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Generic Classification of Davalliaceae

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A generic classification of Davalliaceae is proposed to recognize five genera and two sections for monophyletic groups detected by molecular phylogenetic studies. The delimitation of the taxa, except for *Humata*, differs remarkably from the ones adopted in previous classifications. *Davallia* is divided into sections *Davallia* and *Trogostolon* (stat. nov.), of which the former includes *Scyphularia* and the latter includes *Davallia trichomanoides* and close relatives. *Humata* contains *Davallia corniculata.* The new genus *Araiostegiella* comprises *A. perdurans* and two related species, which have long been assigned to *Araiostegia*. The revived genus *Wibelia* is composed of *W. denticulata* (type) and related species. *Davallodes* is a polymorphic genus that accommodates *Paradavallodes, Araiostegia hymenophylloides* and its close relatives, as well as *Davallodes* s.s. A key to the genera and sections and a set of their diagnostic characters are given and new combinations for the species are presented. The exclusion of *Gymnogrammitis* and *Leucostegia* from the family is also discussed.

Key words: *Araiostegia, Araiostegiella, Davallia,* Davalliaceae, *Davallodes, Humata, Pachypleuria,* taxonomy, *Trogostolon, Wibelia*

Recently published molecular phylogenetic relationships of Davalliaceae are novel in that: (1) none of multispecific genera recognized so far is monophyletic (Tsutsumi & Kato 2005, 2006), and (2) *Gymnogrammitis* (Schneider *et al.* 2002) and *Leucostegia* should be excluded from Davalliaceae (Tsutsumi & Kato 2005, 2006) (Table 1). Tsutsumi & Kato's (2005, 2006) and Tsutsumi *et al.*'s (2008) phylogenetic trees suggest that Davalliaceae comprises five clades, one (*Davallia*) of which has two subclades (Fig. 1). *Davallodes* is basal, and *Wibelia* is second-basal and sister to a clade comprising *Araiostegiella, Davallia*, and *Humata* (for the revised definition of the genera and sections of *Davallia*, see below). Tsutsumi & Kato (2005, 2006) examined nearly 5,000 bp of chloroplast DNA for 36 of ca. 130 species of Davalliaceae, which represent most morphologically recognized groups of species (Kato 1985, Kramer 1990). Tsutsumi *et al.* (2008) analyzed four more species, which included types of genera or close relatives of them. Trees yielded by the analyses had a corresponding topology for major clades. Therefore, addition of more species into the analysis is not likely to result in substantial alteration of the phylogenetic relationships of Davalliaceae.

The relationships are not congruent with any of the conventional generic classifications, which had been hypothesized based on comparative morphology (Ching 1940, 1959, 1978, Copeland 1947, 1958, Holttum 1949, 1955, Kato 1985, Kramer 1990, Nooteboom 1992, 1994, 1998, Pichi Sermolli 1977, Shieh *et al.* 1994, Tagawa & Iwatsuki 1985, Wu 1999) (Table 1). Here we propose a revised

TABLE 1. Comparison of previous major classifications and present classification of Davalliaceae.

Copeland (1927, 1947)	Holttum (1949, 1955)	Ching (1940, 1978)	Pichi Sermolli (1977)	Kato (1985)	Kramer (1990)	Nooteboom (1992, 1994)	Kato & Tsutsumi (present study)
Araiostegia	*Araiostegia*	*Araiostegia*	*Araiostegia*	*Araiostegia*	*Araiostegia*	*Davallia*	*Davallodes* *Araiostegiella*
Davallia	*Davallia*	*Davallia*	*Davallia*	*Davallia*[1]	*Davallia*	*Davallia*	*Davallia*[2] *Wibelia*
Davallodes	*Davallodes*	*Davallodes*	*Davallodes*	*Davallodes*	*Davallodes*	*Davallodes*	*Davallodes*
Humata	*Humata*	*Humata*	*Humata*	*Pachypleuria*	*Davallia*	*Davallia*	*Humata*
Leucostegia	*Leucostegia*	*Leucostegia*	*Leucostegia*	*Leucostegia*	*Leucostegia*	*Leucostegia*	(excluded)[3]
Parasorus	*Davallia*	*Parasorus*	*Parasorus*	*Parasorus*	*Davallia*	*Davallia*	*Humata*
Scyphularia	*Davallia*	*Scyphularia*	*Scyphularia*	*Scyphularia*	*Davallia*	*Davallia*[4]	*Davallia*
Trogostolon	*Davallia*	*Trogostolon*	*Trogostolon*	*Trogostolon*	*Davallia*	*Davallia*	*Davallia*
—	—	*Paradavallodes*	*Paradavallodes*	*Davallodes*	*Davallodes*	*Davallia*	*Davallodes*
(*Araiostegia*)	—	*Gymnogrammitis*[5]	*Gymnogrammitis*	*Gymnogrammitis*	*Gymnogrammitis*	*Gymnogrammitis*	(excluded)[5]

[1] Divided into sect. *Davallia*, sect. *Cordisquama* and sect. *Wibelia*, of which the middle and part of the last are transferred to *Wibelia* by Kato & Tsutsumi (present study).
[2] Divided into sect. *Davallia* and sect. *Trogostolon.*
[3] Transferred to Hypodematiaceae.
[4] Recognized as *Davallia* sect. *Scyphularia.*
[5] Separated as the monotypic Gymnogrammitidaceae (Ching 1966a, 1978, Wu 1999) but more convincingly transferred to Polypodiaceae (Schneider *et al.* 2002).

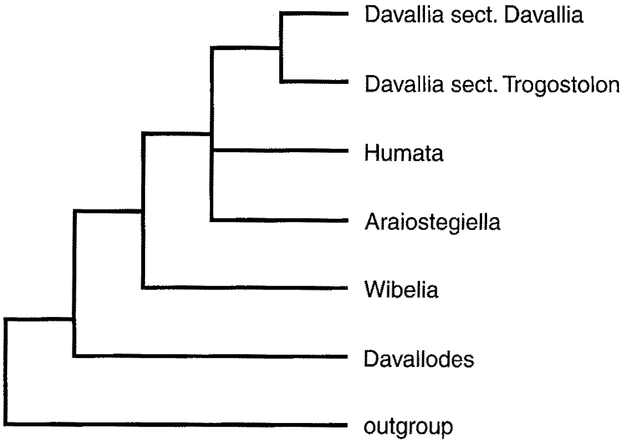

FIG. 1. Phylogenetic tree of Davalliaceae simplified from Tsutsumi & Kato (2005) and Tsutsumi *et al.* (2008).

classification of the family that recognizes those six monophyletic groups as genera and sections (Table 1, Fig. 1). The genus *Davallia* is recognized to comprise two sections, which form the monophyletic *Davallia* and differ from each other only in the scale margin and leaf dissection. Although there are few morphological characters to define the genera or sections clearly, scales, hairs, leaf texture, sori and indusia, and veins, when taken together, are useful (Key and Table 2). Therefore, a matrix of diagnostic characters is more useful for comparison than separate descriptions of the genera and sections (Table 2). New combinations (marked by asterisks below) accompanying the present generic classification are given in Appendix.

