia*, at the same time describing *Davallia intermarginalis* from Java, the type (at Leiden) being closely comparable to Gaudichaud's and Wallich's types. Blume's name was recognized as a synonym at an early stage in subsequent literature.

A beautiful plate of *Davallia pectinata* J. E. Smith was issued by Hooker & Greville (1831, pl. 139). The leaf is narrow-deltoid with many basiscopic lobes on the lowest pair of segments ("pinnae"). It was drawn from a specimen, collected by Menzies in Tahiti and resembles closely J. E. Smith's Nelson type of the same origin.

It is significant that Hooker at that time had no doubts that Menzies' plant is conspecific with both the syntypes of J. E. Smith, as clearly indicated in the elaborate text, accompanying the plate and in which Smith's type-localities are specially mentioned:

"Hab. In insula Otaheite Menzies. In Malacca et in insulis Nicobar dictis. Smith."

Amongst the above basic descriptions Hooker (1846) made a critical choice in his monumental "Species Filicum". He retained two species, *Davallia pectinata* J. E. Smith and *Davallia parallela* "Wall". These taxa were, according to Hooker "undoubtedly nearly allied, but distinct", to be separated by the following characters:

- a. *D. parallela* has the shape of the frond less deltoid, also not so deeply divided and therefore never really pinnate, as in *D. pectinata*.
- b. Margins of segments (pinnae) are horizontally patent and entire, whereas in *D. pectinata* they are spreading and crenate.
- c. Lower margin of lowest pair of segments generally with one solitary lobe, rarely more; in *D. pectinata* pinnatifid with several lobes.
- d. Indusium opening to apex of segments; in *D. pectinata* opening obliquely to the (crenate) margin.

Apart from these two species, Hooker described *Davallia parallela* var. β , based on Cuming 61 from Luzon (BM, L), previously determined by J. Smith (1842) as *Humata pectinata* (J. E. Smith). It has no lobing of the lowest pair of segments, merely auricles.

As to the nomenclature adopted by Hooker: Wallich's name was deemed acceptable and thus "parallela" was given priority over Gaudichaud's epithet "gaimardiana" which is mentioned in synonymy. Blume's spurious conception of "*Davallia pectinata*" was not understood (Hooker had not seen Blume's types). "Java, Blume" is included in the enumeration of collectors and localities mentioned under *D. pectinata* and at the same time *Davallia intermarginalis* Blume is mentioned as a (doubtfully) separate species, the description from the Enumeratio being merely literally cited on the following page of the "Species Filicum".

That Hooker had his doubts on the origin of Smith's Hurloch type — and by inference on Blume's "*Davallia pectinata*" — is indicated by his remark under *D. pectinata*:

"Sir Jas. Smith gives the East Indies as a locality, on the authority of Mr. Hurloch, but perhaps erroneously, for I have never seen it from the Continent of India, only from the Pacific".

This interesting note also clearly shows that Hooker still considered the syntypes of J. E. Smith to be conspecific; moreover, that an initial concept was developing in Hooker's thoughts as to a possible geographical separation of his two species.

At this stage a short review of the generic assignment of the taxa under discussion would be appropriate. Hooker had a very broad and mostly unnatural conception of the genus *Davallia*, as originally conceived by J. E. Smith. However, in the case of *D. parallela* and *D. pectinata*, being definitely Davalliaceous ferns, an inclusion in *Davallia*-proper could be defended, especially as Hooker lists these taxa as belonging to the subgenus *Humata* (Cav.). Still, in Hooker & Baur's (1842) "*Genera Filicum*", *Humata* Cav. is recognized as a proper genus, distinct from *Davallia* J. E. Smith, having an indusium that is free at the sides. As this subject is not falling within the strict scope of this article, it may suffice to say that in modern literature the genus *Humata* is universally recognized. One must add, however, that it is clearly and closely allied to *Davallia* s.str. and although only differing from *Davallia* virtually in one character, is an easily definable group and perhaps is best regarded as a "Genus of convenience", to speak with Copeland.

