Lycopodiaceae in Brazil. Conspectus of the family
I. The genera Lycopodium, Austrolycopodium, Diphasium, and Diphasiastrum

Abstract

A conspectus of the Lycopodiaceae in Brazil is presented, following a generic classification based on anatomy, chromosome numbers, spores and gametophytes, as well as recent molecular studies. The species of Lycopodiaceae occurring in Brazil, traditionally treated conservatively, were grouped in three genera: Lycopodium, Lycopodiella, and Huperzia. Within each genus, the diversity (treated under various subgenera, sections, and subsections) has been discussed. In our new approach, these three genera are treated as subfamilies Lycopodiodeae (four genera in Brazil), Lycopodielloideae (three genera in Brazil), and Huperzioideae (two genera in Brazil). Branching patterns and morphological diversity of vegetative leaves and sporophylls, as well as morphology of sporangia and spores in the different groups, are discussed in a brief review. We provide keys to identification of subfamilies and genera represented in Brazil. The species of Lycopodiodeae, genera Lycopodium (s.str.), Austrolycopodium, Diphasium, and Diphasiastrum (one species in each of the first three genera, two in Diphasiastrum - one of them new) are treated in detail, with descriptions, illustrations (or references to illustrations), and comments on habitat and distribution.

Key words: taxonomy, lycophytes, diversity, floristics, phytogeography.

Introduction

The Lycopodiaceae s. lat. comprise approximately 400 living species, about half of them in the Neotropics. They are considered to be descendants of a basal line of tracheophytes, with a history of 390 million years (Wikström & Kenrick 2001). Earlier they were commonly referred to the informal group of “fern allies” together...
with Isoetaceae and Selaginellaceae. However, molecular studies clearly place the lycophytes as a monophyletic group of microphyllous seedless vascular plants, with a remote relationship to the megaphyllous ferns (Pteridophyta s.str.).

The homosporous lycophytes have traditionally been treated as a single monophyletic family Lycopodiaceae without close relatives, and the species all referred to a single large genus *Lycopodium* (e.g., Tryon & Tryon 1982), or they were subdivided into two families (Rothmaler 1944; Holub 1985) and into four, or, with recent additions, up to 16 genera (Holub 1964, 1983, 1985, 1991; Pichi Sermolli 1977; Øllgaard 1987; Wagner & Beitel 1992; Haines 2003). Øllgaard (1987) revised the classification of Lycopodiaceae in a paper that also served as base of the Index of the Lycopodiaceae (Øllgaard 1989) and the treatment in the “Families and Genera of Vascular Plants” (Øllgaard 1991). An overview of the Neotropical species Øllgaard (1992) summarized our understanding of the floristic diversity of the family in the Neotropics. At the same time, Wagner & Beitel (1992) presented a generic classification for the North-American Lycopodiaceae, based on anatomy, chromosomes, spores and gametophytes. They recognized the subfamilies Huperzioidae (genera *Phlegmariurus* and *Huperzia*), Lycopodioidae (*Lycopodium* s.str. and *Diphasiastrum*), and Lycopodielloidae (*Pseudolykopodiella*, *Lycopodiella*, and *Palhinhaea*). This classification is supported by molecular data (Wikström & Kenrick 2000). Øllgaard (2012a,b) subsequently has presented additional nomenclatural changes for neotropical species, in line with current ideas of generic circumscription.

Brazil, with its hugely diverse flora, includes in the southeastern region one of three main regional centers for neotropical fern species richness and endemism, as discussed by Tryon (1972), with two components, one represented by the Atlantic Forest in the “Serra do Mar” and “Serra da Mantiqueira” mountain ranges and another by the habitats of the “Cadeia do Espinhaço” (extending from the State of Minas Gerais to the State of Bahia), including rocky grassland formations (“campos rupestres”). A few elements of the Guayan secondary center (sensu Tryon 1972) can be found in the mountains in northernmost Brazil, while the highest mountains in the southeastern region present “sub-paramo” conditions and account for the presence some Andean elements. This diversity of habitats and conditions for species richness and endemism are also reflected in the lycopod diversity. From the ca. 200 neotropical species, the recent list of plants from Brazil (still based on the three genera system for Lycopodiaceae) includes 54 species, of which 27 are considered as endemic (Windisch & Ramos 2010).

The study of the Brazilian fern flora started quite late, and in the case of Lycopodiaceae there are very few records in the early literature. The collections and observations by Georg Marckgrav, member of the entourage of artists and scientists brought along by the Prince Maurice de Nassau as governor (1637 to 1644) of the Dutch settlement in northeastern Brazil, resulted in the publication of the “Historia Rerum Naturalium Brasiliae” including the description of 298 plant species (Marckgraw 1648). Almost one and a half centuries later, a major natural history survey was conducted by Alexandre Rodrigues Ferreira in his “Viagem Filosófica” to the Amazon and Central Brazil (1783 to 1792). However, due to the political turmoil in Napoleonic times, Ferreira never published his floristic or taxonomic results (Franca 1922). The attempt by José Mariano da Conceição Vellozo (1742–1811) to publish the “Flora Fluminensis” (for the region of Rio de Janeiro) was ill-fated, with the first of the plates being printed 18 years after his death, while the text was published only in 1881. In this flora, the Lycopodiaceae is treated under Musci and represented only by *Lycopodium cernuum*. Neither Swartz (1806) nor Poiret (1814) cited Brazilian lycopods. This situation changed substantially in the first decades of the nineteenth century, with the visits by Chamisso, St. Hillaire, Langsdorff, Raddi, Martius and other naturalists. Giuseppe Raddi collected ca. 4000 specimens in the vicinity of Rio de Janeiro in 1817–1818 and published on 119 pteridophyte species (Raddi 1819, 1825), including ten of Lycopodiaceae.

