BIODIVERSITAS
Volume 27, Number 2, February 2026
Pages: 21

ISSN: 1412-033X
E-ISSN: 2085-4722
https://doi.org/10.13057/biodiv/d270239

Taxonomic reassessment of the *Selaginella* flora of Java, Indonesia

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Manuscript received: 14 June 2025. Revision accepted: 28 February 2026.

Abstract. *Setyawan AD, Chikmawati T, Miftahudin, Sutarno, Sugiyarto, Sunarto. 2026. Taxonomic reassessment of the* Selaginella *flora of Java, Indonesia. Biodiversitas 27 (2): d270239. https://doi.org/10.13057/biodiv/d270239. Selaginella* Beauv. is one of the most taxonomically complex lycophyte genera in tropical Asia, and species delimitation in Java has long been complicated by extensive morphological variation, nomenclatural inconsistency, and contrasting taxonomic interpretations. This study provides a comprehensive floristic and taxonomic reassessment of *Selaginella* in Java based on 1,962 occurrence records from field surveys and herbarium collections. Species diversity, distribution patterns, and taxonomic relationships were evaluated using comparative morphology, ecological evidence, herbarium examination, and contemporary nomenclatural standardization. A total of 21 species are recognized, including 19 native taxa and two introduced or naturalized species (*S. kraussiana* and *S. uncinata*). Updated diagnostic descriptions and identification keys are provided, and several problematic taxa are reassessed. *Selaginella ascendens* and *S. springiana* are interpreted within the *S. intermedia* complex, whereas *S. caudata* and *S. caulescens* are treated within the *S. plana* and *S. involvens* complexes, respectively. Several vegetative characters traditionally used for species delimitation, including branch flattening, foliage density, and leaf overlap, were found to be highly variable and environmentally responsive, whereas stem pubescence, aristate leaf apices, and certain growth-form characteristics remain more reliable for identification. Floristic comparisons indicate strong affinities between the Javan *Selaginella* flora and other regions of Sundaland, particularly Sumatra and Peninsular Malaysia, together with secondary connections to Wallacea and the broader tropical and subtropical regions of Asia. The study provides an updated checklist, identification framework, and taxonomic baseline for future ecological, biogeographical, and evolutionary research on Asian *Selaginella*.

Keywords: Ecological association, Java, Malesia, taxonomy, tropical Asia

INTRODUCTION

Selaginella Beauv. is one of the most diverse and taxonomically complex lycophyte genera in tropical Asia, comprising several hundred species distributed from humid lowland forests to montane ecosystems (Jermy 1990; Weststrand and Korall 2016). The genus is characterized by heterospory, ligulate microphylls, dichotomous branching, and extensive variation in vegetative morphology, particularly among tropical members of subgenus *Heterophyllum* Hieron. (Jermy 1990; Wong 2010). Southeast Asia represents one of the principal centers of diversity for the genus, with high species richness recorded throughout the Malesian region, including Sumatra, Java, Lesser Sunda Islands, Borneo, Sulawesi, Moluccas (Maluku), Peninsular Malaysia, and the Philippines (Alston 1934b, 1935a,b, 1937, 1940; Wong 1982, 2010). Many species inhabit humid understory environments such as shaded ravines, riparian corridors, volcanic slopes, and montane forests, where environmental heterogeneity strongly influences vegetative architecture and foliage organization.

Java occupies an important biogeographic position within Malesia (Malay Archipelago or Maritime Southeast Asia), because the island lies near the transitional boundary between Sundaland and Wallacea while also possessing pronounced elevational and climatic gradients within a relatively limited area (Steenis 1972; Whitten et al. 1996). Unlike Borneo and Sumatra, which still retain extensive humid lowland forests, Java is dominated by volcanic mountains, monsoonal lowlands, fragmented montane forests, agricultural landscapes, and long-disturbed ecosystems shaped by centuries of human activity (Whitten et al. 1996; MacKinnon et al. 1997; Whitten and Damanik 2012). These environmental contrasts create diverse ecological conditions that may promote morphological plasticity and microhabitat differentiation in *Selaginella*. Consequently, Java provides an important setting for evaluating species boundaries, ecological variation, and floristic relationships within tropical Asian *Selaginella*.

Taxonomic studies of *Selaginella* in Java have a long historical association with tropical pteridophyte systematics in Malesia. The first comprehensive treatment was provided by Alston (1935b) in *The Selaginellae of the Malay Islands. I. Java and the Lesser Sunda Islands*, which established the principal framework for subsequent interpretations of Javan taxa using vegetative characters such as branching organization, anisophylly, leaf morphology, ciliation, and strobilus structure. Later revisions from Sumatra (Alston 1937), Sulawesi and Moluccas (Alston 1940), Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), and the Philippines (Alston 1935a), expanded comparative understanding of Malesian *Selaginella* diversity. Additional studies from Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), China (Alston 1934a; Zhang et al. 2013), Hong Kong (Dahlen 1988), Taiwan (Tagawa 1973; Tsai and Shieh 1994), and the Ryukyu, Japan (Tagawa 1963), and further improved knowledge of Asian species variation and

regional distribution patterns.

In Java, numerous studies on the diversity of *Selaginella* have been conducted, but most focused mainly on floristic inventories and regional distribution rather than comprehensive taxonomic reassessment. Previous investigations include studies in Banten (Setyawan 2015a), West Java (Harli 2013), Central Java (Panjaitan 2013), Yogyakarta (Setyawan et al. 2015a), southern West Java (Setyawan 2015b), southern Central Java (Setyawan 2012; Setyawan et al. 2016), Mount Merapi (Setyawan et al. 2012), Mount Lawu (Setyawan et al. 2013), Bromo Tengger Semeru National Park (Setyawan and Sugiyarto 2015), the Dieng Plateau (Setyawan et al. 2015c), and the Sewu karst region (Setyawan et al. 2015b). Although these studies contributed important information regarding species distribution, habitat preference, and morphological variation, they remained largely inventory-based and did not address taxonomic problems such as synonymy evaluation or reassessment of problematic species complexes.

Several studies also indicated that species-level identification in *Selaginella* is often problematic because many taxa exhibit extensive morphological plasticity and overlapping diagnostic characters (Harli 2013; Setyawan et al. 2012, 2013, 2016). Environmental factors such as humidity, canopy openness, substrate condition, and habitat disturbance strongly influence branch flattening, foliage density, leaf overlap, and stem architecture (Wong 2010). Consequently, characters traditionally emphasized in identification keys frequently vary continuously across populations and habitats. Taxonomic uncertainty is particularly evident among several morphologically variable taxa, especially those associated with the *S. plana*, *S. intermedia*, and *S. involvens* groups, where intermediate vegetative forms commonly occur under field conditions. Similar problems have also been documented elsewhere in tropical Asia, where several historically recognized taxa were later reduced to synonymy or interpreted as environmentally induced variants rather than biologically distinct entities (Alston 1935a; Tagawa 1963; Wong 2010).

Despite nearly a century of study since Alston's (1935b) classical treatment, the *Selaginella* flora of Java has not been comprehensively re-evaluated using extensive field observations, herbarium evidence, and contemporary nomenclatural standards. As a result, uncertainties remain regarding species limits, synonymy, and the status of several morphologically variable taxa. An updated floristic and taxonomic synthesis is therefore needed to provide a stable framework for future studies.

Therefore, the present study provides a comprehensive floristic and taxonomic reassessment of *Selaginella* in Java. Specifically, it aims to document the currently accepted flora, provide updated diagnostic descriptions and identification keys, reassess problematic taxa and species complexes, and evaluate floristic relationships within Malesia and tropical Asia. The resulting framework is intended to support future ecological, biogeographical, and evolutionary studies of Javan *Selaginella* (Setyawan et al. 2026).

MATERIALS AND METHODS

Field surveys

Field surveys were conducted across western, central, and eastern Java covering lowland, submontane, and montane ecosystems. Survey localities included humid lowland forests, riparian habitats, volcanic slopes, montane forests, agroforestry systems, plantations, secondary vegetation, roadside embankments, and other disturbed habitats. Observations covered a broad elevational gradient from lowlands to montane areas exceeding 2,000 m asl. (e.g. Setyawan 2012, 2015b, Setyawan et al. 2016), with particular attention to shaded and moisture-rich microhabitats because most tropical *Selaginella* species depend strongly on humid understory conditions (Wong 2010).

Surveys used an exploratory sampling approach to document species occurrence, ecological distribution, and morphological variation across environmental gradients. Sampling sites represented variation in elevation, habitat type, canopy condition, substrate, and land-use systems throughout Java. Ecological information recorded included habitat condition, substrate type, canopy cover, moisture availability, associated vegetation, disturbance level, and microhabitat characteristics. Geographic coordinates and elevational data were recorded in the field, and living populations were photographed in situ to document growth form, branching architecture, foliage arrangement, and ecological context.

Field surveys generated 1,355 occurrence records from 715 localities across Java, forming the principal dataset for taxonomic reassessment and ecological interpretation (Figure 1). Representative specimens were selectively collected for herbarium verification, particularly for morphologically ambiguous taxa and populations showing unusual phenotypic variation. Particular emphasis was placed on documenting variation in morphologically variable taxa, especially *S. plana*, *S. intermedia*, and *S. involvens* groups, which frequently exhibit environmentally influenced vegetative variation and overlapping diagnostic characters across habitats and elevational zones. Comparative ecological observations were also used to assess ecological tendencies among morphologically similar taxa (Tagawa 1963; Wong 2010).

Herbarium studies

A total of 607 herbarium specimens representing 309 localities in Java were examined to evaluate species identity, nomenclatural consistency, distribution patterns, and morphological variability. The herbarium dataset was dominated by collections deposited in Herbarium Bogoriense (BO), which accounted for 559 specimens (>90%), supplemented by specimens from the Natural History Museum, London (BM; 22 specimens), Naturalis Biodiversity Center, Leiden (L; 18 specimens), and a small number of collections from CANB, K, P, S, BGBM, and WRSL.

Historical collections cited in classical taxonomic treatments were re-evaluated whenever available, and field-collected material was compared directly with herbarium specimens and published descriptions. Most specimens contained sufficient locality information to permit retrospective georeferencing, and all occurrence records were verified using specimen labels, historical locality descriptions, and, where available, corresponding GBIF records. Morphological examination focused on branching pattern, growth form, leaf arrangement, anisophylly, leaf margin characteristics, and apex morphology.

Field observations and herbarium records were integrated into a unified dataset comprising 1,962 occurrence records, including 1,355 field observations and

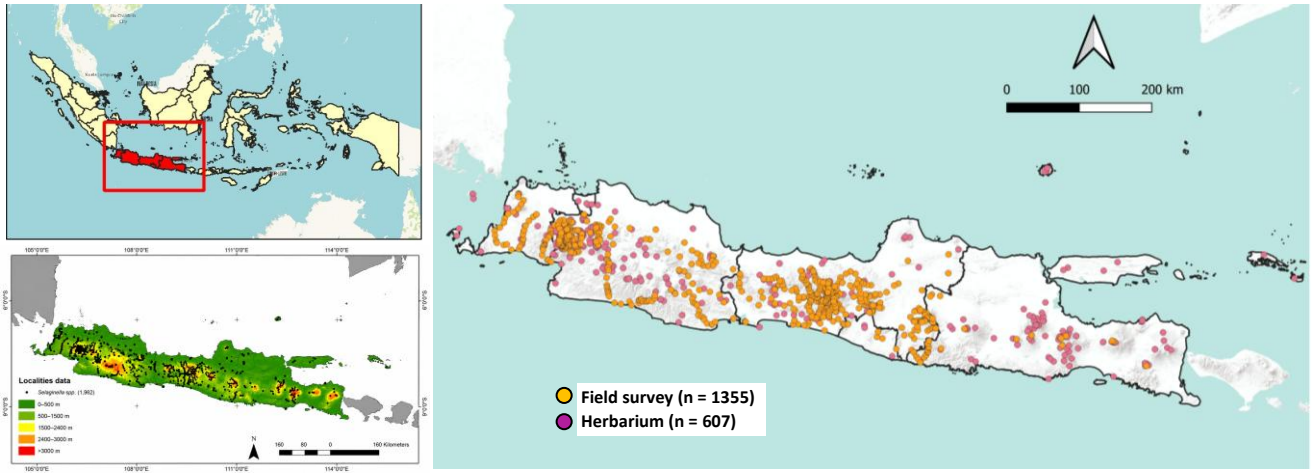

Figure 1. Distribution of *Selaginella* species in Java, Indonesia.