Continuing the historical review on the subject: in the Synopsis of Hooker & Baker (1867) the two species were maintained, but the differentiating characters were for the greater part eliminated. In fact, the only clearly definable feature left was the lobing of the lowest segments: pinnatifid "with lobes sometimes $\frac{1}{2}$ inch long" in *Davallia pectinata*, whereas in *D. parallela* "the lowest pair (is) sometimes auricled". Gone are the differences in frond-form (described as ovate-lanceolate in both species); the orientation of the sori (oblique in both species); the pinnate or pinnatifid condition (being cut down nearly or quite to the rachis in both species). Hooker commented under *D. pectinata*: "Quite similar to the preceding [*D. parallela*] in size and texture".

D. intermarginalis Blume was no longer mentioned. "*D. pectinata* Blume non Smith" was included in the synonymy of *D. contigua* var. *D. blumei* Mett. [= *Prosaptia*] in the Appendix. *D. gaimardiana* (Gaud.) was mentioned in the synonymy of *D. parallela* as oldest name, but not (surprisingly) adopted.

The geographical details were given as: *D. parallela* in Malayan Peninsula and Polynesian Islands; *D. pectinata* in Tropical Polynesian Islands only.

Hooker's views had a deciding influence generally in the last century and in this particular case maybe up till now. To mention a few examples, Brackenridge (1854) recognized *Humata pectinata* "J. Smith" from Tahiti, *H. parallela* "(Wall)" from Samoa, enthusiastically referring to Hooker's (later discarded) differentiation in the "Species Filicum" regarding the orientation of the sori. Presl. (1849) conceived a new genus *Pachypleuria*, differing from *Humata* Cav. mainly in non-dimorphic fronds, and made the new combinations *Pachypleura parallela* (Hooker) Presl and *P. pectinata* (J. E. Smith) Presl, the former being even assigned by Fée (1852) as sole species to yet another genus, *Pteroneuron*, differing by (pseudo) dorsal sori, but neither gave any new ideas on the specific delimitation of the species in question.

The situation seemed to have been consolidated by Christensen (1906) in his Index, where he recognized *Humata gaimardiana* (Gaud.) J. Smith (Syn. *Davallia*

parallela [Wall.] Hooker) and *Humata pectinata* (J. E. Smith) Desv., the former occurring from Burma through Malesia to Polynesia, the latter in Polynesia only.

There is in this period, however, one notable exception. It was Luerssen (1871) who, in his description of the ferns in the Fiji and Samoan Islands, strongly commented on the weak differentiation given by Hooker between *Davallia parallela* and *D. pectinata*:

“Alle angegebenen, sogar von Hooker und Baker noch festgehaltenen Merkmale, welche die *Davallia parallela* Wall von *Davallia pectinata* trennen sollen, taugen nicht”.

which is to say that, according to Luerssen, even the few means of differentiation, maintained in Hooker & Baker's Synopsis, most emphatically do not hold good. His elaborate comments clearly point to the many transitions, even on the same plant, that exist in the characters, supposed to serve as differential, all being variable within the traditional specific delimitation of both taxa.

Luerssen gave a full and complete list of the synonymy, in which *Davallia pectinata* J. E. Smith is included, but nevertheless adopted the later name *Davallia gaimardianum* (Gaud) “Presl”, for which reason is obscure. Presl's combination is even illegitimate according to present rulings, having been published in the Tentamen (1836) with a query-mark and as a synonym in the *Epimelia* (1849).

Apart from Diels (1899) nobody ever took notice of Luerssen's view and it remained a lone cry in the — taxonomic — wilderness, one might say.

Christensen's influence on and significance for modern taxonomic fern-studies has been reemphasized quite recently by Holttum (1975). It is therefore no wonder that the former's specific concept on the subject taxa in the Index (1906) and the modified version in the Third Supplement (1933) — further discussed below — can be retraced in all modern regional floras in the Far East, to mention only: Van Alderwerelt's (1908) *Malayan Ferns*, Backer & Posthumus' (1939) *Varenflora van Java*, Tardieu & Christensen's (1939) *Flore Générale de l'Indochine Vol 7*, Holttum's (1954) *Ferns of Malaya* and Copeland's (1958) *Fern Flora of the Philippines*; and as far as the Pacific is concerned: Copeland's (1929 and 1932) treatises on the ferns of Fiji- and Society Islands, Christensen's (1943) revision of the *Pteridophyta* of Samoa and Brownlie's (1969) *Pteridophyta* of New Caledonia.

In the Third Supplement Christensen also recognized and confirmed several new species that had been described in the meantime as belonging to the same alliance.