Karl Phillip von Martius collected extensively in Brazil from 1817 to 1820, from São Paulo to Bahia and the Amazon (State of Pará). Later he began the publication of the monumental *Flora brasiliensis*, for which Antoine F. Spring prepared the monograph on Lycopodiaceae, (Spring 1840), presenting 20 species (three of them new) based on collections by Beyrich, Freyreiss, Lhotsky, Luschnath, Martius, Maximilian of Wied Neuwied[Neuvied, below], Pohl, Raddi, Schott, and Sellow. The publication in *Flora brasiliensis* was followed by the first part of a worldwide monograph (Spring 1842), completed seven years later (Spring 1849).
A substantial contribution to the knowledge of the Brazilian lycopods was presented by Antoine L.A. Fée in his “Cryptogames Vasculaires du Brésil” (Fée 1869), followed by a supplement (Fée 1872-1873). Fée’s studies were based on material provided by the collectors mentioned above (except for Lhotsky, Lushnath, and Prince Wied-Neuwied) and in addition collections by Glaziou, Blanchet, Claussen, Durville, Gardner, Gaudichaud, Gauthier, Guillemín, Langsdorff, Salzmann, Schott, and Warming. In the first part, Fée included 25 species (two new) of Lycopodium s. lat. In the supplement, 24 species (six of them new) are discussed, based on collections by Glaziou, who was formally cited as contributor in both publications. Glaziou was the director of the Imperial Botanic Gardens of Rio de Janeiro and, in addition to his own collections, had collecting providing specimens, sometimes with dubious locality information, from other regions.

Special mention is due to Alvaro da Silveira from the State of Minas Gerais, which is part of a Brazilian center of fern richness and endemism is found in the rocky grasslands (“campos rupestres”) and mountain tops of the Serra da Mantiqueira. Silveira (1898) described six new species of Lycopodium including a detailed account on their habitats and associated species. Additional information on the lycopods in Minas Gerais was given in a subsequent publication by Silveira (1908). His contact with Hermann Christ led to a contribution by Christ (1900) republished with slight changes (Christ 1902). Sampaio (1914) reassessed the family, surveying the progress made since the publication of the original fascicle by Spring in Martius’s Flora brasiliensis.

Anders Frederik Regnell contributed his own collections during his 43 years in Brazil (from 1841 onwards), most of them spent in Caldas (State of Minas Gerais), and also through his support of other visiting botanists. He provided funds for the work of Karl Mosén and Albert Löfgren, and later through the Regnellian Foundation, which he endowed sponsorship of expeditions to Brazil (Hoehne et al. 1941).

The National Museum in Rio de Janeiro in the late 1800’s established the “travelling naturalist” position (Museu Nacional 2009) held by several important collectors such as Schwacke, Glaziou, Ule, Dusén, and Müller (the last in correspondence with Charles Darwin). Schwacke came to Brazil in 1884, and after his tenure as travelling naturalist (until 1891) transferred to the School of Mines in Ouro Preto, State of Minas Gerais. Ule collected from 1883 to 1900, starting as a teacher in the State of Santa Catarina, becoming a naturalist from the National Museum, and later acting as an independent collector in the Amazon region, with several species known for northern Brazil based only his collections (Hoehne 1941).

Frederico Carlos Hoehne, working at the Botanical Institute of São Paulo, took great interest in the Lycopodiaceae, including their cultivation as decorative plants. His contact with Hermann Nessel led to the publication in Portuguese (Nessel 1927) of a survey of the family in Brazil, including 103 taxa, placed in two genera: Urostachys (illegitimate) and Lycopodium. Nessel’s (1939) book, “Die Bärlappgewächse”, is a major work but of minor importance due to problems with species concepts, data quality, and nomenclature. Nessel left a manuscript, finished before 1942, as a contribution to the “Flora Brasílica” started by Hoehne. This manuscript was translated and published by Hoehne (Nessel 1955) and treated 102 species; it excluded one species (Urostachys sampaioensis) which was based on a sterile specimen of Lamiaceae (Hypitis imbricata Pohl).

Important contributions to the knowledge of Brazilian Lycopodiaceae were given by W. Herter (1909), G. Herter (1949–1950), Holub (1975, 1983; only nomenclature), Pichi Sermolli (1977; nomenclature), Rolleri (1981, 1984), Vasconcellos & Franco (1967; nomenclature), and Wilce (1965, 1972). Information on the ecology and distribution of Brazilian species may be found in diverse regional floristic studies (including checklists, with various degrees of reliability as to identifications), such as Dutra (1938) for Rio Grande do Sul, Angely (1969–70) for the State of São Paulo, Tryon & Conant (1975), Øllgaard (1995), Salino & Almeida (2008). The spores of species occurring in the State of Rio Grande do Sul have been studied by Lorscheitter et al. (1999, 2009), including data on the distribution and ecology. Anatomical data for Brazilian species were presented by Pita et al. (2006a,b). A detailed study of the Lycopodiaceae at the Itatiaia mountain range (States of Rio de Janeiro and Minas Gerais) was published by Ramos & Sylvestre (2010).

