ABSTRACT

TAXONOMY OF NEW WORLD PSEUDOLYCOPODIELLA

by Kelsey Cook

Pseudolycopodiella is a small, pantropical genus of wetland lycopsids that remains largely unstudied. The gross morphology of the plants is strikingly similar across its broad range and systematic work on the genus has been limited in scope, both geographically and taxonomically. Species within the group remain poorly defined, and authors are in disagreement on the number of taxa and their rank. The present work addresses this problem by examining herbarium material of Pseudolycopodiella from throughout its range in the Americas. Study of the morphology of these plants using both a traditional herbarium approach and multivariate statistics has identified ten species, one of which is new. These species, their morphology, and their ranges are presented and discussed.
TAXONOMY OF NEW WORLD PSEUDOLYCOPODIELLA

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**Introduction**

*Pseudolycopodiella* Holub, the slender bog or Carolina clubmoss, is a small genus of terrestrial lycopsids in the Lycopodiaceae. The genus is characterized by prostrate, creeping rhizomes bearing unbranched, erect fertile shoots composed of a slender, unbranched peduncle that is, in most species, sparsely leafy and a single, differentiated strobilus with reniform sporangia. The sporophylls are distinct from the peduncle leaves in color, shape, and texture. Members of the genus have rugulate spores and green, photosynthetic gametophytes that live on the surface of the ground. The genus is found in wet habitats, such as bogs, wet savannahs, ditches, and riversides. It is broadly distributed, with representatives in North, Central, and South America, the Caribbean, sub-Saharan Africa, Madagascar, Asia, Australia, New Zealand, and New Guinea. Their broad range and simple morphology have been obstacles to understanding these plants and their taxonomy.

*Pseudolycopodiella* was historically considered part of a broadly circumscribed *Lycopodium* L. This *Lycopodium sensu lato* has since been broken up into sections, subgenera, or segregate genera by various authors. Information on spore morphology (Wilson 1934, Wilce 1972), leaf anatomy (Chu 1974), sporophyll morphology (Sykes 1906), stem anatomy (Jones 1904), sporangial wall structure (Øllgaard 1975), mucilage canal distribution (Bruce 1976b), branching pattern (Øllgaard 1979), gametophyte structure (Boivin 1950, Bruce 1976c, Holloway 1919), phytochemical distribution (Markham et al. 1983), chromosome number (Wagner 1992), and molecular data (Wikström and Kenrick 1997, Wikström and Kenrick 2000, Yatsentyuk et al. 2001), in addition to observations of gross morphology, have been used to propose and support these different classifications.

*Pseudolycopodiella* was recognized as part of the segregate genus *Lycopodiella* Holub, with which it shares a general body plan, habitat, and gametophyte type, by Pichi Sermolli (1968). Holub (1983) later split *Lycopodiella* to make the new genus, *Pseudolycopodiella*, on the basis of their reniform, isovalvate sporangia, the strong differentiation between peduncle leaves and sporophylls, and the absence of veinal mucilage canals. In contrast, *Lycopodiella sensu stricto* has globose, anisovalvate sporangia, similar peduncle and strobilus leaves, and veinal mucilage canals. Bruce (1976b) and Øllgaard (1987), respectively, treated the group as a section of either *Lycopodium* or *Lycopodiella*. Molecular phylogenetic studies of the Lycopodiaceae have been performed (Wikström and Kenrick 1997, Wikström and Kenrick 2000, Yatsentyuk et al. 2001), but only one species of *Pseudolycopodiella* has been sampled. Hence, the monophyly of the group cannot be ascertained on the basis of currently available molecular information.

Work within *Pseudolycopodiella* has been scattered and mostly limited in scope. In Nessel’s 1939 monograph on the entire Lycopodiaceae, he recognized four species in what is now considered *Pseudolycopodiella*. One of them, *Lycopodium carolinianum* L., was broadly circumscribed. The species was considered widespread and polymorphic. It was interpreted as spanning the globe and including fifteen varieties. Holub (1983, 1985) and Øllgaard (1987) in describing the group, listed included species, but did not discuss them or their relationships.