Classification of Genera and Sections

Key to the Genera and Sections

1. Margin of scales hairy; upper surface of scales verrucose or smooth.
  2. Rhizome less than 3 mm thick; surface of scales verrucose or sometimes smooth; leaves 10-40 cm long, coriaceous; indusia 0.3-1 mm long, attached at base or sometimes at base and part of sides ………… 2. *Humata* (part)
  2. Rhizome usually more than 3 mm thick; surface of scales smooth; leaves 10-120 cm long, chartaceous or subcoriaceous; indusia 1-2 mm long, attached at base and sides ………… 1A. *Davallia* sect. *Davallia*
1. Margins of scales toothed; upper surface of scales smooth.
  3. Scales peltate, indusia attached at base and sides.
    4. Rhizomes more than 3 mm thick; leaves 3- to 4-pinnate, more than 20 cm long, firmly chartaceous or subcoriaceous; indusia usually longer than wide ………… 1B. *Davallia* sect. *Trogostolon*
    4. Rhizomes to 3 mm thick; leaves simple to 2(-3)-pinnate, 10-20 cm long, coriaceous; indusia usually wider than long ………… 2. *Humata* (part)
  3. Scales pseudopeltate, imbricate at base, or peltate (if peltate, pseudoveins present between veins or multicellular hairs present on leaves); indusia variously attached.
    5. Scales pseudopeltate, densely imbricate; leaves glabrous, pinnae sessile, indusia attached at base ………… 3. *Araiostegiella*
    5. Scales peltate or pseudopeltate, imbricate or separate; leaves glabrous or hairy, pinnae of large leaves stalked; indusia attached at base or by base and sides.
      6. Leaves widest at base, glabrous, firmly chartaceous or coriaceous, indusia attached at base and sides ………… 4. *Wibelia*
      6. Leaves equally wide at lower part of frond or gradually narrowed to base, hairy or glabrous, herbaceous or chartaceous, indusia attached at base or at base and sides ………… 5. *Davallodes*

1. **Davallia** Sm.

Davallia Sm., Mem. Acad. Turin 5: 414, 1793; Bedd., Handb. Ferns Brit. Ind. 58, 1883; Copel., Philip. J. Sci. 34: 251, 1927; Gen. Fil. 87, 1947; Fern Fl. Philip. 1: 170, 1958; Tard.-Blot & C. Chr., Lecomte, Fl. Gén. Indo-chine 7(2): 103, 1939; Holttum, Rev. Fl. Malaya 2: 354, 1955; Ching, Fl. Reipubl. Popularis Sin. 2: 297, 1959; DeVol & Yang, Fl. Taiwan 1: 272, 1975; Brownlie, Pterid. Fl. Fiji 162, 1977; Pichi Sermolli, Webbia 31: 343, 1977; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 565, 1985; Tagawa & Iwatsuki, Fl. Thailand 3(2): 157, 1985; Kramer in Kubitzki (ed.) Fam. Gen. Vasc. Pl. 1: 79, 1990, p.p.; Shieh, DeVol & Yang, Fl. Taiwan, 2 ed., 1: 188, 1994; Nooteboom, Blumea 39: 155, 1994, p.p.; Fl. Males. Ser. II, 3: 236, 1998, p.p.; Wu, Fl. Reipubl. Popularis Sin. 6(1): 179, 1999, p.p. —Type: *Davallia canariensis* (L.) Smith.

1A. sect. **Davallia**

Stenolobus C. Presl, Tent. Pterid. 129, pl. 4, f. 30, 1836. —Type: *Stenolobus solida* (Forst.) C. Presl.

Scyphularia Fée, Gen. Fil. 324, pl. 26B, f. 1, 1852; Copel., Philip. J. Sci. 34: 254, 1927; Philip. J. Sci. 73: 356, 1940; Gen. Fil. 88, 1947; Brownlie, Pterid. Fl. Fiji 166, 1977; Pichi Sermolli, Webbia 31: 343, 1977; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 567, 1985. —*Davallia* sect. *Scyphularia* (Fée) Noot., Blumea 39: 208, 1994; Fl. Males. Ser. II, 3: 266, 1998, p.p. —Type: *Scyphularia pentaphylla* (Blume) Fée.

Species assigned to sect. *Davallia*: *Davallia brevipes* Copel., *D. canariensis* (L.) Smith, *D. fejeensis* Hook., D. (= *Scyphularia*) *pentaphylla* Blume, *D. plumosa* Bak., *D. pyxidata* Cav., *D.* (= *Scyphularia*) *simplicifolia* (Copel.) C. Chr., *D. solida* (Forst.) Sw., *D.* (= *Scyphularia*) *triphylla* Hook., *D. wagneriana* Copel. (Genera in parentheses are those that were adopted by previous classifications.)

TABLE 2. Characters of genera and sections of Davalliaceae. **Bold** indicates unique characters to genera or sections.