Øllgaard & Windisch (1987) presented a synopsis of the Brazilian members of the family and recognized 52 species. For that study, a compromise between practical aspects and the phylogeny of the group was adopted, recognizing three genera (subdivided into sections) in Brazil. The bases for such an arrangement were discussed by Øllgaard.
(1987). The acceptance of a single or a reduced number of genera (even considering the diversity in subgenera and sections) tends to obscure the great divergence between the distinct species groups within the family. In the present paper, sections of Øllgaard & Windisch (1987) are considered at the generic level, and previously recognized genera at subfamily rank, adopting the subfamilies and generic concepts of Wagner & Beitel (1992), while including neotropical genera that were not treated in their paper. As the first publication of three, the present paper includes a conspectus of the Lycopodiaceae, keys to the genera occurring in Brazil, and a discussion of the species of the subfamily Lycopodioideae, comprising the genera Lycopodium, Austrolycopodium, Diphasium, and Diphasiastrum).

Materials and Methods

Material from major herbaria in Brazil, and relevant collections and type specimens in European and North American herbaria were consulted (AAU, B, BHCB, BM, BONN, BR, C, CESJ, E,F, FLOR, GH, GU, HB, HBG, HBR, HRCB, ICN, K, L, M, MBM, MG, MO, NY, P, PACA, PAMG, R, RB, S, SI, SJRP, SP, SPF, U, UB, UC, UNB, US, W). Extensive field observations were made, especially by the second author. Only selected representative collections, reflecting general distribution range and morphological variation are cited here. A complete “list of exsiccatea” can be obtained from the authors. References to illustrations are presented, and images of diagnostic characters are presented when no adequate illustrations for the species were found in recent literature. Herbarium acronyms follow “Index Herbariorum” (Thiers continuously updated).

Terminology

Branching patterns – Øllgaard (1979) found three basic branching patterns in the family, corresponding to three subfamilies. Huperzia and Phlegmariurus are characterized by isotomy, i.e., all dichotomies result in branches of equal thickness. Branch pairs may be homoblastic, or heteroblastic. Heteroblasty, i.e., the differentiation of branches to distinct functions, and aspects, occurs in many terrestrial high Andean and in one Brazilian, high-montane species of Phlegmariurus. In these plants, individuals have prostrate or even subterranean, rooting shoots from which erect, aerial shoots bearing sporangia arise.

Subfamilies Lycopodioideae and Lycopodielloideae have anisotomous branching, i.e., dichotomies result in unequally thick branches (=pseudomonopodial growth, according to Wagner & Beitel 1992). In Lycopodioideae, the ramifications are dorsolateral, whereas in Lycopodielloideae they are flabellate in horizontal shoots, and dorsal in erect, aerial, strobiliferous shoots. The erect aerial shoots in Palhinhaea are dorsal in origin and repeatedly ramified forming several flabellate lateral branchlet systems that may ultimately be strobiliferous.

Heterophyll and homophyllly – These characters were used as the main basis for the classification of the species belonging to Huperzia and Phlegmariurus in several earlier treatments (Spring 1842, 1849; Baker 1887; Pritzel 1901; W. Herter 1909; G. Herter 1949–50). In these classifications, the species were keyed as either completely homophyllous (i.e., all leaves uniform), gradually heterophyllous (i.e., with gradually reduced leaves toward the apex of the plant), or heterophyllous (i.e., with sharply distinct, long, expanded leaves in the basal divisions, and small, reduced leaves in the narrow terminal divisions). These characters are highly variable, even within a single species, and are therefore unsuitable as the main basis for subdivision at a higher level; nonetheless, they are still useful for identification.

Isophylly and anisophylly – The vast majority of the species of the family are isophyllous, i.e., the leaves are equal in size and shape at the same point on the stem, but may vary along the stems. Anisophylly, i.e., the development of distinct leaf types at the same point on the stem, resulting in dorsiventral branchlets, is found in Diphasium, and Diphasiastrum, and in some species of Pseudolycopeodia.

Sporophylls – The sporophylls of Huperzieae are scalelike and only slightly or not modified at all. In many species they can be distinguished as sporophylls only by the presence of a sporangium in their axils. Correspondingly, they remain green and photosynthetic long after sporangial dehiscence, in contrast to the ephemeral sporophylls in the other genera. In this subfamily the sporangia are not attached to the sporophyll. The sporophylls of Lycopodiodeae and Lycopodielloideae are highly differentiated, and their condition is invariably correlated with the function of the sporangia, i.e., they are ephemeral structures, wilting during or after dehiscence of the sporangia. There are two
types of sporophyll development in subfamily Lycopodioideae. The most common type is subpeltate, as in *Lycopodium*, *Diphasiastrum*, and *Diphasium* (Fig. 1a), where the sporophyll consists of a stalk, on which the sporangium is borne, and an exterior peltate face. The stalk has a median basiscopic membranous wing adnate to the strobilus axis and to the basiscopic flap of the peltate exterior face. *Austrolycopodium* deviates from other Lycopodioideae by its truly peltate sporophylls, lacking the membranous wings of the three other genera (Fig. 1b). In subfamily Lycopodielloideae the sporophylls are subpeltate, ephemeral organs, as in most of the species of subfamily Lycopodioideae. In *Palhinhaea*, strong development of the lateral flanges of the posterior edge of the basiscopic wing provide an almost complete enclosure of the sporangia, so that the opening for the sporangium above each sporophyll is smaller than the sporangium itself (Fig. 2). In *Lycopodiella* the sporangia are axillary, and not attached to the sporophylls, remaining almost enclosed by free sporophyll bases until sporangial dehiscence.

