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Circumscription of the grammitid fern genus *Oreogrammitis* (Polypodiaceae) with the description of three new genera: *Calligrammitis*, *Devolia*, and *Glabrigrammitis*

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Abstract

Following a recent phylogenetic study, we here review the circumscription of the grammitid fern genus *Oreogrammitis* (Polypodiaceae: Grammitidoideae). We propose three new genera *Calligrammitis*, *Devolia*, and *Glabrigrammitis*, to accommodate the three clades resolved outside of the core *Oreogrammitis*. The taxonomic treatment is presented, and the morphology of each new genus is shown with a color plate.

Keywords: Grammitidoideae, *Grammitis*, polyphyly, Old World

Introduction

The grammitid fern genus *Oreogrammitis* was published by Copeland (1917: 64) based on *O. clemensiae* Copeland (1917: 64) from Mt. Kinabalu, Malaysia. According to Copeland (1917) *Oreogrammitis* is distinguished from *Scleroglossum* (Alderwerelt 1912: 37) by having superficial rather than sunken fused sori. At that time there were only nine genera in Grammitidoideae sensu PPG I (2016) including *Oreogrammitis* itself in comparison with today's 42 genera in the subfamily (Zhou *et al.* 2023). Parris (1983) studied the type species in the field and found that sorus fusion varied with age from discrete when young to complete when mature, and concluded that the genus was not worthy of recognition. Using molecular data, Ranker *et al.* (2004) discovered that *Grammitis s.l.* (Swartz 1800: 3) was polyphyletic and *Grammitis s.s.* probably needed to be restricted to the New-World species with black lamina margins. Parris (2007) re-established *Oreogrammitis* for the portion of the Old-World species of *Grammitis s.l.* with dorsiventral rhizomes and setose sori. In the same work, Parris (2007) described *Radiogrammitis* Parris (2007: 240) and distinguished it from *Oreogrammitis* based on the characters of radial, rather than dorsiventral rhizome, and often absence of rhizome scales in the former.

Molecular phylogenetic analyses by Sundue *et al.* (2014), Bauret *et al.* (2017), and Sirimalwatta (2019) suggested that the three genera, *Oreogrammitis*, *Radiogrammitis*, and *Themelium* Parris (1997: 737) (the ORT clade; Sirimalwatta 2019), though distinguishable from one another morphologically (Parris, 2007), should be united. Knapp & Hsu (2017) described an interesting species from Mainland China, Taiwan, and Japan, *Oreogrammitis orientalis* T.C.Hsu in Knapp & Hsu (2017: 44, 45, 108, 261–263), with simple soriferous lateral veins. Based upon the results of Sundue *et al.* (2014), Kuo *et al.* (2019) transferred seven fern species in Taiwan to *Oreogrammitis* including *Radiogrammitis beddomeana*

(Alderwerelt 1918: 39) Parris (2007: 241) and *R. subnervosa* T.C.Hsu (2017: 46). Parris & Sundue (2020) reduced *Radiogrammitis* and *Themelium* to *Oreogrammitis* and transferred the remaining 36 names to *Oreogrammitis*. Two additional related species, *Grammitis adspersa* Blume (1830: 115) and *G. nuda* Tagawa (1941: 284), were transferred from *Grammitis* to *Oreogrammitis* earlier by Parris (2007, 2013).

In this study, we review the most recent phylogenetic study (Zhou *et al.* 2023) and its consequences focusing on the circumscription of *Oreogrammitis*.

Materials and methods

Morphological data were derived from field observations, herbarium specimen examination, and published studies (e.g., Parris 1983, 2007, Knapp & Hsu 2017). Specimens at CDBI, KUN, MO, P, and PYU were examined. Relevant specimens in JSTOR Global Plants (https://plants.jstor.org/), GBIF (https://www.gbif.org), and some online images (e.g., BM, E, P, K, U) were examined.

Molecular results were derived from Zhou *et al.* (2023) in which six plastid regions of 1003 accessions representing ca. 412 (ca. 45%) species in 41 out of 42 (except *Luisma* M.T. Murillo & A.R. Smith, 2003: 313) genera of Grammitidoideae including 94 accessions representing ca. 67 species of *Oreogrammitis* were sequenced.