607 herbarium or database records. Particular attention was given to morphologically complex taxa exhibiting extensive overlap in vegetative morphology, especially within the *S. plana*, *S. intermedia*, and *S. involvens* groups. Taxonomic decisions were based on comparative evaluation of field populations, herbarium specimens, original species descriptions, regional floristic treatments, and contemporary nomenclatural resources. Specimen identification was conducted through comparison with authenticated herbarium specimens and major regional taxonomic treatments of *Selaginella*, including works covering Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), China (Alston 1934a; Zhang et al. 2013), the Philippines (Alston 1935a), Java and the Lesser Sunda Islands (Alston 1935b), Sumatra (Alston 1937), Celebes and the Moluccas (Alston 1940), the Ryukyu Islands, Japan (Tagawa 1963), Taiwan (Tagawa 1973; Tsai and Shieh 1994; Chang et al. 2010), Thailand (Tagawa and Iwatsuki 1979), Hong Kong (Dahlen 1988), Queensland, Australia (Andrews 1990), and Vietnam (Pham-Hoang 1991). Recent floristic checklists and inventories were additionally consulted to verify nomenclature and regional species occurrence, including Lindsay et al. (2022) for Singapore and Kalyuzhnyi et al. (2024) for Vietnam. Nomenclature followed Plants of the World Online (POWO 2026), supplemented by Hassler (1994-2026) and relevant regional taxonomic literature. Doubtful records lacking reliable herbarium evidence or contemporary field confirmation from Java were treated conservatively.

Morphological examination

Morphological examination focused on vegetative and reproductive characters traditionally used in *Selaginella* taxonomy, including growth habit, stem orientation, branching pattern, rhizophore position, leaf dimorphism, leaf arrangement, leaf shape, leaf apex morphology, ciliation, serration, axillary leaf morphology, and strobilus structure. Additional observations included sporophyll dimorphism and general spore morphology when fertile material was available.

Comparative observations were conducted using fresh material, herbarium specimens, hand lenses, stereomicroscopy, and high-resolution specimen images. Diagnostic characters were evaluated through direct comparison among specimens from different habitats, elevations, and geographic regions in Java. Multiple individuals from representative populations were examined whenever sufficient material was available, particularly for morphologically variable taxa.

Species delimitation emphasized combinations of relatively stable characters rather than isolated traits. This approach was adopted because many vegetative characters in tropical *Selaginella* vary across environmental conditions (Alston 1935a; Wong 2010). Special attention was given to the major morphological frameworks (species complexes) represented by *S. plana*, *S. intermedia*, and *S. involvens*, with emphasis on variation in growth architecture, branching organization, foliage arrangement, and ecological association.

Taxonomic standardization

Accepted names and synonymy were standardized primarily using Plants of the World Online (POWO, accessed January 2026) and the global checklist compiled by Hassler (2024). Historical names and synonymy from classical literature were cross-checked with contemporary nomenclatural treatments to ensure taxonomic consistency.

Taxonomic interpretation and species recognition were based on integrated evaluation of comparative morphology, ecological observations, herbarium evidence, historical taxonomy, and regional distribution patterns. Taxa showing continuous morphological variation without consistent structural or ecological association were interpreted conservatively to reduce potential taxonomic inflation. Taxa showing relatively stable morphological and ecological differentiation were provisionally retained as separate species when sufficient comparative evidence was available. The present study represents a regional floristic and taxonomic reassessment based primarily on comparative morphology, ecological observations, and herbarium evidence rather than a molecular or quantitative species delimitation study.

RESULTS AND DISCUSSION

A total of 21 accepted *Selaginella* species were recognized from Java based on field observations, herbarium examination, comparative morphology, and ecological interpretation. A comprehensive checklist including synonymy, elevational distribution, examined specimens, and distributional notes for all accepted taxa is provided in Table S1. Representative photographs of living specimens are presented in Figure 2.

Key to the species of *Selaginella* in Java

1a. Plants predominantly creeping or prostrate; stems repeatedly rooting along the substrate 2
1b. Plants ascending, erect, suberect, tufted, scandent, or climbing; stems not repeatedly rooting along the substrate 12
2a. Strobili distinctly flattened or dorsiventral; sporophylls clearly dimorphic 3
2b. Strobili tetragonal, quadrangular, or nearly cylindrical; sporophylls monomorphic or nearly uniform..... 8
3a. Leaf margins distinctly ciliate, especially near the basal portions; marginal cilia clearly visible under a hand lens ……..… 4
3b. Leaf margins denticulate, minutely serrulate, sparsely ciliolate, or nearly entire; conspicuous marginal cilia absent or only weakly developed 5
4a. Lateral leaves broadly ovate and strongly overlapping; branches broad, usually ≥5 mm wide including leaves; foliage dense and compact, forming robust flattened mats .... *Selaginella repanda*
4b. Lateral leaves narrower and less strongly overlapping; branches narrower, usually <5 mm wide including leaves; foliage looser and less compact, forming thinner flattened mats ..... *Selaginella ciliaris*
5a. Foliage bluish-green to metallic iridescent under shaded conditions; ultimate branches fan-shaped and strongly flattened ..... *Selaginella uncinata*
5b. Foliage green, yellowish green, or dark green without metallic iridescence; ultimate branches not fan-shaped or not strongly flattened 6
6a. Lateral leaves distinctly separated from one another on ultimate branches; foliage lax and loosely arranged .... *Selaginella remotifolia*
6b. Lateral leaves overlapping or closely arranged along ultimate branches; foliage compact to moderately dense 7
7a. Branch systems strongly dorsiventral and regularly pinnate; ultimate branches broadly flattened; lateral leaves densely overlapping and forming broad, continuous flattened foliage surfaces ..... *Selaginella plana*
7b. Branch systems weakly dorsiventral to dorsiventral and less regularly pinnate; ultimate branches narrower and less strongly flattened; lateral leaves less densely overlapping and not forming broad, continuous flattened foliage surfaces ..... *Selaginella intermedia*
8a. Stems pubescent or hairy under magnification; branch surfaces bearing conspicuous trichomes or short hairs …….. ..... *Selaginella biformis*
8b. Stems entirely glabrous; branch surfaces lacking conspicuous trichomes or hairs 9
9a. Lateral leaves very densely imbricate, producing compact opaque foliage; stems relatively thick and rigid; branches ascending to suberect and forming compact erect shoots ..... *Selaginella opaca*
9b. Lateral leaves less densely imbricate, producing less compact and non-opaque foliage; stems more slender and flexible; branches creeping, ascending, or irregularly branched, not forming compact erect shoots 10
10a. Median leaves with a conspicuous arista extending well beyond the lamina apex; arista persistent and readily visible under a hand lens ..... *Selaginella aristata*
10b. Median leaves acute to shortly acuminate, without a conspicuous arista extending beyond the lamina apex; leaf apices not terminating in a persistent elongate arista 11
11a. Branches slender and loosely organized; lateral leaves weakly overlapping; foliage lax and open ..... *Selaginella alutacea*
11b. Branches compact and relatively rigid; lateral leaves strongly overlapping; foliage dense and compact ..... ……. *Selaginella rothertii*
12a. Plants scandent or climbing over surrounding vegetation; stems elongate and flexible 13
12b. Plants erect, ascending, suberect, or tufted, but not extensively climbing; stems shorter, stiffer, and self-supporting ……..... 14
13a. Foliage metallic bluish-green or iridescent, especially under shaded conditions; lateral leaves with conspicuously auriculate upper bases; stems extensively scandent and climbing over surrounding vegetation ……..... *Selaginella willdenowii*
13b. Foliage green without metallic iridescence; lateral leaves lacking conspicuous auriculate upper bases or with auricles poorly developed; stems ascending, weakly scandent, or less extensively climbing ..... *Selaginella frondosa*
14a. Plants tufted, erect, or forming compact ascending clumps; stems stiff, compact, and regularly pinnate 15
14b. Plants loosely ascending, irregularly branched, or not forming dense compact clumps; stems less stiff, less compact, and irregularly to loosely pinnate 17
15a. Plants very compact and rigid; branches narrow and densely foliated; lateral leaves strongly imbricate, margins slightly spinulose ……..… *Selaginella subspinulosa*
15b. Plants less compact; branches not densely foliated throughout 16
16a. Leaves tightly imbricate and producing compact foliage; plants forming dense erect clumps; stems stiff and densely branched ..... *Selaginella subalpina*
16b. Leaves less tightly imbricate and producing thinner, less compact foliage; plants forming loose erect to ascending clumps; stems more delicate and less densely branched ..... *Selaginella singalanensis*
17a. Lateral leaves with conspicuous auriculate upper bases; auricles conspicuous and well developed; branches broad, ascending, and relatively coarse; foliage compact and densely arranged ..... *Selaginella involvens*
17b. Lateral leaves lacking conspicuous auriculate upper bases; auricles present but narrow or weakly developed; branches narrower and more delicate; foliage less compact and more loosely arranged 18
18a. Branch systems regularly pinnate and strongly flattened in one plane; ultimate branches forming narrow to broad planar sprays 19
18b. Branch systems irregularly branched, weakly flattened, or somewhat bushy; ultimate branches not forming regular planar sprays 20
19a. Stems stiff and relatively rigid; foliage compact and strongly imbricate; branch systems cypress-like and regularly flattened ..... *Selaginella cupressina*
19b. Stems more slender and flexible; foliage thinner and more loosely arranged; branch systems less compact and not distinctly cypress-like ..... *Selaginella zollingeriana*
20a. Plants forming compact mats; leaves small, densely arranged, and strongly overlapping; branch systems regularly pinnate and relatively uniform …… *Selaginella kraussiana*
20b. Plants loosely ascending or forming lax colonies; leaves larger, less densely arranged, and less strongly overlapping; branch systems less regular and more loosely branched ..... *Selaginella ornata*

A. *S. alutacea*

B. *S. aristata*

C. *S. biformis*

D. *S. ciliaris*

E. *S. cupressina*

F. *S. frondosa*

G. *S. intermedia*

H. *S. involvens*

I. *S. kraussiana*

J. *S. opaca*

K. *S. ornata*

L. *S. plana*

M. *S. remotifolia*

N. *S. repanda*

O. *S. rothertii*

P. *S. singalanensis*

Q. *S. subalpina* **R. *S. uncinata*** **S. *S. willdenowii*** **T. *S. zollingeriana***

Figure 2. Representative photographs of 20 *Selaginella* species recorded in Java, Indonesia: A. *S. alutacea*, B. *S. aristata*, C. *S. biformis*, D. *S. ciliaris*, E. *S. cupressina*, F. *S. frondosa*, G. *S. intermedia*, H. *S. involvens*, I. *S. kraussiana*, J. *S. opaca*, K. *S. ornata*, L. *S. plana*, M. *S. remotifolia*, N. *S. repanda*, O. *S. rothertii*, P. *S. singalanensis*, Q. *S. subalpina*, R. *S. uncinata*, S. *S. willdenowii*, and T. *S. zollingeriana*. Representative photographs of 20 of the 21 accepted *Selaginella* species in Java are presented. *Selaginella subspinulosa* is not illustrated due to the lack of suitable photographic material.

***Selaginella alutacea* Spring (Figure 2.A)**

Selaginella alutacea Spring, *Bull. Acad. Roy. Sci. Bruxelles* 10: 233 (1843). Reported in several regional floristic treatments of Malesia (Alston 1934b, 1935b, 1937; Wong 1982, 2010).

Type. Pulo-Pinang (Penang), Malaysia, Gaudichaud 7 (lectotype P).

Diagnostic characters. Plants creeping to loosely ascending, forming thin and relatively delicate mats on moist substrates. Stems slender, glabrous, 1-2 mm wide including leaves, irregularly branched, and rooting intermittently along creeping portions. Branch systems moderately flattened and loosely pinnate. Lateral leaves ovate-lanceolate to asymmetrically ovate, approximately 1.5-3.0 mm long, thin-textured, green to yellowish green, with margins minutely denticulate and occasionally sparsely ciliolate near the basal portions. Median leaves smaller, ovate, acute to shortly acuminate, usually terminating in a narrow apical tip. Strobili slender, tetragonal, generally 5-15 mm long, with monomorphic sporophylls. The species differs from *S. ciliaris* by its weakly developed marginal ciliation and from *S. intermedia* by its narrower branches, smaller foliage, and more delicate overall habit.

Habitat and distribution. Usually found on moist soil banks, shaded ravines, stream margins, and damp rocky substrates in submontane humid forests. The species is most frequently encountered in protected understory habitats with stable moisture conditions but may also occur along semi-open forest trails, roadside embankments, and secondary vegetation margins. In Java, it has been recorded mainly from western and central regions at approximately 467-903 m elevation. Outside Java, the species is also reported from Sumatra (Alston 1937) and Peninsular Malaysia (Alston 1934b; Wong 2010).

Notes. Field identification may be difficult when sterile material is poorly developed because small individuals can resemble juvenile forms of *S. intermedia*. Nevertheless, *S. alutacea* generally maintains a finer branch architecture and more loosely arranged foliage. Available observations suggest that the species is less frequently encountered in strongly disturbed and exposed habitats than *S. plana* or *S. intermedia*, and populations are more commonly associated with continuously moist submontane microhabitats near streams, shaded slopes, and humid ravines.

Specimens examined: ADS 601, ADS 658, ADS 665, ADS 1191, ADS 1261, ADS 1356, and ADS 1358; Bakh. v.d. Brink 6443 (BO!), Bakh. v.d. Brink 7046 (BO!), Bakh. v.d. Brink 4187 (BO!), C.G.G.J. van Steenis 2739 (BO!), Bakh. v.d. Brink 6468 (BO!), Bakh. v.d. Brink 7768 (BO!), Bakh. v.d. Brink 5213 (BO!), and M.A. Donk (BO!).