Character	*Davallia* sect. *Davallia*	*Davallia* sect. *Trogostolon*	*Humata*	*Araiostegiella*	*Wibelia*	*Davallodes*
Rhizome thickness (mm)	2-15	3-12	**0.5-3**	4-6	3-15	3-20
Scale form	Linear-deltoid, sometimes acicular	Linear-deltoid, sometimes acicular	Linear-deltoid, sometimes acicular	Oblong-lanceolate	Linear-deltoid, oblong-lanceolate	**Ovate-lanceolate,** linear-deltoid, sometimes acicular
Scale color	Pale brown to dull brown	Pale brown to dull brown	Pale brown to brown	Brown	Brown	Pale brown to dull brown
Scale base	Peltate	Peltate	Peltate	Pseudopeltate	Peltate or pseudopeltate	Peltate or pseudopeltate
Scale margin	Hairy	Toothed	Hairy, rarely toothed	Toothed	Toothed	Toothed
Scale surface	Smooth	Smooth	**Verrucose,** rarely smooth	Smooth	Smooth	Smooth
Position of abscission layer	Stipe base	Stipe base	Stipe base	Stipe base, **costa base**	Stipe base	Stipe base
Leaf length (cm)	10-120	10-50	(1-)3-35(-80)	20-80	20-160	20-130
Leaf dissection	Simple, imparipinnate, 1-3-pinnate	3- to 4-pinnate	Simple, lobed or pectinate to 3-pinnate	3-4-pinnate	2-3-pinnate	2-4-pinnate
Form of compound leaf	Widest at base	Widest at base	Widest at base	Widest at base	Widest at base	**Equally wide near base or narrowed to base**
Pinna of finely dissected leaf	Stalked	Stalked	Stalked	Sessile	Stalked	Stalked
Leaf texture	Firm-chartaceous to subcoriaceous	Firm-chartaceous to subcoriaceous	**Coriaceous**	Herbaceous	Firm-chartaceous to subcoriaceous	Herbaceous or chartaceous
Multicellular hair on leaf	Absent	Absent	Absent	Absent	Absent	**Present** or absent
Sorus position	At vein bifurcations	At vein bifurcations	At vein bifurcations	At points of vein bending	At vein bifurcations or at points of vein bending	At points of vein bending
Indusium form	Length≧width	Length>width	Length≦width	Length≦width	Length≧width, occasionally length≦width	Length≧width, length≦width
Indusium length (mm)	1-2(-5)	1-2	0.3-1	0.3-1	1-1.5	0.2-1
Indusium attachment	By base and sides	By base and sides	By base, sometimes by base and sides	By base	By base and sides	By base or by base and sides

Notes. Section *Davallia* differs from sect. *Trogostolon* in the scales being hairy or entire at the margin. Section *Davallia* includes *Scyphularia*, which has been characterized by specialized characters such as imparipinnate leaves. *Scyphularia* is not recognized at infrageneric status, e.g., sect. *Scyphularia* (Nooteboom 1994), because it is paraphyletic, that is, does not include *Davallia solida* and related species (Tsutsumi & Kato 2005). The paraphyly is also indicated by the phylogeny where *S. pentaphylla* and *S. pycnocarpa* are sister to *Davallia plumosa*, which was not examined by Tsutsumi & Kato (2005), and *S. triphylla* is basal in the clade of *Davallia* 2 + *Scyphularia* (Tsutsumi *et al.* 2008), i.e., sect. *Davallia* defined here. *Davallia* sect. *Scyphularia sensu* Nooteboom (1994) included *Parasorus*, which is here placed in *Humata*. Sect. *Davallia* ranges widely from Polynesia through southwestern Europe (also Madeira and the Canaries), with many species in tropical Asia.

1B. sect. **Trogostolon** (Copel.) M. Kato & Tsutsumi, **comb. & stat. nov.**

Trogostolon Copel., Philip. J. Sci. 34: 251, pl. 4, 1927; Gen. Fil. 87, 1947; Fern Fl. Philip. 1: 170, 1958; Ching, Fl. Reipubl. Popularis Sin. 2: 283, 1959; Pichi Sermolli, Webbia 31: 343, 1977; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 568, 1985. —Type: *Davallia falcinella* (J. Sm.) C. Presl (= *Trogostolon falcinellus* (J. Sm.) Copel.).

Davallia sect. *Wibelia* (Bernh.) M. Kato, J. Fac. Sci. Univ. Tokyo III, 13: 566, 1985, sens. auct., excl. *D. denticulata* (basion.).

Species assigned to sect. *Trogostolon*: *Davallia assamica* (Bedd.) Baker, *D.* (= *Trogostolon*) *falcinella* (J. Sm.) C. Presl, *D. griffithiana* Hook., *D. mariesii* T. Moore ex Baker, *D. petelotii* Tardieu & C. Chr., *D. platylepis* Baker, *D. sinensis* Ching, *D. stenolepis* Hayata, *D. trichomanoides* Blume, *D. tyermanii* T. Moore.

Notes. Sect. *Trogostolon* is distinguished from sect. *Davallia* in the scales being toothed at the margin; a tooth comprises the outwardly bent ends of adjacent marginal cells. Kato (1985) proposed section *Wibelia*, but the result of a molecular analysis does not support its recognition treatment (see notes under *Wibelia* below). *Trogostolon falcinellus*, type of the section, is characterized by finely dissected leaves and acicular scales, but the characters are shared by consectional species, so cannot define the section. Because of the absence of particular differences that merit generic or sectional recognition, we place *Davallia trichomanoides* and related species in sect. *Trogostolon*.

2. Humata Cav.

Humata Cav, Descr. Plant. 272, 1802; Bedd. Handb. Ferns Brit. Ind. 46, 1883; Tard.-Blot & C. Chr., Lecomte, Fl. Gén. Indo-chine 7(2): 108, 1939; Copel., Gen. Fil. 88, 1947; Fern Fl. Philip. 1: 175, 1958; Holttum, Rev. Fl. Malaya 2: 364, 1955; Ching, Fl. Reipubl. Popularis Sin. 2: 306, 1959; Tagawa, Col. Illustr. Jap. Pterid. 67, 1959; Brownlie, Fl. Nouvelle-Calédonie Dépandances 3. Pterid. 148, 1969; DeVol & Yang, Fl. Taiwan 1: 274, 1975; Brownlie, Pterid. Fl. Fiji 158, 1977; Pichi Sermolli, Webbia 31: 343, 1977; Tagawa & Iwatsuki, Fl. Thailand 3(2): 164, 1985; Shieh, DeVol & Yang, Fl. Taiwan, 2 ed. 1: 190, 1994; Wu, Fl. Reipubl. Popularis Sin. 6(1): 188, 1999. —Type: *Humata ophioglossa* Cav. (= *H. heterophylla* Desv.)

Davallia [unranked] *Pachypleuria* C. Presl, Tent. Pterid. 128, 1836. —*Pachypleuria* (C. Presl) C. Presl, Epim. Bot. 98, 1851; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 567, 1985; in Iwatsuki *et al.* (eds.) Fl. Jap. 1: 74, 1995. —Type: *Pachypleuria pedata* (Smith) C. Presl (= *Humata repens* L. f.).

Pteroneuron Fée, Gen. Fil. 320, pl. 25B, f. 1, 1852. —Type: *Pteroneuron parallelum* Fée.

Parasorus Alderw., Bull. Jard. Bot. Buitenzorg III, 4: 317, t. 14, 1922; Copel., Gen. Fil. 89, 1947; Pichi Sermolli, Webbia 31: 343, 1977; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 568, 1984. **syn. nov**. —Type: *Parasosorus undulatus* Alderw.

Davallia auctt.; Kramer, in Kubitzki (ed.), Fam. Gen. Vasc. Pl. 1: 79, 1990, p.p.; Nooteboom, Blumea 39: 155, 1994, p.p.