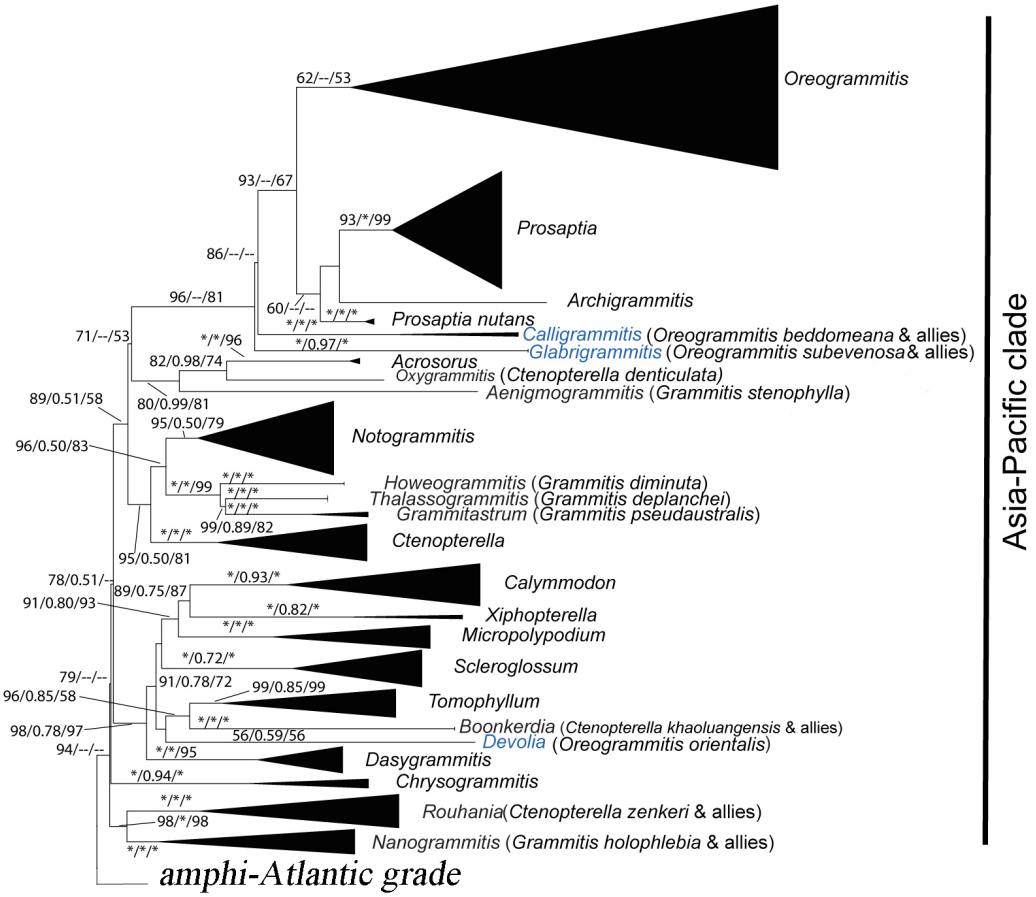

FIGURE 1. Simplified maximum likelihood phylogeny of the Asia-Pacific clade of grammitid ferns (Polypodiaceae) based on six plastid markers (*atpB*, *rbcL*, *rps4*, *rps4-trnS, trnG-R, trnL* & *trnL-F*). Values of maximum likelihood bootstrap support, Bayesian inference posterior probability, and maximum parsimony jackknife support are along/above the branches (Zhou *et al.* 2023). The genera in blue are newly described here.

Results and discussion

Our recent study showed that *Oreogrammitis* sensu Parris (2007, 2013), Kuo *et al.* (2019), and Parris & Sundue (2020) is polyphyletic and resolved this large taxon into four clades: the core *Oreogrammitis*, the *O. beddomeana* clade (*O. beddomeana* (Alderw. 1918: 39) T.C.Hsu (2019: 379), *O. havilandii* (Baker 1894: 253) Parris & Sundue (2020: 48)), the *O. subevenosa* clade (*O. nuda* (Tagawa 1941: 284) Parris (2007: 264), *O. subevenosa* (Baker in Hooker & Baker 1867: 320) Parris (2013: 207)), and the monospecific *O. orientalis* clade (Zhou *et al.* 2023). The *O. beddomeana* clade and the *O. subevenosa* clade are paraphyletic in relation to the core *Oreogrammitis* + (*Archigrammitis* Parris (2013: 135) + *Prosaptia* s.l. (C.Presl 1836: 165–166)). The *O. orientalis* clade is very distantly related to the core group of *Oreogrammitis* and weakly supported as sister to a clade containing *Ctenopterella khaoluangensis* (Tagawa & K. Iwatsuki 1969: 177) Parris (2007: 236) (*Boonkerdia*) and *Tomophyllum* (Fig. 1).