Sporangia – The mature sporangia open by a transversal slit into two nearly equal valves in subfamilies Huperzioidae, Lycopodioidae, and *Pseudolycopodiella*, while in *Lycopodiella* and *Palhinhaea* they are strongly anisovalvate with a small exterior valve. The type of indurations of sporangial wall cells is taxonomically important above species level (Ollgaard 1975).

Spores – External spore morphology was surveyed by Wilce (1972), who recognized five distinct spore groups. The “foveolate-fossulate group” was found in species throughout *Huperzia* and *Phlegmariurus* (in the sense of this paper). Within this group, Wilce distinguished the “Selago

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**Figure 2** – *Palhinhaea steyermarkii*. Ecuador, Napo: Baeza—Tena, 2000 m, Øllgaard et al. 35959 (AAU). Strobilus with coalescent sporophyll bases. Del. K. Tind.
“Rugate” type in *Huperzia* (as here) and the “Phlegmariaria type” in *Phlegmariurus* (as here). In the “Rugate (or “Rugulate”) group”, which occurs throughout subfamily Lycopodielloideae, Wilce distinguished the “Cernuum type”, found in species belonging to *Palhinhaea* (as here), and the “Carolinianum type” in *Pseudolycopodiella* and *Lycopodiella* (both as here). The spore morphology of representative neotropical species has been discussed by Tryon & Lugardon (1990). The reticulate group comprises all Brazilian species belonging to Lycopodiaceae. Optical microscopy and SEM images of species occurring in the State of Rio Grande do Sul are presented by Lorscheitter *et al.* (1999, 2009).

**Taxonomic Treatment**

**Conspectus of the Brazilian Lycopodiaceae**

Equivalent groups of Øllgaard (1987) in parentheses.

- **Subfamily Huperziioideae** sensu Wagner & Beitel (1992)
  - *Huperzia* str. (*Huperzia selago* group)
  - *Phlegmariurus* (all other species groups of *Huperzia* s. lat.)

- **Subfamily Lycopodiioideae** sensu Wagner & Beitel (1992) (*Lycopodium*)
  - *Lycopodium* s. strictiss. (*Lycopodium* sect. *Lycopodium*)
  - *Austrolycopodium* (*Lycopodium* sect. *Magellanica*)
  - *Diphasium* (*Lycopodium* sect. *Diphasium*)
  - *Diphasiastrum* (*Lycopodium* sect. *Complanata*)

- **Subfamily Lycopodielloideae** sensu Wagner & Beitel (1992) (*Lycopodiella*)
  - *Lycopodiella* s. str. (*Lycopodiella* sect. *Lycopodiella*)
  - *Pseudolycopodiella* (*Lycopodiella* sect. *Caroliniana*)
  - *Palhinhaea* (*Lycopodiella* sect. *Campylostachys*)

**Lycopodiaceae** Mirbel, in Lamarck & Mirbel, Hist. Nat. Veg. 4: 293 (1802). Type: *Lycopodium L.*


Terrestrial or epiphytic, erect to pendulous herbs. Stems dichotomously branching, rarely with lateral branching, protostelic, with xylem arranged radially or in parallel bands. Leaves simple, with one simple vein, arranged in low alternating spirals or irregular whorls, or seemingly decussate, homophyllous or heterophyllous, isophyllous or anisophyllous. Sporophylls like the foliage leaves, or modified, sometimes specialized and aggregated into distinct strobili. Sporangia solitary, in leaf axils or on the adaxial side of the sporophyll base, homosporous, unilocular, reniform to subglobular, short-stalked, dehiscing by transverse slits that divide each sporangium into two valves. Spores without chlorophyll, subglobose to tetrahedral, with a trilete scar. Gametophytes monoecious, tuberous, subterranean and holosaprophytic, or surface-living, green, and hemisaprophytic.

**Key to the subfamilies and genera of Lycopodiaceae in Brazil**

1. Stems isomorphously branched throughout, without elongate, indeterminate main stems, rarely heteroblastic, roots usually forming one basal tuft, sporophylls and vegetative leaves alike, or the sporophylls, if smaller, persisting, not subpeltate and ephemeral; sporangia axillary, not attached to the sporophylls; spores foveolate-fossulate (subfamily Huperziioideae).

2. Plants erect, usually with bulbil-producing lateral branchlets. Spores concave between laesurae and truncated corners (Fig. 3b) ................................................................. *Huperzia*

2’. Plants erect or pendulous, without bulbil-producing lateral branchlets. Spores convex between laesurae, with ± plane proximal faces and obtusely angular corners (Fig. 3a) ...... *Phlegmariurus*

1’. Stems anisotomously branched throughout (pseudomonopodial), the branches differentiated into elongate, indeterminate, rhizomatous, or creeping, trailing main stems, rooting at intervals, and usually determinate branchlet systems; sporophylls strongly modified, ephemeral, unlike vegetative leaves, subpeltate or peltate, aggregated in compact, terminal strobili; sporangia borne on sporophyll bases or axillary; spores reticulate or rugate.