Van Alderwerelt van Rosenburgh (1920) proposed *Humata lanuginosa* from Sumatra, syntypes Lörzing 4567, 4764 and Bünнемeyer 3881 (BO, L). In his description there is no character that is in any way new to the taxa discussed, apart from the profuse scabiness and the presence of hairs on the lower surface of the lamina.

There is another point in Van Alderwerelt's publication that deserves special comment. His types are all from Central Sumatra near Toba Lake, from 1100-1800 m, from where several other collections have been made, also from Mt. Dempo and Sibayak at higher altitudes. This is unusual, as elsewhere, also in Sumatra, collections are from the coastal plain or foothills and also often from the sea-shore.

The duplicate of Bünнемeyer's type-specimen, apparently sent to Leiden somewhat later, has the epithet “*lanuginosa*” deleted and “*gaimardiana*” written instead by Van Alderwerelt himself. This tends to show that the author did not believe long in his new creation; as several lamina of the syntypes show multiple lobing and going by the criteria that Van Alderwerelt had used in his *Malayan Ferns*, a rectification in *Humata pectinata* would have been more justified.

Copeland was more prolific. In his work on the Ferns of the Society Islands (1932) he remarks (p. 63):

“Apparently in this group of [*Humata pectinata*] each island has developed a peculiar strain which might be construed as a distinct species”.

but (fortunately) describes and illustrates only two, viz. *Humata huahinensis*, type Grant 5295 from Huahine and *H. melanophlebia*, type Grant 5144 from Tahaa (not seen). This self-imposed restriction is explained on p. 12 where, as on the other islands like Moorea and Bora Bora, “the characteristic representatives are less fixed in their peculiarities and are accordingly left without distinctive names”.

Humata huahinensis is described by Copeland as being very near to *H. pectinata*, but having a black stipe and deviating towards *H. gaimardiana* by being pinnatifid and position of sori, also the closely placed segments.

As to *Humata melanophlebia*, Copeland comments that it is like *H. huahinensis*, but pinnate with more remote pinnae (or segments more distally) which are clearly lobed, mainly basiscopically, the segments becoming inciso-serrate. Copeland (on page 63) mentions Grant's collection 5144 [= type of *H. melanophlebia*] again under *H. huahinensis*. Be that as it may, the proposed elevation to “species” of these Pacific representatives does not thereby become more convincing.

In 1940 Copeland described and illustrated another species, *Humata tenuivenia*, type Brass 14082 from New Guinea:

“*Humata pectinatae* affinis, venis tenuibus inconspicuis, soris perlatiis curvis, indusiis brevibus distincta”.

The (iso)types (L and BO) and the photograph show these specimens to be robust plants from a shady wet habitat (“low epiphyte in coastal swamp-forest”). Copeland specially comments on the curved sori which can face the margin and apex or, in extreme cases, is curved so far that it faces at an angle to the costa too.

A few years earlier Copeland had been the instigator of yet another name. He had requested Alston to have a new look at J. E. Smith's types of *Davallia pectinata*. As a result, Alston (1933, l.c.) lectotypified *Davallia pectinata* J. E. Smith on the Hurloch specimen, dispersing Hooker's previous doubts as to the origin by showing that it came most probably from the Nicobar Islands and in any case from Western regions, not from the Pacific. Arguing further, Alston came to the conclusion that the name *Humata gaimardiana* (Gaud.) J. Smith (of Christensen's Index with a predominantly Western distribution) must in fact be replaced by *Humata pectinata* (J. E. Smith) Desv. and that the other syntype of J. E. Smith (Hooker's and Christensen's *Humata pectinata* with a Pacific distribution) had no name. Alston thus reversed the ideas hitherto current on geographical distribution, but maintained the traditional separation of two specific entities.

The new name Alston introduced was *Humata banksii* and the typification is based on the Tahiti collection No. 1769 (BM) by Banks, “Nelson's specimens being poor, both in the herbaria Smith and Banks”. Alston's description emphasizes “profundae pinnatis” and “inferioribus margine inferiore pinnatifidis”, otherwise does not give any further characters of differentiation from his *H. pectinata*. Actually Alston followed the description as included by Hooker & Baker in the Synopsis for (their) *Davallia pectinata*. Completely absent are comments on notably geographical distribution, or a comparison with e.g. Copeland's previously described species (1932) of which *H. huahinensis* is practically identical with Banks' plant. It is, as if Alston was wary to incriminate himself further in sorting out the antecedents of his new proposal.