The long branch and isolated relationships of each of the three clades outside of the core group of *Oreogrammitis* suggest that none of them can be placed in any existing genera taxonomically. To maintain the monophyly of *Oreogrammitis*, we propose to establish three new genera, *Calligrammitis* (*O. beddomeana*, *O. havilandii*), *Devolia* (*O. orientalis*), and *Glabrigrammitis* (*O. nuda, O. subevenosa*), to accommodate the three clades outside of the core group of *Oreogrammitis*. *Glabrigrammitis* is resolved as sister to *Calligrammitis* + (*Oreogrammitis* + (*Archigrammitis* + *Prosaptia* s.l.)).

Calligrammitis is similar to those species assigned to *Radiogrammitis* in having radial rhizomes but is distinguishable from the latter by having no scales (vs. often having scales in the latter) on rhizomes and in lacking sporangial setae (Parris *et al.* 2015).

Devolia differs from *Oreogrammitis* in having rhizome scales sometimes with an apical seta, and branched hairs with setae as branches (Knapp & Hsu 2017), whereas *Oreogrammitis* has glabrous rhizome scales and usually lacks branched hairs with setae as branches.

Glabrigrammitis differs from *Oreogrammitis* in glabrous, rather than setose sporangia and also differs from nearly all species of *Oreogrammitis* in having branched hairs with setae as branches.

Both *Calligrammitis* and *Glabrigrammitis* are resolved in a clade which also contains *Archigrammitis*, *Oreogrammitis*, and *Prosaptia s.l.* (Zhou *et al.* 2023). *Calligrammitis*, *Devolia,* and *Glabrigrammitis* can be easily distinguished from *Archigrammitis* and *Prosaptia* by having rhizome scales absent or, if present, without marginal setae.

Taxonomic treatment

The currently defined *Oreogrammitis* is thus divided into four genera with three new genera described below.

Calligrammitis Parris, Sundue, Li Bing Zhang, X.M.Zhou & Ralf Knapp, ***gen. nov.*** Type: *C. beddomeana* (Alderw.) Parris, Sundue, Li Bing Zhang, X.M.Zhou & Ralf Knapp ≡ *Polypodium beddomeanum* Alderw., Bull. Jard. Bot. Buitenzorg sér. 2, 28: 39. 1918 (Fig. 2).

Etymology—Greek, *calli* = beautiful, and *Grammitis*, a genus of ferns in which both species were previously placed.

Diagnosis—*Calligrammitis* differs from other genera of Grammitidoideae by the following combination of characters: rhizomes radial, rhizome scales absent, stipes present, fronds not articulated to rhizome, laminae simple, without sclerotic margin, sometimes slightly crenulate, setae present, branched hairs with setae as branches present, basally stellate hairs present, veins simple, 1-forked or pinnately branched, hydathodes sometimes present at vein endings on adaxial surface of lamina, sporangia glabrous.

Species of *Calligrammitis* were placed in *Radiogrammitis* (Parris 2007) and/or *Oreogrammitis* (Knapp & Hsu 2017, Kuo *et al.* 2019). More recently Parris & Sundue (2020) synonymized *Radiogrammitis* with *Oreogrammitis*. *Calligrammitis* differs from similar species of *Oreogrammitis* that lack rhizome scales and sporangial setae by the presence of basally stellate hairs. It is closely related to *Prosaptia*, which also has branched hairs with setae as branches and lacks sporangial setae, but can be easily distinguished from it by having radial rhizomes without rhizome scales, and superficial sori on the abaxial surface of the lamina, while *Prosaptia* has dorsiventral rhizomes with stipes articulated to prominent phyllopodia and clathrate ciliate rhizome scales, with sori sunken in marginal pouches or in pits on the abaxial surface of the lamina or superficial on the abaxial surface of the lamina.

Description—Lamina narrowly lanceolate to narrowly oblanceolate, or narrowly oblanceolate to linear-oblanceolate, texture membranous to coriaceous, setae usually of two different lengths; veins visible or not in transmitted light. Sori ± circular to broadly elliptic, superficial, one or more rows on each side of the midrib.

Taxonomy—*Calligrammitis* contains two species in Taiwan Island, Southeast Asia, New Guinea, and Sri Lanka (Parris *et al.* 2015, Kuo *et al.* 2019).