More detailed studies have been regional in nature. Ballard (1950) examined the members of the group in Africa by studying herbarium specimens. He concluded that there
there were two taxa on the continent, *Lycopodium sarcocaulon* A. Braun & Welw. ex Kuhn and *Lycopodium carolinianum* var. *tuberosum* (Kuhn) Verdc., the latter considered highly variable. Bruce (1976a) did a focused study on *L. carolinianum* in the eastern United States, with an emphasis on their anatomy. Chromosome squashes revealed the presence of diploid and tetraploid individuals within the study area, as well as triploid hybrids. He observed that the tetraploids had larger spores than diploids, and the triploids had high levels of spore abortion, but otherwise found no morphological differences between the cytotypes.

There is considerable disagreement amongst authors on the numbers, circumscriptions, and ranks of *Pseudolycopodiella* taxa. For example, Nessel (1939) recognized fifteen varieties within his *Lycopodium carolinianum*. On the other hand, Holub (1983, 1985) treated some of the same taxa as species and recognized no varieties. In the *P. iuliformis* (Underw. & F. E. Lloyd) Holub group of northern South America, Øllgaard (1992) recognized a single species with two varieties. Vareschi (1969) accepted three separate species in this group. Estimates of the total global species diversity of the group has ranged from four (Nessel 1939), around ten (Arana & Øllgaard 2012), to twelve (Wagner & Beitel 1993). No broad scale review in a modern systematic framework has been done on *Pseudolycopodiella* to clarify the number of taxa and the boundaries between them.

The goal of the present work is to delineate taxa of *Pseudolycopodiella* in the New World, which contains most of its diversity, and to provide a taxonomic treatment of the group. This study is novel in using quantitative data and methods in addition to qualitative observations. It also differs in that it surveys a large portion of the group’s geographic distribution.

**Materials and Methods**

Over 1000 sheets of herbarium material representing about 700 collections were examined from various herbaria (AAU, F, FLAS, GA, GH, MICH, MO, MU, NCU, NY, US, abbreviations from Index Herbariorum, http://sweetgum.nybg.org/ih/). The material spans the entire known range of *Pseudolycopodiella* in the New World. Of these, 262 collections in good condition with all necessary material (fertile; all organs present and visible) were used to take measurements of morphological characters with the help of a dissecting microscope. For the sake of this study, each of the collections was treated as an operational taxonomic unit (OTU).

The quantitative characters that were used in statistical analyses are listed in Table 1. **List of quantitative characters** and described below. Figure 1. **General morphology of Pseudolycopodiella** outlines the organography of *Pseudolycopodiella* and the pertinent terminology.

Lengths and widths of six laterally positioned and six dorsally positioned leaves on the prostrate, indeterminate shoot, or rhizome, and six leaves of the upright, determinate shoot, or peduncle, were taken for each collection. Leaves near the growing shoot apices were avoided to ensure that the measured leaves were fully mature and expanded. Peduncle leaf measurements were taken from leaves toward the middle of the peduncle. One to five sporophylls were also measured per collection. Sporophyll lengths excluded the
membranaceous flap found at their bases. An attempt was also made to measure sporophylls with the flap and to measure the flap by itself, however; they are very brittle and variable in length, so this was abandoned. Length to width ratios were also calculated for each kind of vegetative leaf and for sporophylls. The averages for the lengths, widths, and ratios for each type of leaf were used in further analyses.

Peduncle width was measured at the mid-length of the peduncle. Separate measurements were taken that included or excluded the peduncle leaves. Peduncle length was measured from the point of insertion on the rhizome to the base of the strobilus. Strobilus length and width measurements were taken in the same way. Up to three measurements of each character were taken on each collection depending upon the availability of material.

A single rhizome width measurement was taken per collection. This was taken from a mature, typical-looking portion of the rhizome and excluded leaves.

Numbers of leaf ranks were recorded for the strobilus, peduncle, and rhizome. Leaves occur in alternating pseudowhorls or spirals. For rhiomes and peduncle leaves, the number of leaves in a single pseudowhorl or spiral was recorded. For strobili, because the pseudowhorls are so close together, the number of leaves in two adjacent pseudowhorls was recorded.

A proxy for peduncle leaf density was taken by measuring the distance from the base of one pseudowhorl/spiral to the base of the one three whorls up. This was done near the middle of the peduncle for a single peduncle per collection. Higher numbers indicate that the leaves are farther apart and less dense.