Nevertheless, Alston's views, whether stated or only implied, were immediately followed by Christensen (1933) in the third Supplement of the Index and consequently in all the more local Flora's mentioned previously: Western plants now indiscriminately being called *Humata pectinata* (J. E. Smith) Desv., Eastern (Polynesian) plants referred to *Humata banksii* Alston.

But, Copeland did not agree. His comment on the Humatae in the "Oleandrid Ferns of New Guinea" (1940) may be appropriately quoted in full at the end of this historical survey:

"This is the largest and most difficult genus of the group. Typically epiphytes, the individuals are subject to wide variations in exposure, and some of them are very responsive to these differences. Independent of the environment, some species seem to be notably variable . . . Smith combined a Malayan and a Tahitian plant in describing *Davallia* (*Humata*) *pectinata*. *H. parallela* (Wall) Brack. and *H. gaimardiana* (Gaud.) J. Sm. were subsequently described in the same group. With many specimens from the Society Islands, it seemed to me that each island had its own, more or less distinct form, none of these like the comparatively uniform Malayan plant. It occurred to me that the Malayan plant might be the real *H. pectinata*, so I invited comparison of types by Mr. Alston. The result was his finding the Tahiti specimens [*sic*!] to be of two species, *H. pectinata* and *H. banksii*. It is my conclusion, not his that the Malayan plant must be *H. parallela*, for I have no Malayan specimen duplicated by any from Tahiti.

Some characters which usually serve as specifically diagnostic, serve so badly in *Humata*. Size varies greatly as a matter of plasticity (response to environment). So with size does the dissection of the frond; and so probably do texture and laxness. Paleae are likely to be deciduous. And dimorphism is subject to some reversion.

In the light of the foregoing discussion it will be understood that considerable work on this genus leaves me ill-satisfied. The presentation here given is the best I can make with the present material".

One could have full sympathy with this lament, were it not that in the ensuing key, size, dissection of frond, degree of scaliness and dimorphism figure prominently as differentiating characters. Of the 21 species, Copeland distinguishes in New Guinea alone, not less than six are described as new, of which one, *Humata tenuivenia* falls within the affinity of the taxa under review, as discussed above.

Copeland's confused rejection of Alston's interpretation of J. E. Smith's types was, for that matter, corrected later (1958) in the Fern Flora of the Philippines, where he uses the name *Humata pectinata* (J. E. Smith) Desv. for Philippine specimens, mentioning *Davallia parallela* "Wall" as a synonym.

Observations

When looking back on the features that have been used to distinguish between the taxa, as discussed heretofore, a hard core of only two characteristics remain, viz. the lobing of lowest pair of segments and the pinnatifid against the pinnate condition.

As to the last feature, the wing alongside the rachis is always distally broader than below and is, even in the most deeply incised leaves, never entirely absent. One cannot talk therefore of a real pinnate condition, it is always pseudo-pinnate and this variable point of distinction is in reality non-existent.

As to the (basiscopic) lobing of the lowest pair(s) of segments, transitions can be found on the same rhizome sometimes, from non- one-, two- to multi-lobed. A clinal pattern can be observed, whereby the multilobed basal segments become less frequent from East to West (nearly absent in Malaya and the Philippines), whereas the non-lobed or auricled/one lobed segments decrease from West to East, to being virtually absent in the Eastern Pacific.

The same pattern of gradual transitions can be found in the length of the lowest segments, being either longer, equal to, or shorter than the next pair, this making the overall leaf-shape either narrow deltoid, lanceolate/linear or narrow-ovoid. The sinuses vary in width from nearly equal to the width of the segments to mere slits, variable even on the same leaf or plant.

The above observations make differences in leaf-morphology unfit for the proper distinction of species and the recognition of *Humata banksii* Alston (and *Humata huahinensis* Copel.) seems to be based on weak ground.

Humata melanophlebia Copel. is an extreme case, where the lobing is also conspicuous on the next lower pair(s) of segments and more or less extended to the acroscopic side of the segments as well.

Differences in scaliness have hardly been used in proposing separate taxa, the variability in caducity and density having been generally understood. Van Alderwerelt's "hairs", described in *Humata lanuginosa*, are nothing but the highly dissected, hyaline squamules generally found — but not so obvious — on the underside of the lamina.