***Selaginella aristata* Spring (Figure 2.B)**

Selaginella aristata Spring, *Bull. Acad. Roy. Sci. Bruxelles* 10: 232 (1843). Recognized in several floristic accounts of Malesia (Alston 1935a,b, 1937) and East Asia (Tagawa 1973; Chang et al. 2010).

Type. Philippines, Manila, H. Cuming 1996 (syntype P; iso-syntypes E, LE).

Habitat and distribution. Primarily associated with humid lowland and submontane environments, especially along shaded ravines, moist volcanic slopes, rocky stream banks, irrigation embankments, and moist roadside slopes. The species is frequently encountered in humid semi-open habitats with persistent moisture, including agricultural terraces, forest margins, and riparian embankments, although some populations also occur in more protected understory habitats. In Java, it has been recorded at elevations of approximately 115–1369 m a.s.l., indicating a broad distribution across lowland and submontane habitats, particularly in western and central Java. Additional occurrences are also reported from other parts of Malesia such as Sumatra (Alston 1937) and the Philippines (Alston 1935a), as well as Taiwan (Tagawa 1973; Chang et al. 2010).

Habitat and distribution. Primarily associated with humid lowland to montane environments, especially along shaded ravines, moist volcanic slopes, rocky stream banks,

irrigation embankments, and moist roadside slopes. The species is frequently encountered in humid semi-open habitats with persistent moisture, including agricultural terraces, forest margins, and riparian embankments, although some populations also occur in more protected understory habitats. In Java, it has been recorded from approximately 115-1369 m elevation and is distributed mainly in western and central montane regions. Additional occurrences are also reported from other parts of Malesia such as Sumatra (Alston 1937) and the Philippines (Alston 1935a), as well as Taiwan (Tagawa 1973; Chang et al. 2010).

Notes. Among Javan species, *S. aristata* is relatively distinctive because of its persistent aristate median leaves, which remain visible even in smaller or sterile specimens. Some montane populations may superficially resemble slender forms of *S. intermedia*, particularly under shaded conditions, but *S. intermedia* generally lacks the consistently elongated arista characteristic of *S. aristata*. Although the species is most commonly associated with humid submontane and montane habitats, several populations also occur in semi-open disturbed environments with stable moisture availability, including roadside embankments, irrigation margins, and agricultural slopes.

Specimens examined: ADS 69, ADS 196, ADS 219, ADS 272, ADS 317, ADS 358, ADS 398, ADS 521, ADS 579, ADS 704; Bakh. v.d. Brink 2951 (BO!), C.A. Backer & O. Posthumus 572 (BO!), C.G.G.J. van Steenis 1702 (BO!), E. Jacobson (BO!), Rant (BO!), van Leeuwen (BO!), and Verdoorn (BO!).

***Selaginella biformis* A.Braun ex Kuhn. (Figure 2.C)**

Selaginella biformis A.Braun ex Kuhn. *Forschungsreise S.M.S. Gazelle iv. Teil. Botanik (Algen)* 6: 17 (1889). Basionym: *Lycopodium biforme* Hook. & Grev. Frequently treated in regional floristic revisions of Malesia (Alston 1935a,b), mainland Southeast Asia (Tagawa and Iwatsuki 1979; Pham-Hoang 1991; Kalyuzhnyi et al. 2024), and East Asia (Tagawa 1963; Dahlen 1988; Zhang et al. 2013)

Type. Philippines**,** H. Cuming 2016 (lectotype B; isolectotypes BM, E, P).

Diagnostic characters. Plants creeping to ascending, moderately robust, forming spreading colonies or loose mats on moist substrates. Stems distinctly pubescent to sparsely hairy, a feature that readily separates the species from most other Javan *Selaginella*, which are predominantly glabrous. Branch systems flattened, irregularly pinnate, and relatively broad, usually 2-5 mm wide including leaves. Lateral leaves ovate-lanceolate to asymmetrically ovate, approximately 2-4 mm long, green to dark green, with margins denticulate to ciliolate, especially near the basal portions. Median leaves smaller, ovate, acute to shortly aristate, more closely appressed to the stem. Strobili tetragonal, relatively compact, generally 8-18 mm long, with monomorphic sporophylls. The combination of pubescent stems, broad flattened branches, and ciliolate leaf margins distinguishes the species from glabrous taxa such as *S. intermedia* and *S. plana*.

Habitat and distribution. The species occurs mainly in humid submontane habitats, particularly along stream margins, damp forest trails, shaded ravines, and secondary forest edges. It is frequently associated with moist soils and partially open understory conditions rather than deeply shaded forest interiors. In Java, *S. biformis* has been recorded at approximately 748-798 m elevation and appears locally distributed in humid upland environments. Outside Java, the species is also distributed in other parts of Malesia, i.e. the Philippines (Alston 1935a); as well as Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), China (Zhang et al. 2013), Hong Kong (Dahlen 1988); and the Ryukyu, Japan (Tagawa 1963).

Notes. Stem indumentum remains one of the most reliable characters for identifying *S. biformis*, even in incomplete or sterile material. Although branch density and foliage size may vary among populations, the presence of pubescence consistently separates the species from morphologically similar creeping taxa. Some robust specimens may resemble broad forms of *S. intermedia*, but the latter lacks the characteristic hairy stems and generally possesses smoother foliage surfaces. Available records from Java indicate that the species is primarily associated with humid submontane habitats with persistent moisture and partially open microhabitats rather than broad lowland distribution.

Specimens examined: ADS 609, ADS 661, ADS 1229; A.H.G. Alston 12675 (BO!), Bakh. v.d. Brink 802 (BO!), Bakh. v.d. Brink 1453 (BO!), Bakh. v.d. Brink 5991 (BO!), Bakh. v.d. Brink 6623 (BO!), Bakh. v.d. Brink 6625 (BO!), Bakh. v.d. Brink s.n. (BO!), C.A. Backer 22463 (BO!), C.A. Backer 22864 (BO!), and W.F. Winckel 1764 (BO!).

***Selaginella ciliaris* (Retz.) Spring (Figure 2.D)**

Selaginella ciliaris (Retz.) Spring, *Bull. Acad. Roy. Sci. Bruxelles* 2: 95 (1843). =Basionym: *Lycopodium ciliare* Retz. Included in numerous floristic treatments of Malesia (Alston 1934b, 1935a,b, 1937, 1940; Lindsay et al. 2022; Wong 1982, 2010), mainland Southeast Asia (Tagawa and Iwatsuki 1979; Pham-Hoang 1991; Kalyuzhnyi et al. 2024), East Asia (Tagawa 1973; Dahlen 1988; Tsai and Shieh 1994; Chang et al. 2010; Zhang et al. 2013) and tropical Australia (Jones and Clemesha 1981; Andrews 1990).

Type. Eastern Ceylon (Sri Lanka), König s.n. (lectotype LD; isolectotype K).

Diagnostic characters. Plants creeping and mat-forming, relatively delicate, commonly rooting along prostrate stems. Branch systems flattened and regularly pinnate, usually 2-4 mm wide including leaves. Stems slender, glabrous, and moderately branched. Lateral leaves ovate to ovate-lanceolate, approximately 1.5-3.5 mm long, distinctly ciliate along the margins, particularly near the basal portions; marginal cilia generally visible under hand lens and representing one of the most reliable diagnostic features of the species. Median leaves smaller, ovate, acute to shortly acuminate, with denticulate to sparsely ciliolate margins. Strobili flattened to weakly quadrangular, slender, usually 5-12 mm long. The species differs from *S. repanda*

by its narrower lateral leaves, finer branch systems, and more delicate creeping habit.

Habitat and distribution. Commonly encountered in moist lowland and submontane environments, including stream banks, damp soil slopes, open ravines, wet forest trails, and disturbed secondary habitats. The species frequently colonizes exposed moist soils following disturbance and may develop extensive ground cover in partially open vegetation. In Java, it occurs over a broad elevational range of approximately 3-1,412 m a.s.l., reflecting its wide ecological tolerance and ability to occupy both natural and disturbed habitats. It is widely distributed throughout the island and is also broadly recorded across Malesia, including Sumatra (Alston 1937), Sulawesi (Alston 1940), Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), Singapore (Lindsay et al. 2022), and the Philippines (Alston 1935b), as well as Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), China (Zhang et al. 2013), Taiwan (Tagawa 1973; Tsai and Shieh 1994; Chang et al. 2010), Hong Kong (Dahlen 1988), and Queensland, Australia (Andrews 1990).

Notes. Among creeping Javan taxa, *S. ciliaris* is most easily recognized by its conspicuously ciliate leaf margins combined with its delicate mat-forming growth. Small specimens may occasionally resemble juvenile forms of *S. repanda*, but *S. repanda* generally possesses broader foliage, thicker branches, and a more robust overall appearance. The species also appears more tolerant of periodically disturbed habitats than several forest-restricted creeping taxa.

Specimens examined: ADS 46, ADS 202, ADS 258, ADS 342, ADS 430, ADS 529, ADS 688, ADS 845, ADS 1059, ADS 1456; Bakh. v.d. Brink 1172 (BO!), Bakh. v.d. Brink 6318 (BO!), Banjoemas 2436 (BO!), C.A. Backer 33511 (BO!), C.A. Wisse 804 (BO!), C.G.G.J. van Steenis 6688 (BO!), Junghuhn 253 (BO!), Klei 98 (BO!), Koorders 31443 (BO!), and R. Brinkman 75 (BO!).

***Selaginella cupressina* (Willd.) Spring (Figure 2.E)**

Selaginella cupressina (Willd.) Spring, *Flora* 21: 211 (1838). Recognized in regional floristic treatments of Malesia (Alston 1934b, 1935a,b, 1940; Wong 2010).

Type. Moluccas (Maluku Islands), Indonesia, s. coll. s.n. (holotype B).

Diagnostic characters. Plants erect to ascending, relatively robust, forming compact tufted clumps with a distinctly cypress-like appearance. Stems stiff, glabrous, densely branched, and usually 3-6 mm wide including leaves. Branch systems narrow, compact, and regularly pinnate to subpinnate, producing a dense vertical architecture unlike the flattened creeping habit of many lowland taxa. Lateral leaves strongly imbricate, ovate-lanceolate, approximately 2-4 mm long, acute, green to dark green, with margins entire to minutely denticulate. Median leaves smaller, closely appressed, acute to shortly acuminate. Strobili tetragonal, compact, terminal on ultimate branches, generally 10-20 mm long. The species is readily distinguished by its erect tufted growth, rigid stems, and densely compact branching pattern resembling small conifer shoots.

Habitat and distribution. The species occurs mainly in humid submontane to montane environments, particularly on volcanic slopes, rocky ridges, mossy forest margins, and other humid upland habitats. *Selaginella cupressina* is commonly associated with well-drained volcanic substrates, exposed montane slopes, humid ravines, and semi-open upland terrain, although some populations may also occur in shaded forest margins with persistent humidity. In Java, the species is recorded mainly from montane regions and is also reported from several other parts of Malesia, including Sulawesi and adjacent islands (Alston 1940), Peninsular Malaysia (Alston 1934b) and the Philippines (1935a).

Notes. Compared with morphologically variable creeping species such as *S. plana* or *S. intermedia*, *S. cupressina* shows relatively stable structural morphology across habitats. Compact individuals occurring on exposed volcanic slopes may appear reduced in size, but the characteristic erect cypress-like architecture generally remains consistent. The species may occasionally resemble compact forms of *S. rothertii*, although *S. rothertii* generally possesses flatter branch systems and less rigid foliage organization. Because confirmed collections from Java remain relatively limited, additional herbarium reassessment and field observations may help clarify the full range of morphological variation of the species in montane habitats.

Specimens examined: Tjiming Hs. 2000 (BO!).

***Selaginella frondosa* Warb. (Figure 2.F)**

Selaginella frondosa Warb., *Monsunia* 1: 105, 117 (1900). Treated in several regional floristic accounts of Malesia (Alston 1934b, 1935a,b, 1940; Wong 1982, 2010) and mainland Southeast Asia (Pham-Hoang 1991; Kalyuzhnyi et al. 2024).

Type. Sumatra, Indonesia, Forbes 1688 (syntype P).

Diagnostic characters. Plants ascending to weakly scandent, moderately robust, often forming loosely spreading colonies in humid forest habitats. Stems glabrous, relatively thick, and irregularly branched, usually 3-7 mm wide including leaves. Branch systems broad, flattened, and fern-like in appearance. Lateral leaves ovate-lanceolate to oblong-lanceolate, asymmetrical, approximately 3-6 mm long, green to dark green, with margins denticulate to sparsely ciliolate near the basal portions. Median leaves smaller, ovate, acute to shortly acuminate, more closely appressed to the stem. Axillary leaves relatively broad and frequently overlapping adjacent branches. Strobili tetragonal, moderately robust, generally 10-25 mm long. The species differs from *S. willdenowii* by its non-iridescent foliage, broader fern-like branch systems, and shorter ascending stems that are less extensively climbing.