Species assigned to *Humata: H. angustata* (Wall. ex Hook. & Grev.) J. Sm., *H. botrychioides* Brack., *H. brackenridgei* (Brownlie) M. Kato, *H. caroliniensis* Hosokawa, *H.* (= *Davallia*) *corniculata* (T. Moore) M. Kato & Tsutsumi*, *H. heterophylla* Desv. (= *H. ophioglossa* Cav.), *H. macrostegia* Tagawa, *H. microsora* Copel., *H. parvula* Wall. ex Hook. & Grev., *H. pectinata* J. Sm., *H. pusilla* Mett., *H. pusilloides* Copel., *H. polypodioides*

Brack., *H. repens* L. f., *H.* (= *Davallia*) *seramensis* (M. Kato) M. Kato & Tsutsumi*, *H. sessilifolia* (Blume) Mett., *H. tenuis* Copel., *H. trifoliata* C. Presl, *H. trukensis* H. Ito ex Nakai, *H.* (= *Parasorus*) *undulata* (Alderw.) M. Kato & Tsutsumi*, *H. vestita* Blume.

Notes. Kato (1985) transferred *H. ophioglossa*, the type species of *Humata*, to *Davallia* sect. *Wibelia*, while referring *Humata repens* and related species to *Pachypleuria*. The species of *Pachypleuria sensu* Kato differ from *H. ophioglossa* by the scales being hairy at the margin, verrucose or sometimes smooth on the surface, the leaves coriaceous, the sori relatively small, and the indusia fixed at the base and free on the sides (but sometimes partially fixed at the sides). The verrucose scales, which are unique in the Davalliaceae, support the monophyly of the *H. repens* group, but do not necessarily indicate separation of *Pachypleuria* from *Humata* at the genus level (see below).

In a recent molecular phylogeny, *Humata ophioglossa* (= *H. heterophylla*) is sister to *H. polypodioides*, which is placed outside *Davallia* (Tsutsumi *et al.* 2008) (Fig.1). Although the sequence (4,786 bp) of five continuous chloroplast DNA regions of *H. heterophylla* differs from that of *H. polypodioides* by only 3 bp, they are distinct in leaf morphology: the fertile leaf is lobed and the sterile leaf is simple in *H. heterophylla*, while both leaves are more or less monomorphic and 2-pinnate in *H. polypodioides*. The molecular data do not support Kato's (1985) generic level separation of *H. heterophylla* from *Pachypleuria*, which includes the remaining majority of *Humata* with 2-pinnatifid to 3-pinnate, subdimorphic or dimorphic leaves. The genus *Humata* recognized by, e.g. Copeland (1947), Holttum (1955) and Ching (1959) is paraphyletic in a strict sense, or monophyletic, except that *H.* (= *Davallia*) *corniculata* is nested within the clade of *Humata* (Tsutsumi & Kato 2005). The clade is divided into two subclades, one comprising *H. repens, H. vestita* and related species, along with *H.* (= *D.*) *corniculata*, and the other comprising *H. heterophylla*, *H. polypodioides* and *H. sessilifolia*.

Humata includes species with the small, simple leaves and discrete sori close to adjacent ones, and probably also *Parasorus undulatus* with simple leaves and coenosori comprising marginal sori connate side by side (see Appendix). Kato (1985, 1989), however, placed *Parasorus* under *Davallia* sect. *Davallia sensu* Kato, and Nooteboom (1994) assigned it to *Davallia* sect. *Scyphularia*. The simple leaved species, e.g. *H. angustifolia*, *H.* (= *Davallia*) *seramensis*, and *H.* (= *Parasorus*) *undulata*, may be related to the heterophyllous *H. heterophylla*, because they also share acicular, peltate scales and sori fixed at the base and partly at the sides. Young plants of *Parasorus undulatus* were described to have interrupted, small sori (van Alderwerelt van Rosenburgh 1922), which are similar to the discrete sori of *Humata*, in particular *H. angustifolia* and *H. seramensis*. This inferred relationship among the single leaved species should be verified by another line of evidence, e.g. molecular phylogeny.

Humata is distributed as widely as *Davallia* in eastern and southeastern Asia, extending west to tropical west Africa and the southern Indian Ocean islands, east and south to the western and southern Pacific islands and northern Australia, and north to Japan (Nooteboom 1994).

3. **Araiostegiella** M. Kato & Tsutsumi, **gen. nov.**

Araiostegiae (= *Davallodi*) paleis pseudopeltatis, lobis folii angustissimis uninerviis similis, sed a generibus aliis pinnis subtiliter dissectis sessilis, paleis basi pinnulis, a *Davallode* pro parte paleis pseudopeltatis, indusiis basi fixis differt.

Typus. *Araiostegiella perdurans* (Christ) M. Kato & Tsutsumi*.

Rhizomes long-creeping, dorsiventral, densely scaly throughout, with leaves separated narrowly or widely. *Scales* imbricate, appressed, brown, concolored, membranous, pseudopeltate, oblong-lanceolate, irregularly toothed or subentire at margin, acuminate (neither acicular nor round at apex). *Leaves* medium sized, 3-4-pinnate; basal pinnae largest or as large as second basal pinnae; pinnae sessile, apex acuminate, articulate to rachis particularly in *A. clarkei*; pinnules finely dissected into narrow segments, scaly at base, devoid of multicellular hairs; segments equally or unequally branched, univeined, acute. *Sori* usually located at point of vein bifurcations or at point of vein bending above bifurcations, at sinuses of segments; indusia ovate or laterally elliptic, as wide as long or wider, fixed at base.

Species assigned to *Araiostegiella*: A. *clarkei* (Baker) M. Kato & Tsutsumi*, *A. faberiana* (C. Chr.) M. Kato & Tsutsumi*, *A. perdurans* (Christ) M. Kato & Tsutsumi* (type species).