Actually, often the scales are not, or not well described, a glabrous or subglabrous condition prevailing in mature leaves. But young leaves (and stipes) are always scaly and the reader may be referred to Appendix I, where a full description of the scales can be found.

The venation is always \pm flattened, conspicuous below, \pm parallel with none or 1-2 forkings, 3 forkings only occurring in very large leaves, as in *Humata tenuivenia* Copel. The ancillary veinlet round the (terminal) sorus, basis for Fée's genus *Pteroneuron* can also be absent, or the veinlet is forked far below the sorus, thus becoming just a part of the normally forked venation. Transitions can be found even on the same segments.

The position and orientation of the sorus is also inconstant. It is always intramarginal and the indusium can be semi-circular to crescent-shaped, in extreme cases becoming reniform (*Humata tenuivenia* Copel.). Distally the sorus mostly faces the apex of the segment, lower down (obliquely) the margin.

Conclusion

The above review was made in the framework of a general study of the genus *Humata* Cav. — and other davallioid genera — the results of which will eventually be published in the Flora Malesiana. As such, Van Steenis' forceful, but lucid essay on "Specific Delimitation" is here considered an excellent guide to extricate oneself from further confusion. In itself the present study is an illustration of practically all the pitfalls, so convincingly summed up by Van Steenis, that can beset taxonomy and although his work is mostly based on vast experience in phanerogamic taxonomy, it is certainly also fully applicable to ferns.

Therefore, the author cannot but come to one conclusion, viz. that all the taxa under discussion can best be regarded as one polymorphic species with a wide distribution, for which the name *Humata pectinata* (J. E. Smith) Desv. should be

used. Luerssen's views of nearly a hundred years ago are thus herewith fully confirmed.

Delimitation from allied species like *Humata repens* (Linn. f.) Diels, *H. vestita* (Bl.) Moore and *H. heterophylla* (J. E. Smith) Desv. gives no difficulty and shall not be further elaborated on in this context.

Recognition of infra-specific taxa is omitted; the variable, transitional (and clinal) nature of the characteristics, mentioned hitherto make them unsuitable for the delimitation of recognisable subspecies or varieties.

The geographic distribution of *Humata pectinata* as here construed is a clear-cut case of dependency on certain climatological circumstances. The area covers practically exactly and totally the zone of small seasonal variations in temperature (up to $35^{\circ}\text{ F} = 20^{\circ}\text{ C}$) in the Eastern Tropics and Pacific, with the exception of that part of the zone which is liable to an appreciable monsoon. This explains the striking absence of the species from (East) Java, South-Sulawesi, Lesser Sunda Isles and Southern Moluccas in an otherwise continuous distribution throughout Malesia and Polynesia up to Tahiti. New Caledonia in the South and Taiwan in the North, in both of which islands the species is rare, are only just outside the zone as above referred to. Climatological maps covering the region can be found in Goode (1947).

A special note should be devoted to the occurrence of the species in Java. Although Blume's type of *Davallia intermarginalis* came ostensibly from Western Java, no further collections — apart from an old Junghuhn specimen at BO — have been made in that area for nearly 150 years. Nevertheless, potentially West Java (as against the eastern part of that island) could harbour our species, having only a weak monsoon. Could it have become extinct there by the vast destruction of lowland forest of that island?

The high-altitude collections in Central Sumatra have already been commented upon. This could be a special ecotype, but from New Guinea specimens from medium elevations (1100 m) are also known.

It could be argued that research of a karyological nature, especially cytogenetical, could produce better substantiated and more refined results than is possible by limiting the study to only herbarium material. Whilst this limitation is recognised it is regretted that such an approach is precluded by the unavailability of live material. Whether it would really help in tackling the problem remains to be demonstrated. The mere thought of the difficulties involved in obtaining live plants from the whole distributional area and the time-consuming organization in rigging up a hybridization programme suggests that the above reserve if not illusory would, in practice be hard to tackle in a satisfactory way.

Finally this relatively uncomplicated, but nevertheless perforce lengthy account on how the species *Humata pectinata* has to be construed can be equally repeated for other taxa of the genus. As the publication of such detailed discussions would lead too far and be a tedious repetition, this study may serve as an example as to how the specific concept in the forthcoming treaties of the whole group will be maintained. That a considerable reduction in names will result — as already indicated by Holttum (1954) — is certain.