3. Strobili erect, sessile or pedunculate, borne on branchlet systems that arise in a dorsolateral position on the main stem; side walls of sporangium epidermis cells sinuate, lignified throughout; spores reticulate (subfamily Lycopodiioideae).
4. Leafy branchlet isophyllous, ± terete.
   5. Leaf apices terminating in a colorless membranous or hairlike apex. Sporophylls subpeltate, with a basiscopic membranous wing ...................................................... Lycopodium s. str.
   5’. Leaf apices herbaceous, green. Sporophylls peltate, lacking basiscopic wings ................
   .................................................................................................................. Austrolepodycopodium
4’. Leafy branchlets anisophyllous, with dimorphic or trimorphic leaves, ± flattened and dorsiventral.
   6. Dorsolateral leaves alternate, much larger than the partly membranous ventral leaves ..........
   ...................................................................................................................................... Diphasium
   6’. Leaves decussate, with large lateral leaves and narrow and smaller dorsal and ventral leaves ....
   ...................................................................................................................................... Diphasiastrum
3’. Strobili pendulous and sessile, or strobili erect and terminating simple (or to 2-forked) branches that arise dorsally on the creeping or looping stems; sidewalls of sporangial epidermis cells straight, non-lignified, except for nodular or semiannular internal thickenings; spores rugate (subfamily Lycopodielloideae).
7. Strobili pendulous or nodding, terminating amply branched branchlet systems that are borne on an erect, tree-like main branch, or rarely (P. bradei) strobili ascending, borne on low, ascending, somewhat fan-shaped branchlet systems, lacking an erect main branch; sporangia almost enclosed in cavities formed by the strobilus cortex and coalescent membranous bases of adjacent sporophylls (Fig. 2) .......................................................................................................................... Palhinhaea
7’. Strobili erect, terminating simple or forked erect branches that arise dorsally on the creeping stems; sporangia enclosed or free.
8. Sporangia nearly isovalvate; sporophylls with entire to minutely denticulate-fimbriate margins, arranged in alternating whorls of 2–5, forming 4–10 longitudinal ranks ................................................. Pseudolycoptiella
8’. Sporangia anisovalvate; sporophylls with few to several, prominent and often recurved teeth, arranged in alternating whorls of 5 or more, forming 10 or more longitudinal ranks ................ Lycopodiella

Figure 3 – Spores. a. Phlegmariorus christii; Brazil, Minas Gerais: Serra do Caparaó, ca. 2100 m. Windisch et al. 4966 (AAU). b. Huperzia selago. Denmark. (X 1000)
**Lycopodium** Linnaeus, Sp. Pl. 1100. 1753. – Type: *Lycopodium clavatum* L.

Sporophytes terrestrial, anisotomously branched, with elongate, indeterminate, creeping, or scandent, plectostelic main stems (rhizomes), which, in a dorsolateral position, give rise to usually determinate, ascending to erect, or spreading, repeatedly dorsolaterally branched, branchlet systems. Roots emerging directly along the underside of main stems, with plectostelic main roots. Branchlet leaves uniform terminating in a colorless hair tip or membranous apex. Strobili erect, simple or forked, borne on simple or forked peduncles or rarely sessile. Sporophylls subpeltate with a thin basal decurrent wing, with a basal mucilage-bearing cavity. Sporangia attached to the sporophyll base, reniform, each with a short thick stalk, isovalvate, their epidermal cells with thin, lignified, sinuate side walls, with numerous small in- and evaginations. Spores reticulate on all faces.

The generic description includes only neotropical representatives of the genus, which has probably only two species in South America, and only one in Brazil. The genus occurs on all continents except Australia. *Lycopodium clavatum* is virtually cosmopolitan and quite variable, as indicated by the large number of names referred to this species below. Tetraploids and triploids of this species reported from Japan (Takamiya & Tanaka 1982) seem morphologically recognizable; similar plants also occur in the Neotropics. Chemical differences between Old World and Neotropical populations of *L. clavatum* suggest that genetic variation is involved (Brackman et al. 1974).

**Lycopodium clavatum** L.


*Lycopodium clavatum* L. var. *equisetoides* Nessel, Arch. Bot. São Paulo 1(4): 438 1927. – Syntypes: Brazil, Minas Gerais. s. d., *Wawra s.n.*, (W, not seen); Brazil, São Paulo, 1904, *Grossmann 36* (not seen); Brazil, Paraná: 18 Nov 1898, *Dusén s. n.* (S, not seen; illustrated in Nessel 1955, fig. 103, presumably showing a duplicate specimen from S, now in BONN-Nessel 112 !).


Rhizomes creeping, trailing, or hanging over banks, usually aboveground, rooting with long intervals, 2–3(–4) mm thick excluding leaves. Aerial branches ascending to stiffly erect, to at least 50 cm tall, 1.5–3 mm thick excl. leaves at origin, repeatedly unequally branched, with strongly diverging to almost parallel branchlets. Ultimate branchlets radial. Leaves of main axes and branchlets essentially similar, borne in low alternating spirals or whorls of 6–8(–10), forming 12–16(–20) indistinct longitudinal ranks, patent to ascending or imbricate, linear-acicular, 6–8(–14) mm long, 0.5–0.8 mm wide at the base, terminating in a long hair or membranous apex, with smooth to sparsely denticulate margins. Strobili short- to long-pedunculate. Peduncles terminating main axes of branchlet systems, erect, to 30 cm tall, simple or branched and bearing up to 6 pedicellate strobili. Peduncle leaves distant, adpressed, reduced in length, partially membranous. Strobili 1.5–6(–8) cm long, ca. 4–6 mm diam. (including sporophylls), simple, or sometimes forked. Sporophylls borne in alternating whorls of (4–)5–6, forming (8–)10–12 longitudinal ranks, subpeltate, with a median, basiscopic, membranous wing on the stalk, with triangular-ovate to rhombic-ovate, acuminate exterior face, 3–5(–12) mm long,
ca. 1.4–2 mm wide, with usually broadly scarios, dentate to erose-laciniate margins, and hairlike apex. Sporangia 1.3–1.6 mm wide. Spores reticulate on all faces.