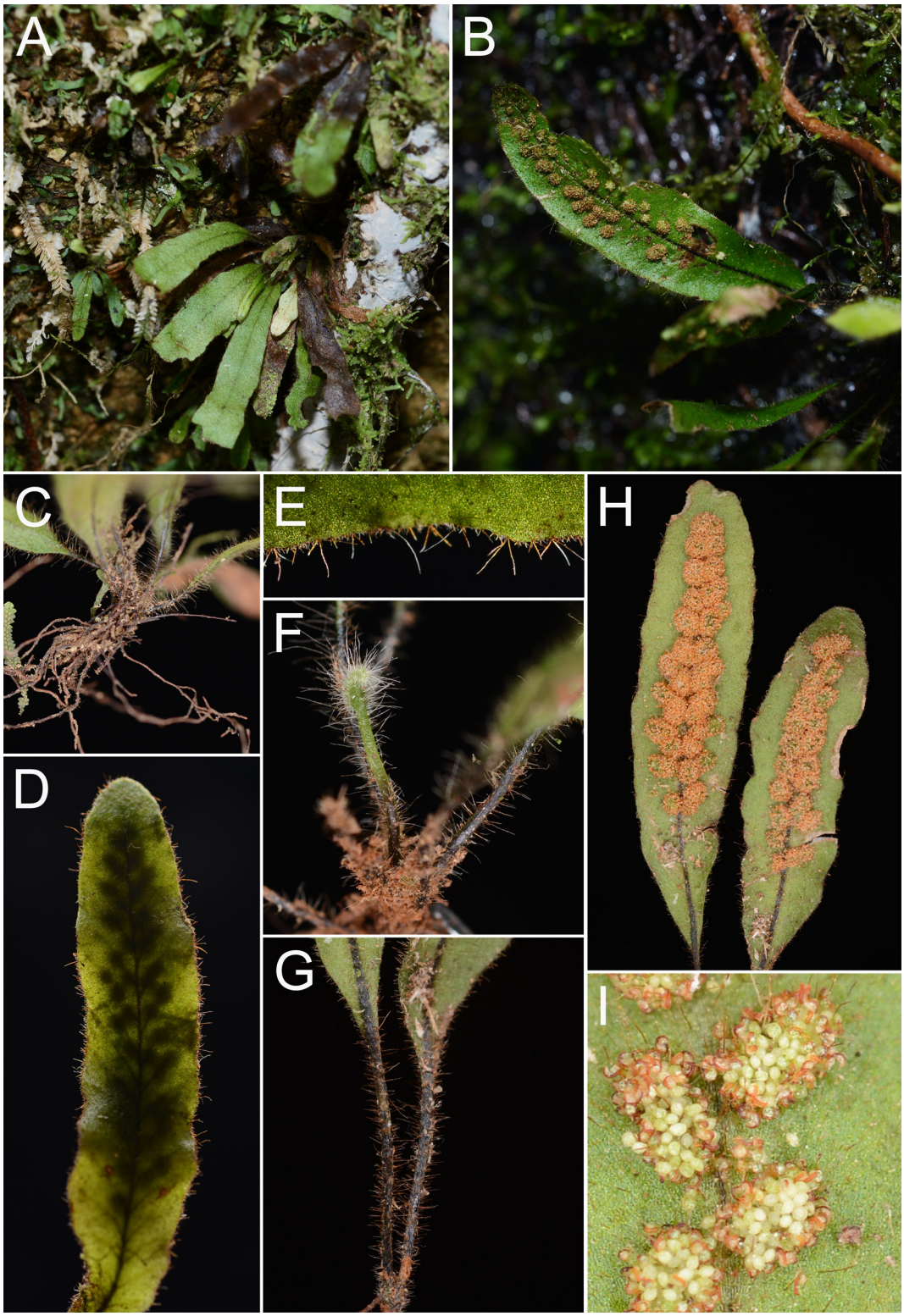

FIGURE 2. *Calligrammitis beddomeana* (Alderw.) Parris, Sundue, Li Bing Zhang, X.M.Zhou & Ralf Knapp.—A, B. Habit and habitats.—C. Lower portion of plant.—D. Adaxial view of lamina.—E. Portion of lamina margin showing hairs.—F. Young shoot of leaf showing hairs.—G. Stipes.—H. Abaxial view of laminae showing sori.—I. Abaxial view of portion of lamina showing sori (photo credit: Ralf Knapp).