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APPENDIX I

NOMENCLATURE

Humata pectinata (J. E. Smith) Desv. (1827). Prodr.: 323. — *Davallia pectinata* J. E. Smith (1793) Mém. Ac. Turin 5: 415; *Trichomanes* Poir. in Lam (1808) Encycl. 8: 78; *Pachypleuria* Presl. (1849) Epim.: 98 — Type: Hurlach/Soc. Unit. Frat. s.n. from Ind. Or. (probably Nicobar Isl.) as lectotypified by Alston (1933) Phil. Journ. Sc. 50: 175, t. 1 fig. 1.

Nephrodium gaimardianum Gaud. (1827) Freyc. Voy. Bat.: 335, t. 12 fig. 1; *Nephrolepis* Presl. (1836) Tent.: 79; *Humata* J. Smith (1842) London Journ. Bot. 1: 425; *Davallia* [Presl. (1836) Tent.: 128 (comb. ill.)] Kuhn (1869) Zool. Bot. Ges. Wien: 580 — Type: Gaudichaud (Gaimard) s.n. from P. Lawak = Rawak/Waigeu/W. Irian.

Davallia parallela [Wallich (1828) List No. 251 (nomen nudum)] Hooker (1846) Sp. Fil.: 153, t. 42a; *Pachypleuria* Presl. (1849) Epim.: 98; *Pteroneuron* Fée (1852) Gen. Fil.: 320, t. 25b; *Humata* Brack. in Wilkes (1854) U.S. Expl. Exp. 16 Bot.: 229; *Oleandra* Keys. (1873) Pol. Cyath. Herb. Bung.: 41 — Type: Wallich 251 Singapore.

Davallia parallela var. β Hook. (1846) Sp. Fil.: 153 — Type: Cuming 61 Luzon.

Davallia intermarginalis Blume (1828) Enum.: 230; *Pachypleuria* Presl. (1849) Epim.: 98; *Humata* Moore (1861) Index: 296 — Type: Blume s.n. Java.

Humata lanuginosa v.a.v.R. (1920) Bull. Jard. Bot. Bzg. 3/2: 155 — Syntypes; Lörzing 4567, 4764, B. Baroe/Sumatra; Bünnemeyer 3881 G. Malintang/Sumatra.

Humata huahinensis Copel. (1932) Bish. Mus. Bull. 93: 11, t. 12b — Type: Grant 5295 Huahine/Soc. Isl.

Humata melanophlebia Copel. (1932) Bish. Mus. Bull. 93: 11, t. 12a — Type: Grant 5144 Tahaa/Soc. Isl.

Humata banksii Alston (1933) Phil. Journ. Sc. 50: 176 — Type: Banks 1769 Tahiti/Soc. Isl.

Humata tenuivenia Copel. (1940) Phil. Journ. Sc. 73: 350, t. 3 — Type: Brass 14082 Idenburg R./W. Irian.

DESCRIPTION

Rhizome upto several metres long-creeping, slender (1½–2½ mm), blackish with white-chalky patches, dictyostelic and dorsiventral, vascular tissue much dissected with two main bundles; bearing articulated fronds, on short phyllopodia, 2–5 cm or more apart; thickly set with appressed, imbricated scales, 4 to 5 mm long, \pm 1 mm wide at the oblong peltate base, from there tapering to the acute apex, castaneous, the thin margin often hyaline/whitish, when young bearing marginal crinkly hairs which are mostly soon deciduous, the edge becoming entire at an early stage.

Stipe thin (1 mm ϕ) but firm, as long as, or somewhat shorter than the lamina, green to reddish brown when living, brown to blackish when dried, sulcate; vascular tissue with mostly three bundles, becoming fused upwards; loosely set with caducous scales and often entirely glabrous with age; scales like those of rhizome but not so appressed and more rounded, becoming smaller, paler, the edge more dissected.

Lamina firm, coriaceous, (5) 7–18 cm long, 4–6 (8) cm wide, narrowly deltoid, lanceolate/linear to narrowly ovate, dark green above, paler below, pinnatifid/pectinate with truncate/cordate base and short coadunate apex; segments many (12–30) which are sessile and confluent by a narrow wing along the rachis; wing occasionally inconspicuous between the lowest pairs of segments (the lamina then becoming pseudo-pinnate) but always widening upwards; sinuses deep and narrow, to about as wide as the pinnae but usually much narrower, becoming distally shallower towards the crenate to entire apex; rachis prominent, green to brown/blackish, sulcate except at the apex; scales loosely covering the young unfolding leaves, equal to those on the stipe, however, especially on the lamina becoming even more hyaline and dissolute, variously deciduous but mostly leaving a few traces on lower surface of rachis and costa, as well as on the margins of the often (sub) glabrous lamina.