Habitat and distribution. The species is primarily associated with humid lowland and submontane forests, particularly along ravines, moist slopes, stream margins, shaded forest edges, and humid riparian corridors. It commonly occurs in sheltered understory habitats with

stable moisture conditions and is less frequent in highly disturbed or exposed environments. In Java, it has been recorded at elevations of approximately 107-262 m a.s.l., indicating a strong association with humid lowland habitats. *S. frondosa* has been recorded from several regions across the island and is also known from other parts of Malesia, including Sulawesi (Alston 1940), the Philippines (Alston 1935a), and Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), as well as Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024).

Notes. Among larger Javan taxa, *S. frondosa* is recognizable by its broad flattened branches and frond-like appearance. Sterile specimens may occasionally resemble juvenile or weakly developed forms of *S. willdenowii*, particularly in shaded habitats, but *S. willdenowii* generally develops more elongate scandent stems and characteristic metallic bluish-green iridescence. Compared with *S. plana*, the present species possesses broader foliage organization and a more ascending growth habit rather than extensive creeping mats. Available observations also suggest stronger association with persistently humid forest microhabitats than with semi-open disturbed environments.

Specimens examined: ADS 112, ADS 450, ADS 482, and ADS 1469.

***Selaginella intermedia* (Blume) Spring (Figure 2.G)**

Selaginella intermedia (Blume) Spring, *Bull. Acad. Roy. Sci. Bruxelles* 10: 144 (1843). =Basionym: *Lycopodium intermedium* Blume. Widely treated in floristic revisions of Malesia (Alston 1934b, 1935a,b, 1937, 1940; Lindsay et al. 2022; Wong 1982, 2010), mainland Southeast Asia (Tagawa and Iwatsuki 1979; Pham-Hoang 1991; Kalyuzhnyi et al. 2024), and East Asia (Chang et al. 2010).

Type. Java, Indonesia, Blume s.n. (lectotype L; isolectotype P).

Diagnostic characters. Plants creeping to ascending, highly variable in overall morphology, forming loose mats or spreading colonies across moist substrates. Stems glabrous, flattened, irregularly pinnate to broadly flabellate, usually 3-8 mm wide including leaves. Branch systems moderately broad but generally less regularly flattened than in *S. plana*. Lateral leaves ovate-lanceolate to asymmetrically elliptic, approximately 2-5 mm long, green to dark green, overlapping to moderately spaced, with margins denticulate or sparsely ciliolate near the basal portions. Median leaves ovate, acute to acuminate, lacking the conspicuous elongated arista characteristic of *S. aristata*. Strobili flattened to weakly quadrangular, slender, generally 8-20 mm long, with dimorphic to weakly dimorphic sporophylls. The species differs from *S. plana* by its less regularly organized branch systems and generally narrower foliage arrangement, while differing from *S. alutacea* by its broader branches and more robust habit.

Habitat and distribution. This species occupies a broad ecological range extending from lowland forests to montane habitats. It commonly occurs along humid ravines, moist stream banks, volcanic slopes, shaded forest trails, riparian embankments, secondary vegetation, and other humid microhabitats with persistent moisture. Compared with several disturbance-tolerant creeping taxa, *S. intermedia* appears more frequently associated with shaded understory habitats and humid ravine systems, although some populations may also persist in partially disturbed environments. In Java, it has been recorded at elevations of approximately 244-1,131 m a.s.l., indicating a broad distribution across lowland and submontane environments. The species is widely distributed throughout Java and broadly recorded across tropical and subtropical Asia and Malesia, including Sumatra (Alston 1937), Sulawesi (Alston 1940), Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), Singapore (Lindsay et al. 2022), and the Philippines (Alston 1935a), as well as Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), and Taiwan (Chang et al. 2010).

Notes. *Selaginella intermedia* represents one of the most taxonomically problematic species in the Javan flora because its morphology overlaps extensively with *S. plana* and several related creeping taxa. Intermediate forms are frequently encountered in humid forest habitats, particularly where environmental gradients influence branch flattening and leaf overlap. In comparison with *S. plana*, the present species usually possesses less rigid branch organization, narrower foliage arrangement, and stronger association with shaded humid microhabitats. Robust specimens may also resemble *S. opaca*, although *S. opaca* generally develops darker opaque foliage and more densely imbricate lateral leaves. Because many traditionally used vegetative characters vary continuously, ecological tendency, microhabitat association, and overall branch architecture remain important supplementary criteria for identification.

Specimens examined: ADS 123, ADS 441, ADS 590, ADS 1104, ADS 1195, ADS 1237, ADS 1255, ADS 1349, ADS 1371, and ADS 1389; Bakh. v.d. Brink 2638 (BO!), Bakh. v.d. Brink 6869 (BO!), C.A. Backer 9364 (BO!), C.A. Backer 9936 (BO!), C.G.G.J. van Steenis s.n. (BO!), Docters van Leeuwen 453 (BO!), J.J. Afriastini 1 (BO!), O. Posthumus 1615 (BO!), W.S. Hoover et al. 31332 (BO!), and W.S. Hoover et al. 32272 (BO!).

***Selaginella involvens* (Sw.) Spring (Figure 2.H)**

Selaginella involvens (Sw.) Spring, *Bull. Acad. Roy. Sci. Bruxelles* 10: 136 (1843). =Basionym: *Lycopodium involvens* Sw. Discussed extensively in floristic and nomenclatural studies across Malesia (Alston 1934b, 1935a,b, 1937, 1940; Wong 1982, 2010), mainland Southeast Asia (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), East Asia (Tagawa 1963, 1973; Tsai and Shieh 1994; Chang et al. 2010; Zhang et al. 2013), and tropical Australia (Andrews 1990).

Type. Japan, ex herb. Swartz / Thunberg s.n. (lectotype B).

Diagnostic characters. Plants ascending to erect, moderately robust, usually forming loose clumps rather than extensive creeping mats. Stems glabrous, relatively thick, and irregularly pinnate to broadly flabellate, generally 4-9 mm wide including leaves. Branch systems flattened but less regularly organized than in *S. plana*. Lateral leaves ovate to ovate-lanceolate, asymmetrical,

approximately 3-6 mm long, green to dark green, with margins entire to minutely denticulate; basal portions frequently slightly auriculate, especially on larger branches. Median leaves ovate, acute to shortly acuminate, closely appressed to the stem. Strobili tetragonal, compact, usually 10-25 mm long. The species is characterized by its robust ascending habit, relatively broad branch systems, partially auriculate leaf bases, and foliage that becomes slightly involute when dry.

Habitat and distribution. *Selaginella involvens* occurs primarily in humid submontane forests, particularly along shaded ravines, moist volcanic slopes, riparian forest margins, and rocky upland habitats with relatively stable atmospheric humidity. Several populations, however, have also been recorded at lower elevations in humid forest environments. Compared with *S. plana* and *S. intermedia*, *S. involvens* shows a stronger association with submontane habitats and is less frequently encountered in highly disturbed lowland areas. In Java, the species has been recorded at elevations of approximately 351–1493 m a.s.l., indicating a broad distribution across lowland and submontane environments, with most records concentrated in upland forest habitats. The species is also widely distributed throughout Malesia, including Sumatra (Alston 1937), Sulawesi and the Moluccas (Alston 1940), the Philippines (Alston 1935a), and Peninsular Malaysia (Alston 1934b; Wong 1982, 2010). Beyond Malesia, it is also recorded from tropical and subtropical Asia, including Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), China (Zhang et al. 2013), Taiwan (Tagawa 1973; Tsai and Shieh 1994; Chang et al. 2010), and the Ryukyu Islands of Japan (Tagawa 1963), as well as tropical Queensland, Australia (Andrews 1990).

Notes. The circumscription of *S. involvens* has historically been problematic because of long-standing confusion with *S. tamariscina* and several morphologically similar Asian taxa (Tagawa 1963). Within Java, some montane specimens may resemble robust forms of *S. intermedia*, but *S. involvens* generally develops thicker stems, broader ascending branches, and more compact foliage organization. In comparison with *S. plana*, the species is usually less regularly pinnate and more erect in overall habit. The slightly auriculate leaf bases and involute appearance of dried foliage are also useful supplementary characters for identification. Field observations further suggest that the species is more consistently associated with persistently humid ravines and volcanic upland habitats than with semi-open disturbed environments.

Specimens examined: ADS 17, ADS 97, ADS 290, ADS 420, ADS 517, ADS 627, ADS 989, ADS 1096, ADS 1139, ADS 1443; A.H.G. Adelbert 138 (BO!), C.A. Backer & O. Posthumus 15 (BO!), C.G.G.J. van Steenis 11187 (BO!), C.G.G.J. van Steenis 12656 (BO!), J. Viets 30 (BO!), J.D. Dangelo 97 (BO!), Koorders 19843b (BO!), Luadil 584 (BO!), P. Buwalda 7519 (BO!), V.M.A. Begemi 16 (BO!), and W.S. Hoover et al. 32127 (BO!).

***Selaginella kraussiana* (Kunze) A.Braun (Figure 2.I)**

Selaginella kraussiana (Kunze) A.Braun, *Index Sem. Hort. Bot. Berol.* 1859: 22 (1860). =Basionym: *Lycopodium kraussianum* Kunze. Commonly recognized as an introduced or naturalized species in tropical regions outside its native African range (Esler 1987; Andrews 1990; Zhang et al. 2013; Middleton et al. 2019; Anderson 2025).

Type. Port Natal (KwaZulu-Natal), South Africa, Gueinzius s.n. (lectotype K; isolectotype P).

Diagnostic characters. Plants creeping and densely mat-forming, relatively delicate, often producing extensive carpets on moist substrates. Stems slender, glabrous, repeatedly branched, and rooting profusely along creeping axes, usually 1-3 mm wide including leaves. Branch systems flattened and regularly pinnate, forming compact foliage mats. Lateral leaves small, ovate to ovate-lanceolate, approximately 1-2.5 mm long, asymmetrical, green to yellowish green, with margins entire to minutely denticulate. Median leaves distinctly smaller, closely appressed, acute to shortly acuminate. Strobili slender, tetragonal, terminal on ultimate branches, generally 5-12 mm long. The species is distinguished by its compact carpet-forming habit, small densely arranged leaves, and vigorous vegetative branching pattern.

Habitat and distribution. In Java, *Selaginella kraussiana* is primarily associated with anthropogenic and semi-disturbed habitats, including botanical gardens, shaded plantations, urban green spaces, moist roadside embankments, secondary vegetation, and cultivated ornamental settings. It commonly occurs in humid environments with persistent soil moisture and partial canopy cover. In Java, the species has been recorded mainly from cultivated and semi-natural habitats ranging from lowland to montane areas, approximately 75-1,500 m a.s.l. (Setyawan et al. 2025). The herbarium specimens examined in the present study was derived from cultivated material growing at approximately 750 m a.s.l. Unlike many native forest species, *S. kraussiana* readily colonizes cultivated and managed habitats and can persist in highly modified landscapes. The species is considered introduced and locally naturalized in Java (Setyawan et al. 2025). Native to southern and eastern Africa, *S. kraussiana* has been widely cultivated as an ornamental groundcover and has subsequently become naturalized in numerous regions outside its native range, including New Zealand (Esler 1987), Singapore (Middleton et al. 2019), Queensland, Australia (Andrews 1990), and China (Zhang et al. 2013). Its introduced distribution now extends across much of Europe, North America, South America, Australia, and New Zealand (Anderson 2025).

Notes. The species spreads efficiently through vegetative fragmentation and stolon-like creeping stems, allowing rapid local expansion in suitable habitats. Small individuals may superficially resemble delicate forms of *S. intermedia* or juvenile *S. plana*, but *S. kraussiana* generally develops more compact mats, smaller foliage, and highly regular pinnate branching. In contrast to most native Javan species, it is strongly associated with ornamental cultivation and human-modified environments, where escaped populations may establish persistent ground cover in moist semi-shaded habitats.

Specimens examined: ADS 163, ADS 466.

***Selaginella opaca* Warb. (Figure 2.J)**

Selaginella opaca Warb., *Monsunia* 1: 108, 122 (1900). Recognized in regional floristic treatments of Malesia (Alston 1935a,b, 1937, 1940).

Type. Sulawesi (Celebes), Indonesia, Warburg 15724 (syntype B).

Diagnostic characters. Plants creeping to ascending, moderately robust, usually forming broad mats or loosely spreading colonies on moist forest substrates. Stems glabrous, relatively thick, and strongly flattened, generally 4-9 mm wide including leaves. Branch systems broad and regularly pinnate, often more compact than in *S. intermedia*. Lateral leaves ovate to broadly ovate-lanceolate, approximately 3-6 mm long, densely arranged, asymmetrical, dark green, with margins entire to minutely denticulate. Median leaves smaller, ovate, acute to shortly acuminate, closely appressed to the stem. Strobili flattened to weakly quadrangular, relatively robust, usually 10-22 mm long. The species is distinguished by its opaque dark-green foliage, relatively thick stems, and densely imbricate lateral leaves that produce a compact flattened appearance.