Calligrammitis beddomeana (Alderw.) Parris, Sundue, Li Bing Zhang, X.M.Zhou & Ralf Knapp, ***comb. nov.*** Basionym: *Polypodium beddomeanum* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 28: 39. 1918. Type: Ceylon (Sri Lanka), Bogawantalawa, *Wall 30* (holotype BO1546078!) ≡ *Grammitis beddomeana* (Alderw.) Ching, Bull. Fan Mem. Inst. Biol. Bot. 10: 240. 1941 ≡ *Radiogrammitis beddomeana* (Alderw.) Parris, Gard. Bull. Singapore 58(2): 241. 2007 ≡ *Oreogrammitis beddomeana* (Alderw.) T.C.Hsu, Taiwania 64(4): 379. 2019 = *Grammitis alepidota* M.G.Price, Philipp. Agric. 57: 34. 1973. Type: Philippines, Luzon, Mt Banahaw, Quezon side, just below summit, 2100 m, 28 March 1972 (holotype PNH114298!; isotypes K000009164!, L, US2858242!) ≡ *Radiogrammitis alepidota* (M.G.Price) Parris, Gard. Bull. Singapore 58(2): 241. 2007. This species occurs in Sri Lanka, Taiwan Island, Southeast Asia and New Guinea.

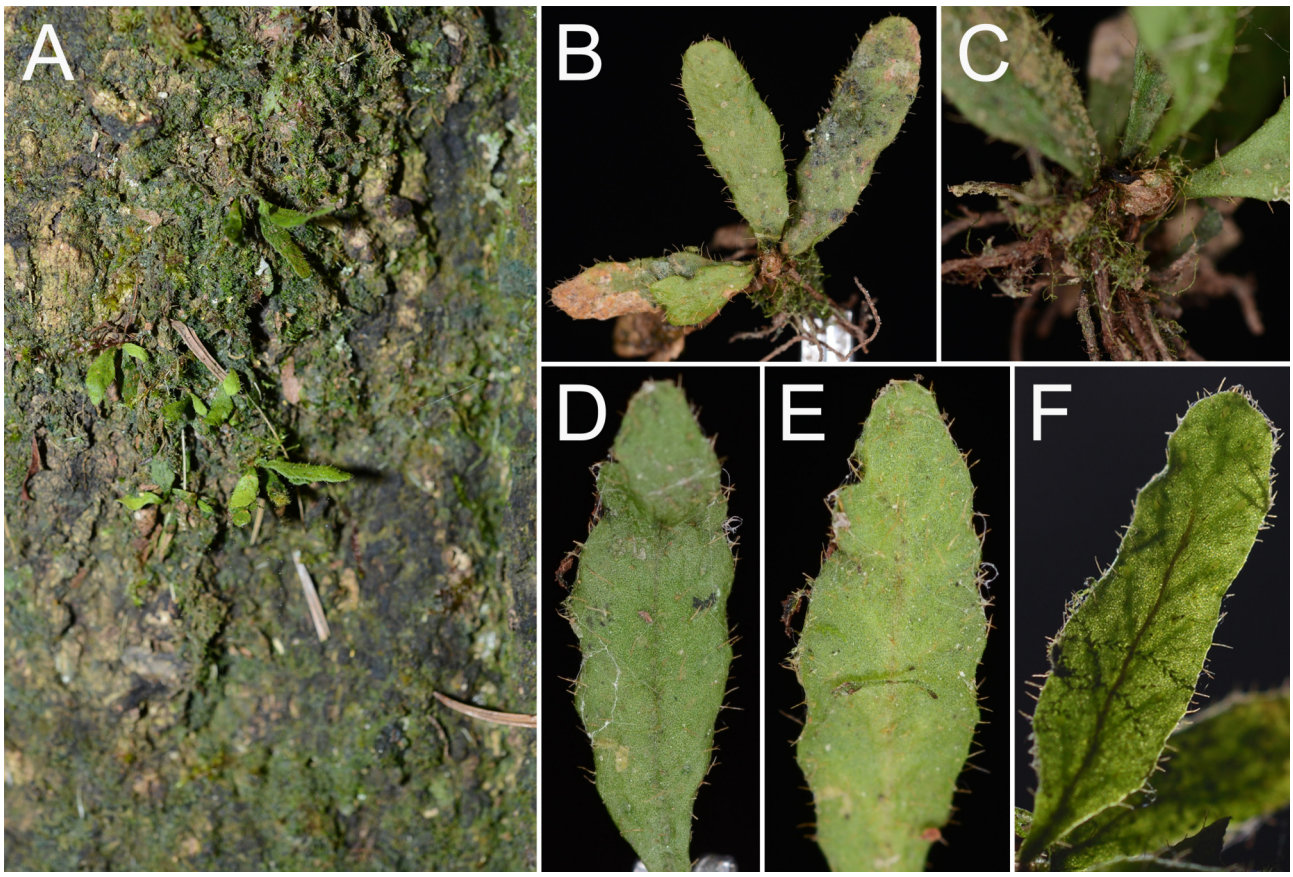

FIGURE 3. *Devolia orientalis* (T.C.Hsu) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Ralf Knapp.—A. Habit and habitat.—B. Habit.—C. Lower portion of plant.—D, F. Adaxial view of laminae. –E. Abaxial view of lamina (photo credit: Ralf Knapp).

Calligrammitis havilandii (Baker) Parris, Sundue, Li Bing Zhang, X.M.Zhou & Ralf Knapp, ***comb. nov.*** Basionym: *Polypodium havilandii* Baker, Trans. Linn. Soc. London, Bot. 4(2): 253. 1894. Type: Malaysia. Sabah Kinabalu, March 1892, *G.D. Haviland 1438* (holotype K000548235!) ≡ *Grammitis havilandii* (Baker) Copel., Gen. Filic. 