Habitats. Terrestrial and rupestral, trailing or scrambling in open and usually humid places such as road cuts, roadsides, rock crevices, trail margins, often in pioneer habitats; alt. ca. 600–2500 m.

*Lycopodium clavatum* is highly variable and adaptive to external factors. Nessel (1927 and 1955) recognized seven and eight varieties respectively. The delimitation of these seems arbitrary, and in our opinion fails to reflect any significant biological or morphological features. At higher elevations in Serra do Caparaó in the State of Minas Gerais forms are encountered that approach the high Andean *Lycopodium clavatum* subsp. *contiguum* (Klotzsch) B. Øllg. in the almost parallel, erect branchlets, and often forked strobili. However, the strobili are invariably pedunculate, and the peduncles often branched. The type of *L. clavatum* var. *minarum* Christ cited above is a robust individual of *L. clavatum* and is not referable to the high elevation forms from Serra do Caparaó.


Sporophytes with subturannce or creeping main stems; isophyllous, the leaves herbaceous throughout; strobili pedunculate or sessile; sporophylls peltate, each with a narrow terete stalk lacking a membranous wing, lacking mucilage cavities; sporangial epidermal cells with thin, evenly sinuate sidewalls; spores reticulate, with medium-sized, irregular meshes, unornamented on proximal faces; gametophytes obconic (in *Austrolycopodium fastigiatum*).

The genus occurs in Australia, Tasmania, New Zealand, Juan Fernandez, Costa Rica, Hispaniola, Andes from Venezuela to Tierra del Fuego, Malvinas, southern and southeastern Brazil, South Georgia, Kerguelen, and Mount Aberdare in Uganda. *Austrolycopodium* superficially resembles *Lycopodium*, and usually has been included with it. Both genera are isophyllous and have pedunculate strobili. However, *Austrolycopodium* is quite distinct, lacking piliferous or membranous leaf apices, having peltate sporophylls, also a different spore type and chromosome number (*Lycopodium s.str. x=34; Austrolycopodium x=31*). The geographical distribution is predominantly austral. The greatest diversity of the group is in Southern South America. The taxonomy of the group is in need of a modern revision.

**Austrolycopodium erectum** (Philippi) Holub, Folia Geobot. Phytotax. 26: 91. 1991. Fig. 4


Gerais, Serra do Caparaô 1900 m, \textit{Schwacke 6205} (lectotype here designated \textit{RB!}, isotype \textit{P!}); Brazil, Rio de Janeiro, Serra da Itatiaia, \textit{Ule 300} (HBG!, \textit{P!}); Brazil, Rio de Janeiro, Serra da Itatiaia, 2100 m, \textit{Ule 3536} (HBG!, \textit{P!}); Brazil, Santa Catharina, Serra Geral, \textit{Ule 2332} (HBG!).

Illustration: Nessel (1955: fig. 105).

Rhizomes subterranean or occasionally aboveground, 1.5–3 mm thick excluding leaves, giving rise to erect, somewhat tree-like aerial shoots, these 1–2 mm thick excl. leaves at origin, to 30(–50) cm tall including peduncles and strobili, repeatedly unequally branched, usually with a well-defined main axis, bearing spreading to ascending branchlet systems. Leaves of main axes subulate, to 6 mm long, to 1.3 mm wide. Branchlets radial, 3–7 mm diam. incl. leaves. Branchlet leaves acicular, somewhat flattened, smooth, with a long pointed, non-piliferous apex, 2.5–5 mm long, (0.4–)0.6–0.8 mm wide. Strobili sessile, or terminating somewhat indistinct, simple or up to 2-forked peduncles, 3–4 mm thick, 1–4(–6) cm long, often forked. Sporophylls borne in alternating whorls of 3 or 4, forming 6–8 somewhat irregular longitudinal ranks, peltate, each with a slender, terete,
wingless stalk, with broadly ovate, short- to long-acuminate exterior face attached to the stalk below the center, with narrowly scarios, shallowly erose-denticulate to almost smooth margins. Sporangia ca. 1.2–1.5 mm wide. Spores reticulate on distal faces, unornamented on proximal faces.


**Habitat.** In Brazil this species occurs terrestrially in high elevation grasslands, 1900–2750 m, in the States of Minas Gerais, Rio de Janeiro, and at a few localities at lower elevations (900–1000 m) in the States of Santa Catarina and Rio Grande do Sul.

This species has been included in *Austrolycopodium fastigiatum* (R. Br.) Holub (type from New Zealand), and the characters separating these, as well as *Austrolycopodium aberdaricum* (Chiov.) Holub from Mount Aberdare in Africa are subtle and overlapping. Some of the dwarfed growth forms of the species are very like *Austrolycopodium magellanicum* (P. Beauv.) Holub, and the delimitation of the two taxa needs more study. The tree-like aspect, and a well developed main axis in the aerial shoots of *A. erectum* is the most conspicuous difference. The material from Santa Catarina and Rio Grande do Sul deviates slightly from the northern populations by narrower leaves and sporophylls borne in whorls of 3, forming 6 irregular ranks. Herter (1950: 99), considered *Lycopodium erectum* Philippi a homonym of *L. erectum* Dill., but apparently Dillenius did not publish this name.