Habitat and distribution. The species occurs mainly in humid submontane to montane forests, especially on moist forest floors, shaded ravines, volcanic slopes, and stream margins with relatively stable moisture conditions. Several populations also extend into lower elevation humid forests, although the species is more commonly associated with humid upland habitats and sheltered understory environments. In Java, *S. opaca* has been recorded from approximately 935-2124 m elevation and appears most frequent in humid montane regions with persistent atmospheric moisture. The species is also reported from other parts of Malesia, including Sumatra (Alston 1937) and Sulawesi and adjacent islands (Alston 1940), and the Philippines (1935a).

Notes. Among the broad creeping species of Java, *S. opaca* is most similar to robust forms of *S. intermedia* and *S. involvens*. However, *S. intermedia* generally possesses looser foliage organization and less opaque leaves, whereas *S. involvens* more commonly develops ascending branches with partially auriculate leaf bases. The present species is usually recognizable by its dark compact foliage, broader branch systems, and strongly overlapping lateral leaves. Sterile specimens from deeply shaded habitats may become particularly broad and flattened, increasing resemblance to members of the *S. plana* complex. Field observations suggest that the species occurs across a relatively broad range of humid upland microhabitats, including semi-disturbed agricultural environments, than previously recognized in classical floristic treatments.

Specimens examined: ADS 12, ADS 57, ADS 153, ADS 275, ADS 421, ADS 519, ADS 581, ADS 992, ADS 1123, ADS 1411; A.H.G. Alston 12498 (BO!), A.M. Noorvoort 312 (BO!), Bakh. v.d. Brink 119 (BO!), C.G.G.J. van Steenis 7160 (BO!), Elbert 185 (BO!), Forbes with 1034 (BO!), J.A. Lorzing 1909 (BO!), J.D. Dongelo 184 (BO!), J.J. Afriastini 551 (BO!), Main 148 (BO!), O. Posthumus 3932 (BO!), and Vermeulen 66 (BO!).

***Selaginella ornata* (Hook. & Grev.) Spring (Figure 2.K)**

Selaginella ornata (Hook. & Grev.) Spring, *Bull. Acad. Roy. Sci. Bruxelles* 10: 232 (1843). =Basionym: *Lycopodium ornatum* Hook. & Grev. Included in several regional floristic treatments of Malesia (Alston 1934b, 1935b; Wong 1982, 2010), mainland Southeast Asia (Tagawa and Iwatsuki 1979; Pham-Hoang 1991), and East Asia (Zhang et al. 2013).

Type. Sumatra, Indonesia, Millett s.n. (lectotype K).

Diagnostic characters. Plants ascending to loosely spreading, moderately delicate, with flattened and irregularly pinnate branch systems. Stems glabrous, relatively slender, and usually 2-5 mm wide including leaves. Lateral leaves ovate-lanceolate to elliptic, asymmetrical, approximately 2-4 mm long, green to dark green, with margins minutely denticulate or sparsely ciliolate near the basal portions. Basal regions of the lateral leaves frequently slightly expanded or weakly auriculate, although less conspicuous than in *S. involvens*. Median leaves ovate, acute to acuminate, smaller and more closely appressed than the lateral leaves. Strobili slender, tetragonal, terminal on ultimate branches, generally 8-18 mm long. The species differs from *S. involvens* by its narrower branch systems, smaller leaves, and more delicate overall habit.

Habitat and distribution. *Selaginella ornata* occurs primarily in humid lowland and submontane forests, particularly on moist soil banks, shaded slopes, stream margins, and forest-edge habitats with relatively stable humidity. The species is more frequently encountered in sheltered understory environments than in highly exposed or disturbed habitats. In Java, it has been recorded at elevations of approximately 222–1457 m a.s.l., indicating a broad distribution across lowland and submontane forests, with most records concentrated in humid upland environments. Beyond Java, *S. ornata* is distributed in other parts of Malesia, including Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), and is also recorded from Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991), and China (Zhang et al. 2013).

Notes. *Selaginella ornata* occupies an intermediate morphological position between slender humid-forest taxa and compact ascending species. The species generally develops a loose shrub-like habit with relatively fragile and easily fragmented branches, whereas *S. involvens* typically forms a more rigid and tree-like ascending structure with denser foliage organization. Compared with *S. intermedia*, *S. ornata* usually possesses less fleshy stems, less clustered growth, weakly auriculate leaf bases, and narrower flattened branches. Field observations suggest that S. ornata commonly occurs in semi-open humid habitats and riparian microhabitats, although substantial morphological overlap remains among these taxa.

Specimens examined: ADS 32, ADS 171, ADS 246, ADS 355, ADS 437, ADS 598, ADS 880, ADS 1094, ADS 1275, ADS 1445; A. Rand (BO!), Bakh. v.d. Brink 5189 (BO!), C.A. Backer 5632 (BO!), C.A. Backer 14269 (BO!), C.G.G.J. van Steenis 10842 (BO!), H. Wiriadinata et al. 31537 (BO!), Koorders 17077 (BO!), M.A. Donk P276

(BO!), O. Posthumus 1814 (BO!), Swartz 2178 (BO!), and W. Meijer 29 (BO!).

***Selaginella plana* (Desv.) Hieron. (Figure 2.L)**

Selaginella plana (Desv.) Hieron., *Nat. Pflanzenfam.* 1(4): 703 (1901). =Basionym: *Lycopodium planum* Desv. ex Poir. One of the most widely treated and taxonomically discussed species in Malesia (Alston 1934b, 1935a,b, 1937, 1940; Lindsay et al. 2022; Wong 1982, 2010).

Type. East Indies (Indiae Orientalis), s. coll. s.n. (lectotype P; isolectotype B).

Diagnostic characters. Plants creeping to ascending, highly variable, usually forming broad mats or loosely spreading colonies over moist substrates. Stems glabrous, relatively robust, strongly flattened, and regularly pinnate to broadly flabellate, generally 5-12 mm wide including leaves. Branch systems broad, conspicuously dorsiventral, and often more regularly organized than in *S. intermedia*. Lateral leaves ovate-lanceolate to asymmetrically ovate, approximately 3-7 mm long, overlapping, green to dark green, with margins entire, denticulate, or sparsely ciliolate near the basal portions. Median leaves ovate, acute to acuminate, closely appressed, usually distinctly smaller than the lateral leaves. Strobili flattened to weakly quadrangular, slender to moderately robust, generally 10-30 mm long. The species is characterized by its broad flattened branch systems, ecological tolerance, and marked structural variability across habitats.

Habitat and distribution. *Selaginella plana* occupies one of the broadest ecological ranges among Javan species. It occurs from lowland to lower montane regions in secondary forests, agroforestry systems, plantations, shaded ravines, stream margins, volcanic slopes, roadside embankments, and disturbed humid habitats. The species frequently colonizes semi-open or partially disturbed environments and is often abundant in areas affected by moderate human activity. In Java, it has been recorded from approximately 8-1216 m elevation and represents one of the most common and widespread *Selaginella* taxa across the island. Outside Java, the species is broadly distributed throughout Malesia, including Sumatra (Alston 1937), Sulawesi, and surrounding islands (Alston 1940), Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), Singapore (Lindsay et al. 2022), and the Philippines (Alston 1935a),

Notes. *Selaginella plana* is most easily confused with *S. intermedia* and *S. opaca*. It differs from *S. intermedia* in its more regularly pinnate branches, broader foliage, and stronger association with disturbed and semi-open habitats, including irrigation channels, agricultural terraces, and other semi-open anthropogenic environments. From *S. opaca*, it differs in its less compact foliage and lower elevational range (usually below 1200 m). Sterile specimens from deeply shaded habitats may exhibit narrower branches, requiring careful comparison with *S. intermedia*.

Specimens examined: ADS 35, ADS 114, ADS 174, ADS 241, ADS 361, ADS 523, ADS 761, ADS 897, ADS 1136, ADS 1457; A.G.L. Adelbert 278 (BO!), A.G.L. Adelbert 441 (BO!), A.G.L. Adelbert 445 (BO!), A.G.L. Adelbert 463 (BO!), Bakh. v.d. Brink 1570 (BO!), Bakh. v.d. Brink 6116 (BO!), C.A. Backer 12139 (BO!), C.G.G.J. van Steenis 8232 (BO!), Doc. van Leeuwen-Reijnvaan 11771 (BO!), J.H. Kern 7208 (BO!), J.V. Borssum Waalkes 461 (BO!), Koorders 44420 (BO!), M.A. Donk 9 (BO!), O. Posthumus 1308 (BO!), and P. Buwalda 8077 (BO!).

***Selaginella remotifolia* Spring (Figure 2.M)**

Selaginella remotifolia Spring, *Pl. Jungh*. 3: 276 (1854). Recognized in several floristic treatments of Malesia (Alston 1934b; Alston 1935a,b; Wong 1982, 2010), mainland Southeast Asia (Tagawa and Iwatsuki 1979; Pham-Hoang 1991; Kalyuzhnyi et al. 2024), and East Asia (Tagawa 1963, 1973; Tsai and Shieh 1994; Chang et al. 2010; Zhang et al. 2013)

Type. Angkola Superior (Tapanuli), Sumatra, Indonesia, Junghuhn s.n. (holotype L).

Diagnostic characters. Plants creeping to loosely ascending, relatively delicate, with slender flattened branch systems forming loose mats on moist substrates. Stems glabrous, irregularly pinnate, rooting intermittently along creeping portions, and usually 2-4 mm wide including leaves. Lateral leaves distinctly distant from one another on ultimate branches, representing one of the most diagnostic features of the species. Leaves ovate-lanceolate to elliptic, asymmetrical, approximately 1.5-3 mm long, green to yellowish green, with margins minutely denticulate or sparsely ciliolate near the basal portions. Median leaves smaller, ovate, acute to shortly acuminate, moderately appressed to the stem. Strobili slender, flattened to weakly quadrangular, generally 6-15 mm long. The loose foliage arrangement and clearly separated lateral leaves distinguish the species from most other creeping Javan taxa.

Habitat and distribution. The species is primarily associated with continuously humid submontane to montane habitats, particularly along shaded stream banks, damp rocky slopes, ravines, and forest trails. Several populations also occur in humid lower elevation forests, although the species is most frequently encountered in cool and persistently moist upland environments. In Java, *S. remotifolia* has been recorded from approximately 768-2161 m elevation and appears most common in humid montane regions with stable atmospheric moisture. The species is also recorded from several regions in other parts of Malesia, including Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), the Philippines (Alston 1935a); and is also recorded from Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), China (Zhang et al. 2013), Taiwan (Tagawa 1973; Tsai and Shieh 1994; Chang et al. 2010), and the Ryukyu Islands of Japan (Tagawa 1963).

Notes. Among slender creeping species, *S. remotifolia* is most readily recognized by the distant arrangement of the lateral leaves on ultimate branches. Delicate specimens may resemble narrow forms of *S. intermedia*, but *S. intermedia* generally develops denser foliage organization and broader branch systems. The present species also differs from *S. alutacea* by its looser branching structure and more conspicuously spaced leaves. Because branch

elongation may vary under shaded conditions, reliable identification should emphasize overall foliage arrangement rather than branch length alone. Field observations further indicate that the species occurs in a wider range of humid upland microhabitats, including semi-disturbed riparian and roadside habitats, than previously emphasized in classical floristic treatments.

Specimens examined: ADS 21, ADS 87, ADS 192, ADS 263, ADS 356, ADS 443, ADS 553, ADS 725, ADS 1127, ADS 1416; B.P.G. Hochreutiner 1278 (BO!), C.A. Backer & O. Posthumus 485 (BO!), C.G.G.J. van Steenis 7193 (BO!), Clason-Laarman 80 (BO!), Doc. van Leeuwen-Reijnvaan 11431 (BO!), E. Jacobson 142 (BO!), H.O. Forbes 1064 (BO!), M.A. Donk P275 (BO!), O. Posthumus 3931 (BO!), and W. Meijer 2755 (BO!).

***Selaginella repanda* (Desv.) Spring (Figure 2.N)**

Selaginella repanda (Desv.) Spring, *Voy. Bonite, Bot.* 1: 329 (1846). =Basionym: *Lycopodium repandum* Desv. ex Poir. Included in several regional floristic treatments of Malesia (Alston 1934b, 1935a,b; Wong 1982, 2010), mainland Southeast Asia (Tagawa and Iwatsuki 1979; Pham-Hoang 1991; Kalyuzhnyi et al. 2024), and East Asia (Tagawa 1973; Tsai and Shieh 1994; Chang et al. 2010).

Type. Philippine Islands, Desvaux s.n. (holotype P).

Diagnostic characters. Plants creeping and broadly spreading, relatively robust, commonly forming extensive mats on moist forest substrates. Stems glabrous, flattened, irregularly pinnate to broadly flabellate, generally 5-10 mm wide including leaves. Branch systems broad and relatively loose compared with *S. plana*. Lateral leaves broad ovate to ovate-lanceolate, approximately 3-6 mm long, strongly overlapping, green to dark green, with margins distinctly ciliate, particularly near the basal portions. Median leaves ovate, acute to acuminate, smaller and more closely appressed than the lateral leaves. Strobili flattened to weakly quadrangular, relatively slender, usually 10-20 mm long. The species is distinguished by its broad ciliate leaves, robust creeping habit, and loosely organized branch systems.