Notes. The species of *Araiostegiella* have been traditionally referred to *Araiostegia*, based on similarities in the pseudopeltate, irregularly toothed scales, finely dissected leaves with narrow, univeined segments, and small indusia attached by the base (Copeland 1947, Tagawa & Iwatsuki 1970, Ching 1978, Kato 1985). Molecular evidence indicates paraphyly of *Araiostegia*, which should be divided into two genera, *Araiostegiella* and *Davallodes* (which includes *Araiostegia hymenophylloides* and allies; see below) (Fig. 1). *Araiostegiella* differs from all other genera in the sessile pinnae and pinnules, even though they are finely dissected, and in the scales borne at the base of the pinnules (Fig. 2, Nooteboom 1992: figs. 2, 4). There are abscission layers at the base of the pinnae, as well as at the base of the stipes, a rare character state in Davalliaceae (Nooteboom 1992: fig. 3). The genus is composed of three species distributed

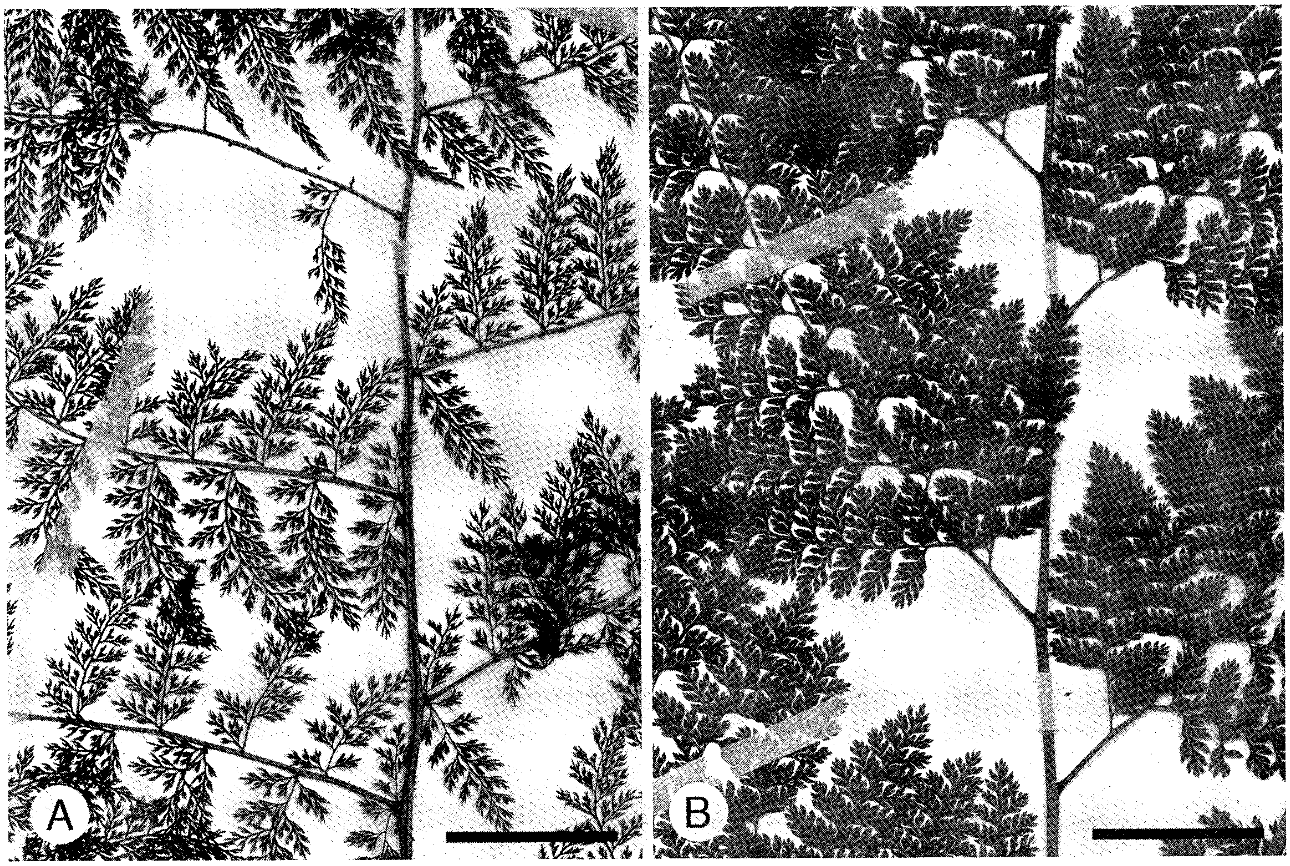

FIG. 2. Parts of leaves of *Araiostegiella perdurans* with sessile pinnae (A: *C.-I Peng 13234* [TNS], Taiwan) and *Davallodes hymenophylloides* with stalked pinnae (B: *S. Matsumoto 780804-4* [TNS], W Malaysia). Scale bars = 2 cm.

from the Himalaya to southern China and Taiwan. Nooteboom (1992, 1994) recognized only a single variable species, *A. clarkei*, but this lumping is not supported by the molecular variation in *A. faberina* and *A. perdurans* (Tsutsumi & Kato 2005, Tsutsumi *et al.* 2008).

4. **Wibelia** Bernh.

Wibelia Bernh., Schrad. J. 1800(2): 122, pl. 1, f. 2, 1801 (non Fée 1852). —*Davallia* sect. *Wibelia* (Bernh.) M. Kato, J. Fac. Sci. Univ. Tokyo III, 13: 566, 1984, excl. syn. et spp. cit. —Type: *Wibelia elata* (Forst.) Bernh. (= *Wibelia denticulata* (Burm.) M. Kato & Tsutsumi*).

Parestia C. Presl, Epim. Bot. 99, 1851. —Type: *Parestia elegans* (Poir.) C. Presl (= *Wibelia denticulata*). **syn. nov.**

Davallia sect. *Cordisquama* M. Kato, J. Fac. Sci. Univ. Tokyo III, 13: 566, 1985. —Type: *Davallia divaricata* Blume. **syn. nov.**

Species assigned to *Wibelia* : *W. chaerophylloides* (Poir.) Steud.*, *W. decurrens* (Blume) M. Kato & Tsutsumi*, *W. denticulata* (Burm.) M. Kato & Tsutsumi* (type species), *W. dimorpha* (Holttum) M. Kato & Tsutsumi*, *W. divaricata* (Blume) M. Kato & Tsutsumi*, *W. embolostegia* (Copel.) M. Kato & Tsutsumi*, *W. epiphylla* (Forst.) M. Kato & Tsutsumi*, *W. formosana* (Hayata) M. Kato & Tsutsumi*.

Notes. *Wibelia* and *Parestia* have long been synonymized under *Davallia*, because their type species, both identified as *Wibelia denticulata*, has been considered to be related to *D. canariensis* (type of *Davallia*) and relatives (Copeland 1947). Kato (1985) recognized *Davallia* sect. *Wibelia* for *W. denticulata*, *Davallia trichomanoides* and others, which were considered to be closely related to each other. Molecular analyses place *W. denticulata* and related species outside of *Davallia*, *Humata*, and *Araiostegiella* (Tsutsumi & Kato 2005, Tsutsumi *et al.* 2008) (Fig. 1). Furthermore, *W. denticulata* and relatives form a monophyletic group with *W. divaricata* and related species, which had been assigned to *Davallia* sect. *Cordisquama* by Kato (1985). As the species of *Wibelia* have usually been placed in *Davallia*, they are hardly distinguished from *Davallia* by gross morphology. But the group of *W. divaricata*, *i.e.*, *Davallia* sect. *Cordisquama*, can be recognized by the pseudopeltate scales and the sori being borne at the bending points of veins. The genus *Wibelia* revised here is separable from *Davallia* sect. *Davallia* by the toothed, peltate or pseudopeltate scales, from sect. *Trogostolon* by the relatively larger leaves (usually more than 50 cm long), from *Humata* by the usually larger leaves, toothed, smooth surfaced scales and indusia fixed at the base and sides, and from *Araiostegiella* and *Davallodes* by a combination of firmly chartaceous or subcoriaceous leaves with deltoid or deltoid-ovate lamina and indusia fixed at the base and sides (Table 2).