**Diphasium** C. Presl ex Rothm., Feddes Repert. 54: 64. 1944. Type: *Diphasium jussiaei* (Poir.) Rothm. (=*Lycopodium jussiaei* Poir.).


Sporophytes with subterranean or creeping to subscandent main stems; branchlets dorsiventral, anisophyllous, with dimorphic leaves, two dorsolateral ranks of broad alternate leaves, and two or three ventral ranks of narrow membranous-tipped leaves; strobili pedunculate or sessile; sporophylls subpeltate; sporangial epidermal cells with sinuate, finely curled side walls; spores reticulate with large meshes and unornamented proximal faces; gametophytes obconic; x = 34–36, ca. 90.

**Diphasium jussiaei** (Desv. ex Poir.) C. Presl ex Rothm., Feddes Repert. 54: 65. 1944. **Fig. 5**


See Øllgaard (1988: 131) for additional synonymy.

**Illustrations:** Nessel (1955: fig. 108); Øllgaard (1988: fig. 25B)

Plants creeping, trailing or hanging over banks. Rhizomes usually aboveground, rigid, 2–4 mm thick. Leaves of main stems radially arranged, uniform, 3–5 mm long, ca. 1 mm wide, linear-lanceolate, each with broadly membranous distal part and apex (sometimes scarios), irregularly obtuse to acute, erose apex. Aerial shoot systems 5–75 cm tall, in large individuals with a main axis almost conform to the rhizome, upward becoming anisophyllous, bearing alternating, fan-shaped branchlet systems. Branchlets dorsiventral, anisophyllous, flattened, 4–6(–8) mm wide (including leaves), with 2 dorsolateral ranks of broad leaves and 2–3 indistinct ventral ranks of narrow leaves. Dorsolateral leaves obliquely elliptic, the acrosopic margin 2–3.5 mm long, 1–1.5 mm wide, upward and ventrally curved, subacute to mucronate to short hair-tipped, basiscopic margin decurrent. Ventral leaves appressed, lanceolate-subulate, with membranous apices. Strobili terminating main aerial axes, or stronger branches, pedunculate. Peduncles to 12 cm long, simple or to 2-forked, bearing 1–3 strobili, terete, with distant, narrow, appressed leaves. Strobili (1–)3–10 cm long, 4–6 mm diam. incl. leaves. Sporophylls borne in alternating whorls of 4, forming 8 longitudinal ranks, subpeltate, with a basiscopic, median, membranaceous, decurrent wing on the stalk, with ovate, more or
less acuminate exterior face, 4–6 mm long, ca. 2 mm wide, with narrowly membranous, shallowly erose, denticulate margins. Sporangia 1.5–2 mm diam. Spores reticulate, with large, regular meshes on distal faces, and unornamented proximal faces.

Distribution. Costa Rica, Jamaica, Hispaniola, Venezuela, Andes south to Bolivia, Brazil (Mount Itaiaia, in the states of Minas Gerais, and Rio de Janeiro, Sao Paulo).

Habitat. Usually a vigorous scrambling to scandent plant, in clearings, on road cuts, rupestral habitats, and open places in montane scrub forests. Elevation 1800–2400 m.

Diphasium jussiaei is closely related to D. scariosum (G. Forst.) Rothm. (Indonesia to New Zealand), and to plants from Chile, Juan Fernandez, and Argentina, recognized as Diphasium gayanum (Remy) Holub. The plants referred to Diphasium jussiaei, including the Brazilian ones, are generally larger and coarser than those species.

Key to the species of Diphasiastrum in Brazil

1. Lateral leaves of terminal branchlets each with long, semiterete, rigid and strongly falcate free blade, nearly equalling to longer than the adnate basal part (Fig. 6a-b) .............. Diphasiastrum falcatum
1. Lateral leaves of terminal branchlets each with the free blade short- to long-deltate, usually shorter than the adnate basal part, often ending a thin and weak long-pointed tip (Fig. 6c-d) ...................... Diphasiastrum thyoides
**Diphasiastrum thyoides** (Willd.) Holub, Preslia 47: 108. 1975.


Illustrations: Mickel & Beitel (1988: fig. 2A); Nessel (1955: fig. 107); Øllgaard (1988: fig. 25A).

Plants with creeping, trailing to scandent aerial parts. Main stems usually aboveground, or hanging over banks, terete, 1.2–2.5 mm diam. (excluding leaves). Main stem leaves relatively distant, borne in irregular spirals, or subverticillate, subulate, appressed to ascending. Aerial shoots arising from the rhizomes in a dorsolateral position, ascending to erect, 10–50 cm tall, with vegetative portions to ca. 30 cm tall. Main upright axis terete to somewhat flattened, bearing lateral, flattened, fan-shaped branchlet systems. Ultimate branchlets flattened, dorsiventral, anisophyllous, 1.5–3 mm wide including leaves, with trimorphic, decussate leaves in 4 ranks. Distal, median branchlet leaves with pointed, subulate to acicular, appressed, 1–2 mm long, free blades, and a conspicuous, ca. 0.4–0.6 mm wide, prominently decurrent base. Lateral branchlet leaves bilaterally compressed, long-decurrent, 2.5–7 mm long incl. bases, the free blades 1–3 mm long, appressed to spreading, acuminate to long-pointed, the leaf bases 0.6–1.5 mm wide. Ventral leaves inconspicuous, acicular, without decurrent base, 1–2 mm long. Strobili pedunculate. Peduncles terminating main erect axis or major axes of distal branchlet systems, 10–25 cm long, terete, with rather distant, subulate, appressed leaves, each bearing 4–9 pedicellate strobili. Strobili 1.5–5 cm long, 2–4 mm diam. incl. sporophylls, often with protracted sterile tips. Sporophylls usually borne in alternating whorls of 3, forming 6 longitudinal ranks, subpeltate, with a basiscopic, median wing on the stalk, with broadly deltate-ovate, long-cuspitate, ca. 2–3 mm long, 1.5–2 mm wide exterior face, with erose-laciniate to almost entire, broadly membranous margins. Sporangia 1.5–2 mm diam. Spores densely reticulate on all faces.