Segments to 6 (8) mm wide, straight and horizontally patent or a little curved upwards, the apex bluntly acute to rounded; edge in barren leaves rarely quite entire, commonly shallowly crenate/sinuate at apex only, less often the incisions becoming more pronounced and continuing to bottom of sinus; in the very slightly and inconspicuously contracted fertile leaves incisions more prominent; the lowest pair of segments variable, either somewhat shorter or equal (ovate-lanceolate form), or if more developed, becoming longer than the next pair of segments (narrow-deltoid form), the basiscopic edge being either entire, auricled, often prominently, or two/multi lobed, the lobes grading to the crenate apex, the lowest segments then becoming unilaterally pinnatifid; venation, apart from the prominent costa,

distinct on lower surface only, the veins coarse, brown and parallel, not or 1, 2, (3) times forked, both upper and lower basal primary veins springing from very base of costa or in larger fronds the lower directly from the rachis.

Sori terminal on the swollen acroscopic (when forked) vein-ending, forming an intra-marginal, often crowded row; away from the apex often with an accessory posterior veinlet running round the sorus to just within the leaf-edge; indusium brown, ± 1 mm wide, finely striated, firm and permanent, semi-circular or crescent-shaped to reniform, the lower straight to convex side attached in the middle for \pm half its length, otherwise the indusium free, opening to the apex or (especially lower down) obliquely to the leaf-edge; sporangia with 12-14 indurated cells; spores monolite, verrucate-rugulate, $20 \times 13 \mu$ with crenulated margin.

GEOGRAPHICAL DISTRIBUTION

From Southern Burma (Mergui), Lower Thailand, South Viet Nam, and Taiwan, throughout Malesia with the exception of those regions with an appreciable monsoon (Middle and Eastern Java, Lesser Sunda Islands, South-Sulawesi and South Moluccas), extending further into Tropical Polynesia to Society Islands in the East and New Caledonia in the South.

ECOLOGY

Epiphyte, high and low, on trees; or terrestrial on boles and rocks, in often exposed habitats near seashore and in light forest, steep banks, even padangs on bare sand, but also known from swamp-forest in shade. Can apparently stand a lot of exposure, the leaves curling up in dry periods [Holtum (1954)]. From sea-level to 800 m, going up to 2000 m in Sumatra and to medium altitudes in New Guinea.

APPENDIX II

ILLUSTRATIONS

Various facies of *Humata pectinata* (J. E. Smith) Desv.

1. Sinclair, S. F. 40582 (1955) North side of Cape Rochado-Malacca-Malaya.
"Rocky wooded seashore. Creeping rhizome on sea cliffs. Fruiting. Fronds curled up with the drought. Flattened by immersing in water".
Two leaves from same rhizome.
2. Lörzing 15533 (1929), East Mt. Sibayak-Sumatra-Indonesia, 1300-1440 m.
"Primary forest, epiphytic, and, in lighter places, on prostrate trunks and rocks. Not rare".
Two fronds from same rhizome.
3. Lütjeharms 4674 (1936), Enggano off West Sumatra-Indonesia.
"Epiphytisch op klapperstammen. Strand bij Kiojoh".
Small leaves on rhizome.
4. Van Niel 3383 (1964), Tutong-Brunei-North Borneo.
"Under clumps of trees in an open vegetation (sand)".
Two leaves on same (branched) rhizome.
5. Cuming 61 (1836), Luzon-Philippines.
No further details — Type *Davallia parallela* var. β Hooker.
One leaf from isotype at L.
6. Brass 14082 (1939), Bernhard Camp-Idenburg River-W. Irian-Indonesia.
"Low epiphyte in flooded rain forest of river-plain at 50 m." — Type *Humata tenuivenia* Copel.
One leaf from isotype at L.
7. Van Balgooy 1983 (1971), W. slope Pahia-Bora²-Society Islands, 300 m.
"Epiphyte, rootstock creeping".
One large, one small leaf from same collection.