Habitat and distribution. The species occurs mainly in humid lowland and submontane forests, particularly along ravines, moist slopes, shaded stream banks, forest trails, wet rocky substrates, and humid riparian embankments. It is strongly associated with continuously humid understory habitats and is less common in open disturbed environments, although several populations may occur along semi-open humid forest margins. In Java, it has been recorded at elevations of approximately 19-1,064 m a.s.l., indicating a broad distribution across lowland and submontane forest environments. *Selaginella repanda* has been recorded from several regions across the island and is also widely distributed in tropical and subtropical Asia, including Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), the Philippines (Alston 1935a), as well as Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991; Kalyuzhnyi et al. 2024), and Taiwan (Tagawa 1973; Tsai and Shieh 1994; Chang et al. 2010).

Notes. *Selaginella repanda* is most similar to robust forms of *S. ciliaris*, but *S. ciliaris* generally possesses narrower leaves, finer branches, and a more delicate mat-forming habit. Compared with *S. plana*, the present species develops more conspicuously ciliate leaf margins and less regularly flattened branch systems. Although branch density may vary among populations, the combination of broad overlapping leaves and distinct marginal ciliation remains relatively stable across habitats with persistent humidity and shaded understory conditions.

Specimens examined: ADS 49, ADS 323, ADS 487, ADS 680, ADS 719, ADS 985, ADS 1028, ADS 1053, ADS 1138, ADS 1450; C.A. Backer 3408 (BO!), C.A. Backer 20069 (BO!), C.A. Backer 27965 (BO!), C.A. Backer 30753 (BO!), Clason-Laarman F18 (BO!), J.D. Dongelo 1964 (BO!), J.G.B. Beumee 5544 (BO!), Mousset 245 (BO!), and W.C. van Kern (BO!).

***Selaginella rothertii* Alderw. (Figure 2.O)**

Selaginella rothertii Alderw., *Bull. Jard. Bot. Buitenz*. sér. 2, 1: 22 (1911). Recognized in the floristic treatment of the *Selaginella* flora of Java Island (Alston 1935b).

Type. West Java, Indonesia, Blume s.n. (holotype L).

Diagnostic characters. Plants creeping to procumbent, moderately robust, usually forming compact colonies or loose mats in humid forest habitats. Stems glabrous, relatively stiff, regularly pinnate to subpinnate, and generally 3-7 mm wide including leaves. Branch systems flattened but narrower and more compact than in *S. plana*. Lateral leaves ovate-lanceolate, asymmetrical, closely arranged, approximately 2-5 mm long, green to dark green, with margins entire to minutely denticulate. Median leaves smaller, ovate, acute to shortly acuminate, closely appressed to the stem. Strobili tetragonal, compact, usually 10-18 mm long. The species is characterized by its relatively rigid foliage, compact branch organization, and narrow flattened branch systems.

Habitat and distribution. The species occurs mainly in humid lowland to submontane forests, especially on volcanic substrates, shaded rocky slopes, moist ravines, forest floors, and humid riparian habitats at lower to middle elevations. Compared with widespread creeping taxa, *S. rothertii* is more frequently associated with relatively humid submontane habitats and stable understory conditions, although available records indicate that the species also occurs at lower elevations and along semi-open humid slopes. In Java, it has been recorded from approximately 182-768 m elevation and appears locally distributed in western and central regions. The species is currently known primarily from Java (Alston 1935b).

Notes. Morphological variation in *S. rothertii* is generally less extensive than in widespread creeping species such as *S. plana* or *S. intermedia*. Compact individuals from exposed submontane habitats may superficially resemble reduced forms of *S. cupressina*, but *S. cupressina* develops denser cypress-like branching and more strongly imbricate foliage. In comparison with S. plana, the present species possesses narrower branch systems and a more compact creeping habit. The compact foliage arrangement and relatively stiff stems are useful supplementary characters for identification in the field. Field observations further suggest stronger association with

persistently humid understory habitats than with strongly disturbed anthropogenic environments.

Specimens examined: ADS 103, ADS 106, ADS 107, ADS 394, ADS 459, ADS 479, ADS 500, and ADS 503.

***Selaginella singalanensis* Hieron. (Figure 2.P)**

Selaginella singalanensis Hieron., *Hedwigia* 50: 18 (1910). Reported in regional floristic treatments of western Malesia (Alston 1935b, 1937).

Type. Mount Singgalang, West Sumatra, Indonesia, Beccari 242 (original material B, FI).

Diagnostic characters. Plants ascending to loosely tufted, relatively slender to moderately robust. Stems glabrous, flattened, irregularly pinnate to subpinnate, and generally 3-6 mm wide including leaves. Branch systems moderately compact but less rigid and less densely organized than in *S. subspinulosa*. Lateral leaves ovate-lanceolate to elliptic, asymmetrical, approximately 2-5 mm long, green to dark green, with margins entire to minutely denticulate. Median leaves ovate, acute to shortly acuminate, usually spreading slightly from the stem rather than being tightly appressed. Strobili tetragonal, slender to moderately compact, generally 8-18 mm long. The species differs from *S. subalpina* and *S. subspinulosa* by its looser branch organization, thinner-textured foliage, and less rigid overall habit.

Habitat and distribution. The species occurs mainly in humid submontane habitats, particularly on moist volcanic slopes, shaded ravines, rocky substrates, forest margins, and humid upland stream corridors. It is generally associated with humid upland environments characterized by persistent atmospheric humidity and stable understory moisture conditions. In Java, *S. singalanensis* has been recorded at elevations of approximately 768–1369 m a.s.l., indicating a predominantly submontane distribution in humid upland forests. The species is known from Java and Sumatra. Alston (1935b) recorded the species from Java under the name *Selaginella modica*, now regarded as a synonym of *S. singalanensis*, while Alston (1937) documented additional records from Sumatra.

Notes. *Selaginella singalanensis* occupies an intermediate position among several montane tufted taxa and may occasionally resemble slender forms of *S. subspinulosa*. However, *S. subspinulosa* generally possesses denser branching, thicker foliage, and more rigid stems. Compared with *S. subalpina*, the present species develops more elongate branches and less compact foliage organization. The slightly spreading median leaves and relatively flexible branch systems are useful field characters for distinguishing the species from other compact upland taxa. Field observations further indicate stronger association with persistently humid montane microhabitats than with exposed or semi-disturbed upland environments.

Specimens examined: ADS 13, ADS 133, ADS 269, ADS 385, ADS 467, ADS 471, ADS 578, ADS 584; C.A. Backer 30731 (BO!), D.R. Pleyte 258 (BO!), J.A. Lorzing 490 (BO!), Junghuhn 255 (BO!), and Kobus Tosari 147 (BO!).

***Selaginella subalpina* Alderw. (Figure 2.Q)**

Selaginella subalpina Alderw., *Bull. Jard. Bot. Buitenzorg,* sér. 2, 20: 26 (1915). Known from montane habitats in Java and recognized in the floristic treatment of the Javan *Selaginella* by Alston (1935b).

Type. Java, Indonesia, s. coll. s.n. (holotype BO).

Diagnostic characters. Plants erect to densely tufted, relatively compact, commonly forming small clumps in humid submontane to montane habitats. Stems glabrous, stiff, regularly pinnate to subpinnate, and generally 3-6 mm wide including leaves. Branch systems narrow, compact, and densely foliated. Lateral leaves ovate-lanceolate, closely imbricate, approximately 2-4 mm long, green to dark green, with margins entire to minutely denticulate. Median leaves smaller, ovate, acute to shortly acuminate, tightly appressed to the stem. Strobili tetragonal, terminal, compact, usually 8-15 mm long. The species is characterized by its compact tufted habit, dense foliage arrangement, and strong association with humid submontane to montane environments.

Habitat and distribution. The species occurs mainly in humid submontane habitats, particularly on moist volcanic slopes, mossy forest floors, shaded rocky ridges, humid ravines, and sheltered upland forest margins at middle elevations. It is strongly associated with humid upland environments characterized by persistent atmospheric humidity, stable understory moisture, and relatively dense canopy cover. In Java, *S. subalpina* has been recorded at elevations of approximately 540–1249 m a.s.l., indicating a predominantly submontane distribution in humid upland forests. The species has been recorded from humid upland forests and mossy habitats in Java (Alston 1935b).

Notes. Compared with widespread lowland species, *S. subalpina* shows relatively limited structural variation across habitats. The species is most similar to *S. subspinulosa*, but *S. subspinulosa* generally develops more rigid branching, denser foliage, and slightly spinulose leaf margins. In contrast, *S. subalpina* possesses softer foliage texture and less rigid branch organization. The compact tufted habit and consistent occurrence in humid submontane and montane forests provide useful supplementary characters for identification. Although often associated with humid submontane and montane forests, currently available records do not indicate restriction to upper montane environments.

Specimens examined: ADS 130, ADS 495, ADS 663, ADS 1210, ADS 1247, ADS 1279, ADS 1303, ADS 1315, ADS 1321, ADS 1338; Blume (BO!), C.A. Backer 10647 (BO!), Hildebrandt (BO!), W.F. Winckel 1594 (BO!), W.F. Winckel 1684 (BO!), and W.S. Hoover et al. 32711 (BO!).

***Selaginella subspinulosa* Spring**

Selaginella subspinulosa Spring, *Pl. Jungh.* 3: 277 (1854). Recognized in the floristic treatment of Javan *Selaginella* by Alston (1935b).

Type. Java, Indonesia, Junghuhn s.n. (holotype L).

Diagnostic characters. Plants erect to densely ascending, relatively compact and rigid, usually forming tight clumps in humid upland habitats. Stems glabrous,

stiff, regularly pinnate, and generally 3-6 mm wide including leaves. Branch systems narrow, compact, and densely foliated. Lateral leaves ovate-lanceolate, strongly imbricate, approximately 2-4 mm long, thick-textured, green to dark green, with margins minutely denticulate to slightly spinulose near the apical portions. Median leaves ovate, acute to shortly acuminate, closely appressed to the stem. Strobili tetragonal, compact, terminal on ultimate branches, usually 8-16 mm long. The species is distinguished by its rigid compact habit, densely overlapping leaves, and subtly spinulose leaf margins.

Habitat and distribution. The species occurs mainly in humid montane and upper submontane habitats, particularly on moist volcanic slopes, mossy forest floors, shaded rocky substrates, humid ravines, and sheltered montane forest margins at middle to upper elevations. Compared with several creeping lowland taxa, *S. subspinulosa* is generally associated with humid montane environments characterized by relatively stable atmospheric humidity and persistent understory moisture. In Java, the species appears locally distributed in montane regions, although currently available records remain limited. The species has been recorded from montane regions of Java (Alston 1935b).

Notes. *Selaginella subspinulosa* closely resembles *S. subalpina*, especially in compact montane populations, but generally possesses more rigid branching, denser foliage organization, and slightly spinulose leaf margins. The foliage texture is also typically firmer and more strongly imbricate than in *S. singalanensis*. Although branch length may vary slightly among populations, the compact rigid architecture remains relatively stable and provides an important field character for species recognition. Available records suggest occurrence in humid montane habitats, although the limited number of confirmed collections from Java still makes its full ecological range and habitat preference uncertain. Because confirmed recent collections from Java remain limited, additional field observations and herbarium reassessment are still needed to clarify the current ecological distribution and morphological variability of the species.

Specimens examined: Anonymous A010414 (BO!), Docters van Leeuwen-Reijnvaan 2568 (BO!), Zollinger 2011 (BO!).

***Selaginella uncinata* (Desv.) Spring (Figure 2.R)**

Selaginella uncinata (Desv.) Spring, *Bull. Acad. Roy. Sci. Bruxelles* 10: 141 (1843). =Basionym: *Lycopodium uncinatum* Desv. ex Poir. The species has been recognized in floristic and taxonomic treatments across mainland Southeast Asia (Kalyuzhnyi et al. 2024) and East Asia (Dahlen 1988; Chang et al. 2010; Zhang et al. 2013).

Type. China, s. coll. s.n. (lectotype P).

Diagnostic characters. Plants creeping and mat-forming, relatively delicate, with slender repeatedly branched stems rooting along the substrate. Branch systems strongly flattened and regularly pinnate, generally 2-5 mm wide including leaves. Foliage characteristically bluish-green to metallic iridescent under shaded humid conditions, representing one of the most distinctive diagnostic features of the species. Lateral leaves ovate-lanceolate, asymmetrical, approximately 1.5-3 mm long, thin-textured, with margins entire to minutely denticulate. Median leaves smaller, ovate, acute to shortly acuminate, closely appressed to the stem. Strobili slender, flattened to weakly quadrangular, terminal on ultimate branches, usually 5-12 mm long. The species is readily recognizable by its iridescent coloration, delicate foliage, and strongly flattened branch systems.

Habitat and distribution. The species is commonly associated with shaded humid habitats, including moist ravines, forest margins, shaded plantations, gardens, humid roadside embankments, ornamental landscapes, and disturbed secondary vegetation. It is frequently cultivated as an ornamental ground cover and occasionally becomes naturalized in semi-natural habitats with persistent humidity. In Java, *S. uncinata* has been recorded at elevations of approximately 107–1359 m a.s.l. and is primarily associated with cultivated, semi-natural, and disturbed habitats in humid lowland and submontane environments. The species is native to southern China (Zhang et al. 2013) and is also recorded from Hong Kong (Dahlen 1988), Taiwan (Chang et al. 2010), and Vietnam (Kalyuzhnyi et al. 2024). It is widely cultivated as an ornamental plant in Southeast Asia (Li and Tan 2005) and has become locally naturalized in parts of Java (Setyawan 2014).