Habitats. Clearings, road banks, open habitats, and secondary scrub in upper montane forest, alt. 400–2450 m.

The present application of the name *Diphasiastrum thyoides* corresponds to the "Lycopodium thyoides-complex" of Wilce (1965: 155-158). The Brazilian material referred to this species is highly variable and may belong to more than one taxon, but also external factors apparently greatly affect the growth habit of the individuals. We have not attempted to treat the infraspecific variation, apart from the description of *D. falcatum* below.

The following names: *Lycopodium complanatum* L. var. *tropicum* Spring, in Martius, Fl. bras. 1: 116. 1840, and *Lycopodium complanatum* L. var. *adpressifolium* Spring, Mem. Acad. Roy. Sci. 15: 102. 1842, are here considered to be synonyms of the present concept of *Diphasiastrum thyoides*. We have not seen the relevant type material.

Spring (1842: 102) placed var. *tropicum* in synonymy under var. *adpressifolium*, and both in synonymy under *L. thyoides* (the latter as as a synonym under *L. complanatum*, making var. *adpressifolium* a superfluous name for var. *tropicum*, and citing Martius (M), and Schott (W not seen) as syntypes. of var. *tropicum*. 

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**Figure 6 – Diphasiastrum – a-b. Diphasiastrum falcatum, holotype in R – a. branchlet upperside; b. branchlet underside. c-d. Diphasiastrum thyoides, Brazil, Rio de Janeiro, Serra do Papagaio, 900 m, Carauta 2969 (AAU) – c. branchlet upper side; d. branchlet underside. Scale in mm.**

Diphasiastrum falcatum B. Øllg. & P.G. Windisch, sp. nov. TYPE: BRAZIL. RIO DE JANEIRO: Serra dos Órgãos, 2000 m, 27.II.193, Brade 12440 (holotype R, isotypes AAU!, HB!). Figs. 6a-b, 7

Species nova Diphasiastro thyoides affinis, a qua differt statura graciliore, foliis lateralibus ramuluiorum ultimorum cum apice libro linearisubulato semitereti, valde falcato rigido, partem adnatum aequante vel superante.

Plants with creeping rhizomes, usually aboveground. Rhizomes terete, 1.5–2 mm diam. excluding leaves. Rhizome leaves relatively distant, borne in irregular spirals, or subverticillate, subulate, appressed to ascending. Aerial shoots arising from the rhizomes in a dorsolateral position, ascending to erect, to 30 cm tall, with vegetative portions to ca. 20 cm tall. Main upright axis terete to somewhat flattened, bearing lateral, flattened, fan-shaped branchlet systems. Lower divisions subsopolystalous, with subulate, irregularly spirally to decussately arranged leaves. Ultimate branchlets flattened to bluntly triangular, dorsiventral, anisophyllous, 1.5–3.2 mm wide including leaves, with trimorphic, decussate or subdecussate leaves in 4 ranks. Distal, median branchlet leaves linear-subulate, the free part semiterete, falcate, 1–2 mm long, and with a conspicuous, ca. 0.4–0.6 mm wide prominently decurrent base. Lateral branchlet leaves bilaterally compressed, long-decurrent, 3–4 mm long incl. the adnate basal part, the free blades 1.5–2.5 mm long, rigid and strongly falcate, semiterete with a prominent vein ridge on the lower side, linear-subulate, the adnate leaf bases 1.5–2.5 mm long, with almost parallel to somewhat diverging margins, often curved down. Ventral branchlet leaves subulate, with slightly decurrent base, their free part 1–1.5 mm long. Peduncles terminating main erect axis or major axes of distal branchlet systems, to 12 cm long, to 4-forked, terete, with rather distant, subulate, appressed leaves, each bearing up to 6 pedicellate strobili. Strobili 1–2.5 cm long, 2–2.5 mm diam. incl. sporophylls. Sporophylls usually borne in alternating whorls of 3 or 4, forming 6–8 longitudinal ranks, subpellate, with a basiscopic, median wing on the stalk, with broadly deltate-cordate, slightly acuminate, ca. 2–2.5 mm long, ca. 1–1.3 mm wide exterior face, with almost entire, narrowly membranous margins. Sporangia 1–1.3 mm wide. Spores normally developed, reticulate on all faces.


This species has some features resembling juvenile plants of Diphasiastrum thyoides (Willd.) Holub due to the subulate and irregularly spiraled leaves of the basal divisions and central axes of

Figure 7 – Diphasiastrum falcatum – holotype in R.
the branchlet systems. However the 3 collections are all fertile, and the terminal branchlets are distinct, especially due to the rather full, rigid, and strongly falcate free blades of the lateral leaves. No collections intermediate between this species and *D. thyoides* have been observed.

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