211. 1947) ≡ *Radiogrammitis havilandii* (Baker) Parris, Gard. Bull. Singapore 58(2): 242. 2007 ≡ *Oreogrammitis havilandii* (Baker) Parris & Sundue, Phytotaxa 436(1): 48. 2020 = *Polypodium multisorum* Copel., Philipp. J. Sci., C Bot. 12(1): 61. 1917. Type: [Malaysia, Sabah] Mt Kinabalu, Paka Cave, *Topping 1665* (lectotype MICH1190874!; designated by Parris, 1990; isotypes BM!, US!). This species occurs in Malaysia.

Devolia Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Ralf Knapp, ***gen. nov.*** Type: *D. orientalis* (T.C.Hsu) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Ralf Knapp ≡ *Oreogrammitis orientalis* T.C.Hsu, Ferns Fern Allies Taiwan Second Suppl. 44. 2017. (Fig. 3).

Etymology—In honor of the late professor Charles E. DeVol (1903–1989) based at NTU for his contributions to oriental botany, especially to the Flora of Taiwan. He was one of the five committee members of Flora of Taiwan and a specialist of pteridophytes.

Diagnosis—*Devolia* differs from other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, not articulated to rhizome, rhizome scales glabrous or with an apical seta, concolorous, stipes absent or very short, fronds not articulated to rhizome, laminae simple, without sclerotic margin, setae present, branched

hairs with setae as branches present, veins simple, vein endings with hydathodes present on adaxial surface of lamina, sporangia glabrous.