Wibelia is predominant in Asia and the Pacific, but only *W. chaerophylloides* occurs widely in tropical and southern Africa (Schelpe & Anthony 1986). *Wibelia chaerophylloides* is an independent species close to *W. denticulata* (Tsutsumi *et al.* 2008), although the two have been treated as conspecific (e.g. Nooteboom 1994).

5. **Davallodes** Copel.

Davallodes Copel., Philip. J. Sci. 3C: 33, 1908; Philip. J. Sci. 34: 251, pl. 4, 1927; Gen. Fil. 87, 1947; Fern Fl. Philip. 1: 168, 1958; Tard.-Blot & C. Chr., Lecomte, Fl. Gén. Indo-chine 7(2): 115, 1939; Ching, Fl. Reipubl. Popularis Sin. 2: 281, 1959; Holttum, Kew Bull. 27: 245, 1972; Pichi Sermolli, Webbia 31: 343, 1977; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 564, 1985; Tagawa & Iwatsuki, Fl. Thailand 3(2): 155, 1985; Kramer in Kubitzki (ed.) Fam. Gen. Vasc. Pl. 1: 78, 1990; Nooteboom, Blumea 37: 176, 1992; Fl. Males. Ser. II, 3: 268, 1998. —*Microlepia* [unranked] *Davallodes* Copel., Polypod. Philip. Is., Bur. Gov. Lab. Publ. 28 : 55, 1905. —Type: *Davallodes hirsuta* (J. Sm. ex C. Presl) Copel., '*hirsutum*'.

Araiostegia Copel., Philip. J. Sci. 34: 240, pl. 1, 2, 1927, p.p.; Univ. Calif. Publ. Bot. 12: 397, 1931, p.p.; Gen. Fil. 85, 1947; Fern Fl. Philip. 1: 166, 1958, p.p.; Holttum, Rev. Fl. Malaya 2: 364, 1955; Ching, Fl. Reipubl. Popularis Sin. 2: 285, 1959, p.p.; Tagawa & Iwatsuki, Acta Phytotax. Geobot. 24: 178, 1970, p.p.; Fl. Thailand 3(2): 150, 1985, excl. *Gymnogrammitis*, p.p.; DeVol & Yang, Fl. Taiwan 1: 270, pl. 95, 1975, p.p.; Pichi Sermolli, Webbia 31: 343, 1977, p.p.; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 564, 1985, p.p.; Kramer in Kubitzki (ed.) Fam. Gen. Vasc. Pl. 1: 78, 1990, p.p.; Shieh, DeVol & Yang, Fl. Taiwan, 2 ed., 1: 186, 1994, p.p.; Wu, Fl. Reipubl. Popularis Sin. 6(1): 167, 1999, p.p. —Type: *Araiostegia hymenophylloides* (Blume) Copel. **syn. nov.**

Paradavallodes Ching, Acta Phytotax. Sin. 11: 18, 1966; Pichi Sermolli, Webbia 31: 343, 1977; Wu, Fl. Reipubl. Popularis Sin. 6(1): 162, 1999. —Type: *Paradavallodes multidentata* (Hook.) Ching, '*multidentatum*'. **syn. nov.**

Species assigned to *Davallodes*: *D.* (= *Araiostegia*) *beddomei* (Hope) M. Kato & Tsutsumi*, *D. borneensis* (Hook.) Copel., *D. burbidgei* C. Chr. & Holttum, *D. hirsuta* (J. Sm. ex C. Presl) Copel. (type species), *D.* (= *Araiostegia*) *hymenophylloides* (Blume) M. Kato & Tsutsumi*, *D.* (= *Araiostegia*) *imbricata* (Ching) M. Kato & Tsutsumi*, *D. membranulosa* (Wall. ex Hook.) Copel., *D.* (= *Paradavallodes*) *multidentata* (Hook.) M. Kato & Tsutsumi*, *D.* (= *Araiostegia*) *pseudocystopteris* (Kunze) M. Kato & Tsutsumi*, *D.* (= *Araiostegia*) *pulchra* (D. Don) M. Kato & Tsutsumi*, *D.* (= *Araiostegia*) *yunnanensis* (Christ) M. Kato & Tsutsumi*.

Notes. The genus *Davallodes* emended here is difficult to define by a single character, but instead a combination of characters must be used, which are shown in the Key and in Table 1.

In molecular phylogenetic analyses, Tsutsumi & Kato (2005) and Tsutsumi *et al.* (2008) showed that *D. gymnocarpa* is a member of *Davallodes*, but did not examine *Davallodes hirsuta*, the type of *Davallodes*. Because the two species are probably close or conspecific (Nooteboom 1992), *Davallodes* is the oldest, available name at the genus level for the clade comprising *Araiostegia* clade 1 + *Davallodes* + *Paradavallodes* (Tsutsumi & Kato 2005, Tsutsumi *et al.* 2008).

This revised genus comprises all species of *Davallodes*, *Paradavallodes multidentata* (type), *Araiostegia hymenophylloides* (type) and closely related species, but excludes *A. perdurans* and its close relatives, which are assigned to *Araiostegiella* above. *Davallodes* is basal in the phylogenetic tree of the Davalliaceae (Fig. 1; Tsutsumi & Kato 2005, Tsutsumi *et al.* 2008). *Davallodes* is remarkably polymorphic and shows variation in characters that are discontinuous and shared by different genera (Table 1). Hence, no single character can define *Davallodes*, but specific characters can discriminate the genus from each of the related genera. Species of *Davallodes* that have been assigned to *Araiostegia* are distinguished from *Araiostegiella* by the stalked pinnae (Fig. 2). Most species assigned to *Davallodes* sensu Holttum (1972) differ from *Araiostegiella* in having peltate scales. From *Wibelia*, the species of *Davallodes* are distinguished by the leaves bearing multicellular hairs; from species of other genera by the herbaceous or thinly chartaceous leaves; and from still other species, by the indusia fixed at the base. *Davallodes* sensu Holttum (1972) is unique in its oblanceolate leaves among related genera with finely dissected leaves. There is no clear infrageneric structure in the genus, as neither *Araiostegia* nor *Davallodes* as previously defined is monophyletic (Tsutsumi & Kato 2005, Tsutsumi *et al.* 2008).