Notes. The metallic bluish-green iridescence is most conspicuous under shaded and humid conditions, whereas plants growing in brighter habitats may appear greener and less reflective. Among Javan taxa, *S. uncinata* is unlikely to be confused with native species because of its distinctive coloration and delicate branch organization. Sterile specimens in poor condition may superficially resemble small forms of *S. kraussiana*, but *S. kraussiana* lacks the characteristic iridescent foliage and usually develops denser carpet-forming mats with smaller leaves. Field observations further indicate strong association with cultivated semi-shaded habitats and persistently humid anthropogenic environments.

Specimens examined: ADS 286, ADS 454, ADS 455, ADS 631, and ADS 1473.

***Selaginella willdenowii* (Desv.) Baker (Figure 2.S)**

Selaginella willdenowii (Desv.) Baker, *Gard. Chron.* 1867 (30): 783 (1867). =Basionym: *Lycopodium willdenowii* Desv. ex Poir. Widely treated in floristic studies of Malesia (Alston 1934b, 1935a,b; Lindsay et al. 2022; Wong 1982, 2010), mainland Southeast Asia (Tagawa and Iwatsuki 1979; Pham-Hoang 1991), East Asia (Tagawa 1963; Chang et al. 2010; Zhang et al. 2013) and tropical Australia (Andrews 1990).

Type. East Indies (Indiae Orientalis), s. coll. s.n. (lectotype P).

Diagnostic characters. Plants scandent to climbing, relatively robust, frequently extending over shrubs, rocks, or surrounding vegetation. Stems elongate, flexible, glabrous, irregularly pinnate to broadly flabellate, and generally 5-12 mm wide including leaves. Branch systems broad and strongly flattened. Foliage characteristically

metallic bluish-green to iridescent under humid shaded conditions, usually darker and structurally more robust than in *S. uncinata*. Lateral leaves ovate-lanceolate, asymmetrical, approximately 3-7 mm long, with slightly auriculate upper bases and margins entire to minutely denticulate. Median leaves smaller, ovate, acute to acuminate, closely arranged along the stem. Strobili tetragonal, relatively slender, generally 10-25 mm long. The combination of long scandent stems, broad flattened branches, and iridescent foliage readily distinguishes the species from other Javan taxa.

Habitat and distribution. The species occurs mainly in humid lowland to lower montane forests, particularly along ravines, moist forest margins, shaded rocky slopes, riparian habitats, and humid stream corridors with stable atmospheric humidity. It is commonly associated with dense canopy cover and often climbs over surrounding vegetation in sheltered forest interiors. In Java, *S. willdenowii* has been recorded from approximately 28-1151 m elevation and appears widely distributed across humid forest habitats from lowland to submontane regions of western Java. The species is widely distributed across tropical and subtropical Asia. In addition to Java, it has also been reported from Sumatra (Alston 1937), Peninsular Malaysia (Alston 1934b; Wong 1982, 2010), Singapore (Lindsay et al. 2022), the Philippines (Alston 1935a), Thailand (Tagawa and Iwatsuki 1979), Vietnam (Pham-Hoang 1991), China (Zhang et al. 2013), Taiwan (Chang et al. 2010), and the Ryukyu Islands of Japan (Tagawa 1963).

Notes. Among the scandent species of Java, *S. willdenowii* is most distinctive because of its metallic iridescent foliage combined with elongate climbing stems. The species may occasionally resemble robust forms of *S. frondosa*, but *S. frondosa* generally possesses shorter ascending branches and lacks the conspicuous bluish iridescence characteristic of *S. willdenowii*. Compared with *S. uncinata*, the present species is substantially larger, more robust, and more extensively scandent in growth habit. Field observations indicate strongest development in persistently humid shaded habitats with stable canopy cover and high atmospheric moisture. Available elevational records indicate broad ecological tolerance across humid forest habitats, although the species is most characteristic in shaded lowland and submontane environments.

Specimens examined: ADS 108, ADS 393, ADS 603, ADS 667, ADS 829, ADS 953, ADS 1178, ADS 1288, ADS 1369, ADS 1471; A.G.L. Adelbert 272 (BO!), A.H.G. Alston 12386 (BO!), A.H.G. Alston 12877 (BO!), A.P.G. Bijhouwer 265 (BO!), Bakh. v.d. Brink 5502 (BO!), C.A. Backer 4123 (BO!), J.A. Lorzing 2510 (BO!), M.A. Donk 33 (BO!), S.J. van Ooststroom 12590 (BO!), and W.F. Winckel 966 (BO!).

***Selaginella zollingeriana* Spring (Figure 2.T)**

Selaginella zollingeriana Spring, *Pl. Jungh.* 3: 278, no. 11 (1854). The species was included in the classical revision of Javan *Selaginella* by Alston (1935b).

Type. Java, Indonesia, Zollinger 2419 (holotype P).

Diagnostic characters. Plants ascending to spreading, moderately delicate, usually forming loose colonies on moist forest substrates. Stems glabrous, flattened, irregularly pinnate, and generally 2-5 mm wide including leaves. Branch systems relatively narrow and moderately compact. Lateral leaves ovate-lanceolate to elliptic, asymmetrical, approximately 2-4 mm long, green to dark green, with margins minutely denticulate or weakly ciliolate near the basal portions. Median leaves ovate, acute to shortly acuminate, closely arranged but not strongly imbricate. Strobili slender, tetragonal, terminal on ultimate branches, usually 8-18 mm long. The species differs from *S. ornata* and *S. intermedia* by its narrower branch systems, relatively delicate foliage, and more compact ascending habit.

Habitat and distribution. The species occurs mainly in humid submontane to lower montane forests, particularly on shaded slopes, moist volcanic substrates, ravines, forest margins, and humid upland stream corridors with stable humidity conditions. Compared with several widespread lowland taxa, *S. zollingeriana* appears more consistently associated with humid upland environments and sheltered understory habitats. In Java, it has been recorded from approximately 983-1222 m elevation and appears locally distributed in western and central montane regions. The species has been recorded from Java and the Lesser Sunda Islands (Alston 1935b).

Notes. *Selaginella zollingeriana* may occasionally resemble slender upland forms of *S. ornata* or *S. intermedia*, especially under deeply shaded conditions. However, the species generally develops narrower branch systems, more delicate foliage organization, and a relatively compact ascending habit. Compared with *S. singalanensis*, it possesses less rigid branching and thinner foliage texture. Field observations further suggest relatively consistent association with persistently humid and shaded upland microhabitats. Available elevational records indicate relatively consistent ecological association with humid submontane and lower montane habitats in Java, although currently available collections remain limited compared with widespread taxa such as *S. plana* or *S. intermedia*.

Specimens examined: ADS 118, ADS 286, ADS 488, ADS 649, ADS 816, ADS 1007, ADS 1195, ADS 1328; Bakh. v.d. Brink 5866 (BO!), C.A. Backer 15114 (BO!), C.G.G.J. van Steenis 10284 (BO!), Koorders 18641 (BO!), M.A. Donk P281 (BO!), and O. Posthumus 2485 (BO!).

Discussion

Taxonomic reassessment of the Selaginella flora of Java

The present study recognizes 21 accepted species of *Selaginella* in Java based on integrated evaluation of field observations, herbarium specimens, comparative morphology, ecological information, and contemporary nomenclatural standards. This revised checklist represents a conservative reassessment of Javan *Selaginella* diversity and updates species concepts that have undergone substantial changes since the classical treatments of the twentieth century. While most historically recognized taxa are retained, several names previously treated as distinct species are not accepted because their diagnostic characters

overlap extensively with broader and more variable species complexes.

The taxonomic foundation for *Selaginella* in Java was established by Alston (1935b), who recognized 23 species from Java and the Lesser Sunda Islands based largely on herbarium morphology. Subsequent compilations, particularly Hassler's global checklist (1994-2026), incorporated nomenclatural revisions and expanded geographic information, whereas Plants of the World Online (POWO 2026) provided a globally standardized framework for accepted names and synonymy. Comparison among these sources and the present reassessment reveals broad agreement regarding the core composition of the Javan flora, but also identifies several problematic taxa. *Selaginella ascendens* and *S. springiana* are interpreted here within the *S. intermedia* complex, whereas *S. caudata* and *S. caulescens* are treated within the *S. plana* and *S. involvens* complexes, respectively. In contrast, *S. grabowskyi*, *S. strobiformis*, and *S. tamariscina* are excluded because they lack reliable supporting evidence from Java.

Nomenclatural standardization played an important role in reconciling inconsistencies among historical treatments and modern databases. Following POWO (2026), supported by Hassler (1994-2026) and regional taxonomic literature, orthographic variants, outdated combinations, and conflicting synonymies were standardized. The present study adopts a conservative taxonomic philosophy in which species delimitation is based on combinations of relatively stable morphological characters supported by herbarium, ecological, and distributional evidence. Such an approach reduces the risk of taxonomic inflation arising from environmentally induced morphological variation and provides a more stable framework for interpreting the *Selaginella* flora of Java (Jermy 1990; Wong 2010; Weststrand and Korall 2016).

Species complexes and problematic taxa

Several *Selaginella* taxa in Java form morphologically overlapping groups that complicate species delimitation and contribute to contrasting interpretations among historical and contemporary taxonomic treatments (Table 1). These difficulties arise primarily because many vegetative characters traditionally used for species identification, including branch architecture, foliage density, leaf overlap, and growth habit, vary considerably across environmental conditions and often fail to provide clear boundaries between closely related taxa.

The most problematic group is the *Selaginella plana* complex, comprising *S. plana*, *S. caudata*, and *S. stipulata*. *S. plana* is one of the most widespread species in Java and exhibits substantial variation in branching pattern, foliage compactness, and leaf arrangement across diverse habitats. In Java, the species occurs from lowland disturbed habitats and agroforestry systems to humid submontane forests, where local environmental conditions appear to influence vegetative architecture. Characters historically used to distinguish *S. caudata* and *S. stipulata* frequently occur within the morphological range of *S. plana* and show no consistent discontinuities among examined specimens. Consequently, neither field observations nor herbarium material support their recognition as distinct species. Both taxa are therefore interpreted here as components of a broadly circumscribed *S. plana* complex, consistent with previous observations that vegetative morphology in tropical *Selaginella* is often strongly influenced by environmental conditions (Jermy 1990; Wong 2010).

Table 1. Principal species complexes and problematic taxa of *Selaginella* in Java and their taxonomic interpretation in the present study

Species complex	Historically recognized taxa	Main diagnostic characters traditionally used	Major source of taxonomic uncertainty	Interpretation adopted in the present study
S. plana complex	*S. plana*, *S. caudata*, *S. stipulata*	Branch flattening, foliage density, leaf arrangement, stem robustness	Continuous morphological variation across habitats; no stable discontinuities among examined specimens	*S. plana* retained; *S. caudata* and *S. stipulata* not maintained as distinct species
S. intermedia complex	*S. intermedia*, *S. ascendens*, *S. springiana*	Growth habit, branch architecture, foliage compactness, leaf morphology	Extensive overlap in morphology and ecological distribution; absence of consistent diagnostic boundaries	*S. ascendens* and *S. springiana* treated within *S. intermedia*
S. involvens complex	*S. involvens*, *S. caulescens*, *S. cupressina*	Ascending habit, compact foliage, branch organization, leaf overlap	Overlapping vegetative characters and limited availability of verified comparative material	*S. caulescens* included within *S. involvens*; *S. cupressina* provisionally retained pending further study
Taxonomically uncertain taxa	*S. cupressina*, *S. subspinulosa*	Mainly distinguished by growth form and foliage architecture	Insufficient collections and limited field observations from Java	Provisionally retained pending additional herbarium and field evidence
Excluded taxa from the Javan flora	*S. grabowskyi*, *S. strobiformis*, *S. tamariscina*	Reported in historical or secondary sources	Lack of reliable herbarium specimens or verified contemporary records from Java	Excluded from the accepted flora of Java

A second problematic group is the *Selaginella intermedia* complex, including *S. intermedia*, *S. ascendens*, and *S. springiana*. These taxa were historically separated using differences in growth habit, branch organization, and foliage morphology (Alston 1935b). However, examination of a broader geographic and ecological dataset revealed extensive morphological continuity among them. Populations assigned to *S. intermedia* encompass much of the variation attributed to *S. ascendens* and *S. springiana*, while all three taxa occupy similar habitats, particularly humid forests, ravines, and submontane environments. Across Java, morphologically intermediate populations were observed in moist forest understories, riparian habitats, and volcanic mountain systems, where no clear ecological or geographical segregation could be identified. No consistent morphological, ecological, or geographical boundaries were identified, supporting their treatment as a single, broadly defined species complex. Similar patterns have been reported in other Asian *Selaginella* groups where environmentally responsive vegetative characters obscure species limits (Tagawa 1963; Wong 2010; Weststrand and Korall 2016).