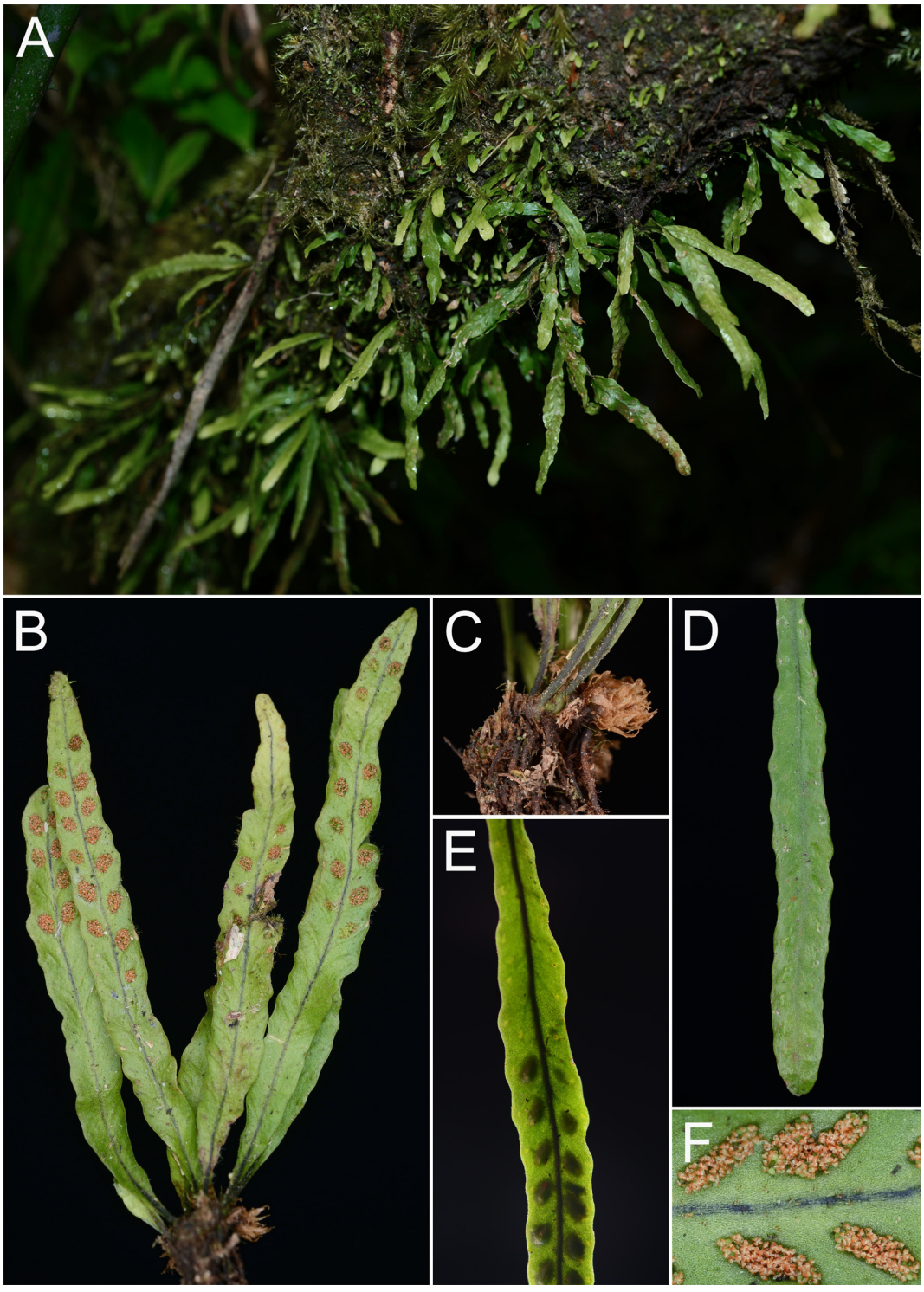

FIGURE 4. *Glabrigrammitis nuda* (Tagawa) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Parris.—A. Habit and habitat.—B. Habit.—C. Lower portion of plant showing rhizome.—D. Adaxial view of sterile lamina.—E. Adaxial view of portion of fertile lamina.—F. Abaxial view of portion of lamina showing sori (photo credit: Ralf Knapp).

Description—Rhizome scales medium yellowish-brown. Stipes very short or absent. Laminae oblanceolate-oblong, apex obtuse, base long-attenuate, margin entire; midrib sometimes slightly prominent and concolorous to slightly darker on abaxial surface, not evident or slightly immersed on adaxial surface; veins extending beyond sori, ending with very evident hydathodes, visible in transmitted light. Sori superficial close to or slightly spaced from midrib in apical 1/6 to 1/2 of lamina, 1–9 in each row, one row each side of midrib. Lamina hairs pale yellowish brown,

setae frequent on all parts of lamina, slightly denser at margin and around sori; forked hairs scattered along abaxial surface of midrib and sometimes occasional on other parts of lamina (Knapp & Hsu, 2017).

Taxonomy—Currently only one species is known from East Asia.

Devolia orientalis (T.C.Hsu) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Ralf Knapp, ***comb. nov.*** Basionym: *Oreogrammitis orientalis* T.C.Hsu, Ferns Fern Allies Taiwan Second Suppl. 44. 2017. Type: China, Guangxi Zhuang Autonomous Region, Jinxiu Yao Autonomous County, Mt. Shengtang (ShengTangShan), 1800–1900 m, 2 April 2013, *T.C.Hsu 6455* (holotype TAIF; isotypes AK, IBK, TAIF, TNM). This species occurs in Taiwan Island, Mainland China (Guangxi), and Japan (Knapp & Hsu, 2017).

Glabrigrammitis Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Parris, ***gen. nov.*** Type: *G. subevenosa* (Baker) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Parris ≡ *Polypodium subevenosum* Baker, Syn. Fil. (Hooker & Baker) 320.1867 (Fig. 4).