In a molecular phylogenetic tree, *Paradavallodes multidentata* (type) is nested within the genus *Davallodes* emended here (Tsutsumi *et al.* 2008). Previous taxonomic treatments of it, however, differed among authors. *Paradavallodes* was recognized as a genus intermediate between *Araiostegia* and *Davallodes* (Ching 1966b, 1978, Pichi Sermolli 1977, Wu 1999). Many other authors placed *P. multidentata* in *Araiostegia* (e.g. Copeland 1927, 1947, Tagawa & Iwatsuki 1970, Sen *et al.* 1972, Kato 1975, 1985, Kramer 1990, Nooteboom 1992). Nooteboom (1994) included *Paradavallodes* (as *Araiostegia*) in *Davallia* s.l. *Davallodes membranulosa*, one of four species referred to *Paradavallodes* by Ching (1966b), is not close to *P. multidentata,* as suggested by scale characters (Kato 1975). It was placed in *Davallodes* (Copeland 1947, Kato 1975, 1985, Kramer 1990) or *Araiostegia* (Sen *et al.* 1972, Holttum 1972, Nooteboom 1992). We conclude that, although *P. multidentata* and *D. membranulosa* share hairy leaves, *Paradavallodes* is an artificial assemblage in the genus *Davallodes*.

Genera excluded

Gymnogrammitis Griffith

Not. Pl. Asiat. 2: 608, 1849; Icon. Pl. Asiat. 2: pl. 129, f. 1, 1849; Tard.-Blot & C. Chr., Lecomte, Fl. Gén. Indo-chine 7(2): 117, f. 14, 1939; Ching, Sunyatsenia 5: 220, 1940; Fl. Reipubl. Popularis Sin. 2: 284, 1959; Acta Phytotax. Sin. 11: 13, 1966; Acta Phytotax. Sin. 16(3): 16, 1978; Pichi Sermolli, Webbia 31: 343, 1977; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 565, 1985; Kramer in Kubitzki (ed.) Fam. Gen. Vasc. Pl. 1: 80, 1990; Nooteboom, Blumea 37: 186, 1992; Wu, Fl. Reipubl. Popularis Sin. 6(1): 198, 1999. —Type: *Gymnogrammitis dareiformis* (Hook.) Ching ex Tardieu & C. Chr.

Notes on the systematic position. The systematic treatment of *Gymnogrammitis*, along with *Araiostegia*, being assigned to Davalliaceae has been widely accepted (Tardieu-Blot & Christensen 1939, Ching 1940, 1959, Sen & Sen 1971, Sen et al. 1972, Pichi Sermolli 1977, Kato 1985, Tagawa & Iwatsuki 1985, Wu 1999). Copeland (1931, 1947) did not recognize the genus, synonymizing it under *Araiostegia* (see also McNeill *et al.* 2006: 245), while Nooteboom (1992, 1994) recognized the genus *Gymnogrammitis* and reduced *Araiostegia* under *Davallia*. Ching (1966a, 1978) and Wu (1999) separated *Gymnogrammitis* as an independent family Gymnogrammitidaceae. Recently, Schneider et al. (2002) provided molecular evidence for the systematic position of *Gymnogrammitis* in Polypodiaceae *s.l.* (Smith *et al.* 2006), which was supported by Tsutsumi & Kato (2006).

The finely dissected leaves and pseudopeltate scales shared by *Gymnogrammitis* and *Araiostegia* are convergences. The sister relationship of *Gymnogrammitis* and *Selliguea* (inclusive of *Crypsinus*) indicates that differences in the genera have been produced by abrupt modifications of characters, e.g. leaf dissection (finely dissected vs. simple or lobed) and venation (free vs. anastomosing). Close comparison among polypods will reveal the evolution of the morphology of *Gymnogrammitis*, by which the genus has long been regarded as non-polypodioid.

Leucostegia C. Presl

Tent. Pterid. 94, pl. 4, f. 11, 1836; Copel., Philip. J. Sci. 34: 252, 1927, Gen. Fil. 86, 1947; Fern Fl. Philip. 1: 167, 1958; Tard.-Blot & C. Chr., Lecomte, Fl. Gén. Indo-chine 7(2): 112, 1939, p.p.; Holttum, Rev. Fl. Malaya 2: 351, 1955; Ching, Fl. Reipubl. Popularis Sin. 2: 296, 1959; DeVol & Yang, Fl. Taiwan 1: 278, 1975; Pichi Sermolli, Webbia 31: 343, 1977; Kato, J. Fac. Sci. Univ. Tokyo III, 13: 564, 1984; Tagawa & Iwatsuki, Fl. Thailand 3(2): 168, 1985; Kramer in Kubitzki (ed.) Fam. Gen. Vasc. Pl. 1: 78, 1990; Nooteboom, Blumea 37: 184, 1992; Fl. Males. Ser. II, 3: 274, 1998; Shieh, DeVol & Yang, Fl. Taiwan, 2 ed., 1: 197, 1994; Wu, Fl. Reipubl. Popularis Sin. 6(1): 178, 1999. —Type: *Leucostegia immersa* (Wall. ex Hook.) C. Presl.

Notes on the systematic position. Leucostegia has long been assigned to Davalliaceae because of their similarities in the creeping, dorsiventral rhizome densely covered by scales, dissected leaves, and marginal sori with cup-shaped or shell-shaped indusia (Copeland 1927, 1947, 1958, Tardieu-Blot & Christensen 1939, Ching 1940, 1959, 1978, Holttum 1949, 1955, Sen *et al.* 1972, Kato 1985, Tagawa & Iwatsuki 1985, Kramer 1990, Nooteboom 1992, 1998, Shieh *et al.* 1994, Wu 1999). In a molecular phylogenetic analysis, Tsutsumi & Kato (2006) showed that *Leucostegia* is close to *Hypodematium* of Hypodematiaceae, which is far from Davalliaceae and included in Dryopteridaceae (Smith *et al.* 2006). Schuettpelz & Pryer (2007) insisted on the monophyly of the two genera and *Didymochlaena* and the exclusion of them from

Dryopteridaceae.