Taxonomic uncertainty is also evident within the *Selaginella involvens* complex. Historically, *S. caulescens* was distinguished from *S. involvens* based on branching pattern and foliage organization (Alston 1935b), but these characters overlap extensively, and many specimens exhibit intermediate morphologies. Accordingly, *S. caulescens* is interpreted here within the *S. involvens* complex. This overlap is particularly evident among specimens collected from humid upland forests and volcanic slopes, where variation in foliage density and branch organization appears continuous rather than discrete. The status of *S. cupressina* remains less certain. Although its erect shoots, compact branching, and characteristic cypress-like appearance support its traditional recognition as a distinct species (Alston 1940; Wong 2010), verified material from Java remains limited. A similar situation applies to *S. subspinulosa*, which is represented by relatively few confirmed collections and remains insufficiently documented in Java. Consequently, both species are provisionally retained pending additional collections and comparative study.

In contrast, several names reported in historical treatments or secondary databases could not be substantiated by reliable evidence from Java. The absence of verifiable specimens is particularly notable given the extensive herbarium and field dataset examined in this study. *Selaginella grabowskyi*, *S. strobiformis* (Hassler 1994-2026), and *S. tamariscina* (Alston 1934b) lack verified herbarium specimens or contemporary field records from the island and are therefore excluded from the accepted flora. These findings highlight the importance of specimen-based verification and critical re-evaluation of historical records in regional floristic studies.

Reliability of morphological characters and phenotypic plasticity

Morphological characters traditionally used in *Selaginella* taxonomy differ considerably in their diagnostic reliability. While some traits remain relatively stable across populations and habitats, others are strongly influenced by environmental conditions and should be interpreted cautiously when used for species delimitation (Jermy 1990; Wong 2010; Weststrand and Korall 2016).

Among the least reliable characters are branch flattening, foliage density, and leaf overlap. These traits vary substantially in response to humidity, canopy cover, substrate conditions, and habitat exposure. Plants growing in shaded and persistently humid environments often develop broader and more flattened branch systems with relatively loose foliage, whereas individuals from exposed slopes, rocky substrates, or disturbed habitats tend to exhibit denser foliage and more compact growth forms. Such variation is particularly evident in widespread species such as *S. plana* and *S. intermedia*, which occur across a broad range of habitats in Java, from humid forest understories and riparian corridors to agroforestry systems and disturbed vegetation. Consequently, specimens from contrasting environments may differ markedly in overall appearance despite belonging to the same species. As a result, branch architecture and foliage organization frequently overlap among species and contribute to the taxonomic difficulties observed in the *S. plana*, *S. intermedia*, and *S. involvens* complexes (Alston 1935b; Wong 2010).

In contrast, several characters appear comparatively stable and retain greater taxonomic value. Stem pubescence consistently distinguishes *S. biformis* from the predominantly glabrous species occurring in Java, while the conspicuous aristate median leaves of *S. aristata* remain among the most reliable diagnostic features in the flora. Iridescent bluish-green coloration is also characteristic of *S. uncinata* and *S. willdenowii*. Although the intensity of iridescence may vary with light conditions, the character remains informative when evaluated together with growth habit and leaf morphology (Wong 2010; Zhang et al. 2013).

These observations indicate that phenotypic plasticity plays an important role in shaping vegetative morphology in Javan *Selaginella*. Consequently, species delimitation is most reliable when based on combinations of relatively stable characters supported by ecological and distributional evidence rather than on individual vegetative traits considered in isolation (Jermy 1990; Wong 2010; Weststrand and Korall 2016).

Endemic, introduced, and geographically restricted taxa

Although the *Selaginella* flora of Java is dominated by widespread Malesian species, several taxa exhibit restricted distributions and contribute disproportionately to the island's biogeographical significance. Among these, *S. rothertii* is of particular interest because available evidence indicates that it is endemic to Java, with no verified records currently known from elsewhere. In contrast, *S. zollingeriana* appears to have a more restricted regional distribution centred in Java and the adjacent Lesser Sunda Islands, including Bali. Both species remain morphologically distinct in historical and contemporary taxonomic treatments (Alston 1935b; Hassler 1994-2026;

POWO 2026). In addition, *S. subalpina* is closely associated with humid montane habitats, including high-elevation forests and volcanic slopes, suggesting specialization to cool and persistently moist environments. Together, these taxa highlight the importance of montane ecosystems as centres of localized diversity and refugia for geographically restricted *Selaginella* species in Java.

A different pattern is observed in *S. willdenowii*. Although widely distributed across western Malesia, including Java, Sumatra and Peninsular Malaysia (Alston 1934b, 1935b, 1937; Wong 2010), as well as mainland Southeast Asia (Tagawa and Iwatsuki K. 1979; Pham-Hoang 1991), and East Asia (Tsai and Shieh 1994, Zhang et al. 2013), its occurrence in Java is largely confined to the humid and mountainous regions of the west. Its apparent scarcity in central and eastern Java likely reflects its preference for shaded, persistently moist habitats and the pronounced west-east precipitation gradient across the island (Steenis 1972; Whitten et al. 1996).

In contrast, *Selaginella uncinata* and *S. kraussiana* represent introduced or naturalized elements of the contemporary Javan flora (Setyawan 2014; Setyawan et al. 2025). Both species are widely cultivated as ornamentals and have become established locally outside cultivation. *S. uncinata* is frequently encountered in shaded and humid habitats near settlements, gardens, and disturbed forest margins, whereas *S. kraussiana* appears less widespread but similarly occurs in anthropogenic environments associated with horticultural introduction. The occurrence of these species demonstrates that the modern Javan flora is dynamic rather than static, with human-mediated dispersal contributing to changes in species composition beyond the native Malesian assemblage (Wong 2010; van Kleunen et al. 2015).

Floristic affinities of the Javan Selaginella flora

The *Selaginella* flora of Java exhibits its strongest floristic affinities with other regions of Sundaland, particularly Sumatra, Peninsular Malaysia, and Borneo. Many species recognized in the present study, including *S. plana*, *S. intermedia*, *S. involvens*, *S. ornata*, *S. remotifolia*, *S. willdenowii*, *S. ciliaris*, and *S. aristata*, are also widely distributed throughout western Malesia (Alston 1934b, 1935a,b, 1937; Wong 1982, 2010). This high degree of species sharing is consistent with the geological history of Sundaland, where repeated land connections during periods of lowered sea levels facilitated floristic exchange among Java, Sumatra, Borneo, and Peninsular Malaysia (Steenis 1972; Hall 2013). The widespread occurrence of these taxa across diverse habitats, from lowland forests to montane environments, suggests long-term regional continuity and supports the interpretation that the Javan flora forms part of a broader Sundaic assemblage characterized by relatively limited endemism.

Beyond Sundaland, the Javan *Selaginella* flora also maintains floristic links with Wallacea and the wider tropical Asian region, although these relationships are generally weaker. Several species extend eastward into Sulawesi, Maluku, and the Lesser Sunda Islands, including *S. cupressina*, *S. ciliaris*, and *S. frondosa* (Alston 1935b, 1940). Among these, *S. ciliaris* exhibits one of the broadest distributions within the genus, occurring throughout much of East Asia and Malesia and extending to New Guinea and northern Australia (Andrews 1990). Its extensive range likely reflects broad ecological tolerance and effective long-distance dispersal facilitated by lightweight spores. Other species, including *S. involvens*, *S. biformis*, *S. uncinata*, and *S. willdenowii*, extend northward into mainland Southeast Asia and East Asia, occurring in Thailand, Vietnam, southern China, Taiwan, and the Ryukyu Islands (Tagawa 1963, 1973; Tagawa and Iwatsuki 1979; Tsai and Shieh 1994; Zhang et al. 2013). Collectively, these distribution patterns indicate that the Javan *Selaginella* flora occupies an intermediate biogeographical position, showing its strongest affinity to Sundaland while retaining secondary connections with Wallacea and the broader tropical and subtropical regions of Asia.

Implications for future integrative taxonomy

The present reassessment provides an updated floristic and taxonomic framework for *Selaginella* in Java, but several species complexes remain incompletely resolved. Future studies should incorporate quantitative morphometric analyses to evaluate morphological variation objectively, particularly within the *S. plana*, *S. intermedia*, and *S. involvens* complexes, where species boundaries remain difficult to define using traditional morphology alone. Additional anatomical investigations, including leaf structure, sporophyll morphology, and spore characters, may provide valuable diagnostic evidence for taxa that exhibit extensive vegetative overlap.

Equally important is the integration of molecular phylogenetic approaches, which have substantially advanced species delimitation and evolutionary interpretation in lycophytes and ferns (Korall and Kenrick 2002; Weststrand and Korall 2016; Zhou and Zhang 2023). Molecular data may help determine whether morphologically variable populations represent environmentally induced forms or independently evolving lineages. Continued herbarium revision is also essential because many historical collections have never been reassessed using contemporary taxonomic concepts. Additional field surveys, particularly in underexplored montane regions and isolated volcanic systems, are needed to clarify the distribution and status of geographically restricted taxa. An integrative framework combining morphology, anatomy, molecular phylogenetics, herbarium evidence, and expanded field sampling will provide the most robust basis for future taxonomic research on Asian *Selaginella*.

In conclusion, the present study provides a comprehensive floristic and taxonomic reassessment of *Selaginella* in Java based on field observations, herbarium evidence, comparative morphology, and contemporary nomenclatural standardization. A total of 21 species are recognized and documented, together with updated diagnostic descriptions and identification keys. The study clarifies the status of several problematic taxa and species complexes, particularly those associated with *S. plana*, *S.*

intermedia, and *S. involvens*, and supports a conservative approach to species delimitation. Floristic comparisons indicate strong affinities between the Javan *Selaginella* flora and other regions of Sundaland, with additional connections to Wallacea and the broader tropical and subtropical regions of Asia. The resulting taxonomic framework provides a foundation for future ecological, biogeographical, and evolutionary studies of Javan *Selaginella*.

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Table S1. Checklist of *Selaginella* in Java, Indonesia

Accepted name	Growth form	General habitat	Elevational range	Altitude (m)	Distribution status in Java
Selaginella alutacea Spring	Creeping to ascending	Humid submontane forests and ravines	Submontane	467-903	Native
Selaginella aristata Spring	Creeping to ascending	Humid lowland and submontane forests, ravines, and moist slopes	Lowland–submontane	115-1369	Native
Selaginella biformis A.Braun ex Kuhn.	Creeping to ascending	Moist forest floors and stream banks	Submontane	748-798	Native
Selaginella ciliaris (Retz.) Spring	Creeping	Moist disturbed habitats, forest margins, and open humid sites	Lowland–submontane	3-1412	Native
Selaginella cupressina (Willd.) Spring	Erect to ascending	Volcanic slopes and humid montane forests	Montane	No data	Native
Selaginella frondosa Warb.	Ascending to scandent	Humid lowland forests, ravines, and riparian corridors	Lowland	107-262	Native
Selaginella intermedia (Blume) Spring	Creeping to ascending	Humid forests, ravines, and disturbed habitats	Lowland–submontane	244-1131	Native
Selaginella involvens (Sw.) Spring	Ascending to erect	Humid lowland and submontane forests	Lowland–submontane	351-1493	Native
Selaginella kraussiana (Kunze) A.Braun	Creeping	Gardens, plantations, urban green spaces, and disturbed habitats	Lowland–submontane	75-1500	Introduced/ Naturalized
Selaginella opaca Warb.	Creeping to ascending	Humid forest interiors, ravines, and montane forests	Submontane–montane	935-2124	Native
Selaginella ornata (Hook. & Grev.) Spring	Ascending	Humid lowland and submontane forests	Lowland–submontane	222-1457	Native
Selaginella plana (Desv.) Hieron.	Creeping to ascending	Forest margins, disturbed habitats, secondary forests, and riparian areas	Lowland–submontane	8-1216	Native
Selaginella remotifolia Spring	Creeping to loosely ascending	Moist ravines, stream banks, and montane forests	Submontane–montane	768-2161	Native
Selaginella repanda (Desv.) Spring	Creeping	Humid forest floors, ravines, and rocky substrates	Lowland–submontane	19-1064	Native
Selaginella rothertii Alderw.	Creeping to procumbent	Humid lowland and submontane forests	Lowland–submontane	182-768	Native
Selaginella singalanensis Hieron.	Ascending to tufted	Humid submontane forests and shaded slopes	Submontane	768-1369	Native
Selaginella subalpina Alderw.	Erect to tufted	Humid upper submontane forests and mossy slopes	Submontane	540-1249	Native
Selaginella subspinulosa Spring.	Erect to ascending	Humid montane volcanic habitats	Montane	No data	Native
Selaginella uncinata (Desv.) Spring	Creeping	Shaded gardens and moist disturbed habitats	Lowland–submontane	107-1359	Introduced/ Naturalized
Selaginella willdenowii (Desv.) Baker	Scandent to climbing	Humid forests, forest margins, and riparian habitats	Lowland–submontane	28-1151	Native
Selaginella zollingeriana Spring	Ascending to spreading	Humid submontane forest interiors	Submontane	983-1222	Native