Etymology—Latin *glabri-*, glabrous, and *Grammitis*, a genus of ferns, referring to the glabrous sporangia in comparison with the setose sporangia in the most similar genus, *Oreogrammitis*.

Diagnosis—*Glabrigrammitis* differs from other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, rhizome scales glabrous, concolorous, stipes absent or very short, fronds not articulated to rhizome, laminae simple, without sclerotic margin, setae present, branched hairs with setae as branches present, hairs pale, veins simple or 1-branched, vein endings with hydathodes present on adaxial surface of lamina, sometimes with a white deposit, sporangia glabrous.

Glabrigrammitis is similar to *Oreogrammitis* but differs in having glabrous, rather than setose sporangia. *Glabrigrammitis* is particularly similar to *O. adspersa*, but *Glabrigrammitis* has glabrous sporangia and always has a white deposit on the hydathodes, while the latter has setose sporangia and sometimes has a white deposit on the hydathodes (Parris, 2013). *Glabrigrammitis* differs from nearly all species of *Oreogrammitis* in having branched hairs with setae as branches.

Description—Rhizomes short creeping. Stipes sometimes with hairs. Laminae linear to linear-oblanceolate, obtuse to acute at apex, margin entire or undulate. lateral veins visible or not transmitted light. Sori circular to elongate, superficial or sunken in lamina, in one row each side of midrib, receptacles sometimes prominent on adaxial surface of lamina.

Taxonomy—*Oreogrammitis subevenosa* was formerly regarded as a synonym of *O. adspersa* (Copeland 1952, Parris 1983, 2007, 2010) but was later separated from it by Parris (2013). Here we recognize two species in *Glabrigrammitis*. *Glabrigrammitis nuda* is distinguished from *G. subevenosa* by broadly elliptic to elliptic sunken sori versus circular to broadly elliptic superficial sori. The former is endemic to Taiwan Island; the latter is in Thailand, Vietnam, Peninsular Malaysia, Java, Borneo, Philippines, Maluku, New Guinea, and Solomon Islands.

Glabrigrammitis nuda (Tagawa) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Parris, ***comb. nov.*** Basionym: *Grammitis nuda* Tagawa, Acta Phytotax. Geobot. 10(4): 284. 1941. Type: Formosa (Taiwan), Takaio, between Daizyurin and Taito border, Tyosyo-gun, c. 1000 m, 22 January 1939, *Tagawa 2092* (holotype KYO!) ≡ *Oreogrammitis nuda* (Tagawa) Parris, Gard. Bull. Singapore 58(2): 264, 2007. This species is endemic to Taiwan Island.

Glabrigrammitis subevenosa (Baker) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Parris, ***comb. nov.*** Basionym: *Polypodium subevenosum* Baker, Syn. Filic. (Hooker & Baker) 320. 1867. Type: [Malaysia] Penang, *Mactier s.n.* (holotype K001044343!; isotypes E00195211!, 00195212!) ≡ *Grammitis subevenosa* (Baker) C.Chr. & Tardieu, Notul. Syst. (Paris) 8: 179. 1939 ≡ *Oreogrammitis subevenosa* (Baker) Parris, Fern Gaz. 19(6): 207. 2013 = *Grammitis sessilifolia* J.Sm., Hist. Filic. 181. 1875, *nom. nov. pro Polypodium sessilifolium* Hook., Sp. Filic. 4: 168. 1863 *non* Liebm. 1849. Type [Malaysia] Malacca, *Cuming 382* (lectotype K000784941!; **designated here** by Parris to replace *Cuming 222* K000784942!, selected as lectotype by Parris, 1983; the latter is the specimen illustrated by Hooker, tab. CCLXXII A, but is not listed as a type) = *P. malaicum* Alderw., Malayan Ferns 577. 1909, *nom. nov. pro P. sessilifolium* Hook. 1863 *non* Liebm. 1849 ≡ *G. malaica* (Alderw.) Tagawa, Acta Phytotax. Geobot. 8: 173. 1939, *nom. superfl. pro G. sessilifolia* J.Sm. = *P. maxwellii* Baker, Bull. Misc. Inform., Kew 1893: 221. 1893. Type: Borneo, Sarawak, Mt Gading, 1891, *Hose 296* (holotype K000547579!; isotypes E00194230!, SAR! both 1892, but labelled as type by Hose) ≡ *G. maxwellii* (Baker) Parris, Fern Gaz. 12(2): 118. 1980. This species occurs in Southeast Asia, Malesia, and Solomon Islands.

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