Leucostegia and *Hypodematium* share long creeping rhizomes densely covered by basifixed scales, simple, dorsiventral dictyosteles, and sori fixed at the base (in *L. immersa*; fixed at the base and sides in *L. pallida*) (Pérez Arbeláez 1928, Kato & Mitsuta 1980, Kato 1985). They are also similar in the lithophytic growth form: *Leucostegia* grows often on rocks and is also terrestrial and epiphytic, while *Hypodematium* grows in crevices of limestone. The similarities in the rhizome, stele and scale are likely adaptations to similar habitats.

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APPENDIX. New combinations that accompany the proposed generic classification of Davalliaceae.

Araiostegiella clarkei (Baker) M. Kato & Tsutsumi, **comb. nov.** —*Davallia clarkei* Baker, Syn. Fil. 91, 1874. —*Araiostegia clarkei* (Baker) Copel., Philip. J. Sci. 34: 241, 1927; Noot., Blumea 37: 170, f. 3, 1992; Wu, Fl. Reipubl. Popularis 6: 173, 1999 (as *A. hookeri*); Noot., Blumea 39: 176, 1994, p.p.

Araiostegiella faberiana (C. Chr.) M. Kato & Tsutsumi, **comb. nov.** —*Davallia clarkei* Baker var. *faberiana* C. Chr., Acta Horti Gothob. 1: 73, 1924. —*Araiostegia faberiana* (C. Chr.) Ching in C. Chr., Ind. Fil. Suppl. 3: 120, 1934; Tagawa & Iwatsuki, Fl. Thailand 3(2): 152, f. 11, 2, 1985; Wu, Fl. Reipubl. Popularis Sin. 6: 174, 1999.

Araiostegiella perdurans (Christ) M. Kato & Tsutsumi, **comb. nov.** —*Davallia perdurans* Christ, Bull. Herb. Boissier 6: 970, 1898. —*Araiostegia perdurans* (Christ) Copel., Univ. Calif. Publ. Bot. 12: 397, 1931; Ching, Fl. Reipubl. Popularis Sin. 2: 294, 1959; Wu, Fl. Reipubl. Popularis 6: 175, f. 31, 1-10, 1999.

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Davallodes beddomei (Hope) M. Kato & Tsutsumi, **comb. nov.** —*Davallia beddomei* Hope, J. Bomb. Nat. Hist. Soc. 12: 527, t. 1, 1899. —*Araiostegia beddomei* (Hope) Ching, Fl. Reipubl. Popularis Sin. 2: 288, 1959; Wu, Fl. Reipubl. Popularis Sin. 6: 171, 1999.

Davallodes hymenophylloides (Blume) M. Kato & Tsutsumi, **comb. nov.** —*Aspidium hymenophylloides* Blume, Enum. Pl. Jav. 172, 1828. —*Araiostegia hymenophylloides* (Blume) Copel., Philip. J. Sci. 34: 241, 1927; Fern Fl. Philip. 1: 166, 1958; Holttum, Fl. Malaya 2: 363, f. 210, 1955. —*Davallia hymenophylloides* (Blume) Noot., Blumea 39: 186, 1994.

Davallodes imbricata (Ching) M. Kato & Tsutsumi, **comb. nov.** —*Araiostegia imbricata* Ching, Fl. Reipubl.

Popularis Sin. 2: 291, 1959; Tagawa & Iwatsuki, Fl. Thailand 3(2): 152, f. 11, 3, 1985; Wu, Fl. Reipubl. Popularis Sin. 6: 173, 1999.

Davallodes multidentata (Wall. ex Hook.) M. Kato & Tsutsumi, **comb. nov.** —*Davallia multidentata* Wall. ex Hook. in Hook. & Baker, Syn. Fil. 91, 1868; Noot., Blumea 39: 188, 1994. —*Araiostegia multidentata* (Wall. ex Hook.) Copel., Philip. J. Sci. 34: 241, 1927; Ching, Fl. Reipubl. Popularis 2: 295, 1959; Sen *et al.*, Kew Bull. 27: 232, 1972; Noot., Blumea 37: 173, 1992. —*Paradavallodes multidentata* (Wall. ex Hook.) Ching, Acta Phytotax. Sin. 11: 20, 1966; Wu, Fl. Reipubl. Popularis Sin. 6: 164, f. 30, 5-8, 1999, '*multidentatum*'.

Davallodes pseudocystopteris (Kunze) M. Kato & Tsutsumi, **comb. nov.** —*Davallia pseudocystopteris* Kunze, Bot. Zeit. 6: 68, 1850. —*Araiostegia pseudocystopteris* (Kunze) Copel., Philip. J. Sci. 34: 241, 1927; Ching, Fl. Reipubl. Popularis Sin. 2: 287, 1959; Tagawa & Iwatsuki, Fl. Thailand 3(2): 155, f. 11, 4, 1985; Wu, Fl. Reipubl. Popularis Sin. 6: 169, 1999.

Davallodes pulchra (D. Don) M. Kato & Tsutsumi, **comb. nov.** —*Davallia pulchra* D. Don, Prodr. Fl. Nepal. 11, 1825. —*Araiostegia pulchra* (D. Don) Copel., Philip. J. Sci. 34: 241, 1927; Ching, Fl. Reipubl. Popularis Sin. 2: 288, 1959; Tagawa & Iwatsuki, Fl. Thailand 3(2): 154, 1985; Wu, Fl. Reipubl. Popularis Sin. 6: 170, 1999.

Davallodes yunnanensis (Christ) M. Kato & Tsutsumi, **comb. nov.** —*Davallia yunnanensis* Christ, Bull. Herb. Boissier 6: 970, 1898. —*Araiostegia yunnanensis* (Christ) Copel., Philip. J. Sci. 34: 241, 1927; Ching, Fl. Reipubl. Popularis Sin. 2: 290, 1959; Wu, Fl. Reipubl. Popularis Sin. 6: 172, 1999.

Humata corniculata (T. Moore) M. Kato & Tsutsumi, **comb. nov.** —*Davallia corniculata* T. Moore, Ind. Fil. 292, 1861; Holttum, Fl. Malaya 2: 359, 1955; Noot., Blumea 39: 177, 1994.

Humata seramensis (M. Kato) M. Kato & Tsutsumi, **comb. nov.** —*Davallia seramensis* M. Kato, J. Fac. Sci. Univ. Tokyo, sect. III, 14: 223, f. 2, 1989; Noot., Blumea 39: 210, 1994.

Humata undulata (Alderw.) M. Kato & Tsutsumi, **comb. nov.** —*Parasorus undulatus* Alderw., Bull. Jard. Bot. Buitenzorg, ser. 3, 4: 317, f. 14, 1922. —*Davallia undulata* (Alderw.) Noot., Blumea 39: 211, 1994.

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