For selected specimens, the diameters of twenty-five spores were measured using a light microscope. Measurements excluded the ornamented perispore but included the endospore wall. The spores were collected with a probe or tweezers and mounted in Hoyer’s medium. Spores were measured between 12 and 48 hours after mounting. This allowed time for the spores to settle but avoided any significant swelling caused by the mounting medium. Scanning electron micrographs were also taken of selected, representative specimens. For this, spores were mounted on stubs using double-sided carbon adhesive and were sputter coated with gold. They were imaged using a Zeiss SUPRA 35 VP.

Additionally, various qualitative characters were examined and noted for each collection. These included leaf shape, sporophyll margin, phyllotaxy, branching pattern, rhizome cross-sectional shape, plant color, and leaf curvature. These data were not used in statistical analyses because they could not be quantified or categorized in meaningful ways that were usable in the analyses.

Data analysis involved both a traditional neural taxonomic approach and statistical analyses. The traditional approach involved repeatedly examining herbarium specimens and looking for discrete morphological groups of specimens that were distinct from other such groups. Such groups were thought of as provisional taxa.

Multivariate techniques, including Principal Components Analysis and Cluster Analysis, were used to analyze the quantitative data of provisional taxa. Principal Components Analysis (Jolliffe 2002) works by taking multivariate data and using it to create new, uncorrelated variables, called Principal Components (PCs). The PCs contain decreasing portions of the variation present in the original data, so most of the variation is usually contained in the first few PCs. This makes it possible to look at only a few PCs, as opposed to the original dataset with many variables, with minimal loss of information.
### Table 1. List of quantitative characters analyzed

1. dorsal leaf length
2. dorsal leaf width
3. dorsal leaf length:width ratio
4. lateral leaf length
5. lateral leaf width
6. lateral leaf length:width ratio
7. peduncle leaf length
8. peduncle leaf width
9. peduncle leaf length:width ratio
10. peduncle height
11. peduncle width; excluding leaves
12. peduncle width; including leaves
13. sporophyll length
14. sporophyll width
15. sporophyll length: width ratio
16. strobilus height
17. strobilus width; excluding sporophylls
18. strobilus width; including sporophylls
19. rhizome width
20. peduncle leaf density
21. rhizome leaf ranks
22. peduncle leaf ranks
23. sporophyll ranks
24. spore diameter
Figure 1. General morphology of *Pseudolycopodiella* (*J. Prado 422 NY*). A. Plant habit. B. Details of the strobilus, highlighting the sporophylls, or sporangia bearing leaves. C. Details of the peduncle, highlighting the pseudowhorls of small leaves. D. Details of the rhizome, highlighting the leaves borne on the lateral and dorsal surfaces.

Hierarchical Cluster Analysis uses multivariate data to create dendrograms. The distance in multivariate character space between all possible pairs of OTUs is calculated and put in a matrix. The two OTUs with the smallest distance between them are joined together into a cluster. The distance matrix is then recalculated, with the new cluster treated as a single unit. This process continues until all OTUs are associated in a single cluster. The order in which OTUs are grouped is used to make the dendrogram. Because there are many algorithms to calculate distances and produce a dendrogram, three methods were employed; average linkage (Sokal and Michener 1958), centroid method (Milligan 1979), and Ward’s method (Ward 1963). The different outputs were compared so that conclusions were not made based on what might be a relic of a particular method.
Some groups of characters are directly correlated with each other. For example, leaf length and width measurements are used to calculate length to width ratios. Using all three together in a multivariate analysis is problematic because it is sampling the same character more than once, which may bias the analyses. To overcome this problem, separate analyses were performed with just lengths and width, just ratios, and with both. The results of all analyses were compared and taken into consideration.

Additionally, scatterplots comparing pairs of characters and distributions of individual characters were examined. All of these analyses were used to visualize the data and identify distinct groupings of data points. Statistical analyses were done in JMP Version 11.0.0 (SAS Institute Inc.) and R (R Development Core Team 2008) with the package “beanplot” (Kampstra 2008).

Distribution maps were made using R with the packages “maps” (Brownrigg 2014b) and “mapdata” (Brownrigg 2014a). Latitude, longitude, and elevation data were taken directly from specimen labels when available. When they were not present on a label, data were approximated using available locality information and Google Earth (Google Inc. 2015).

Results and Discussion


**Rhizome Phyllotaxy**

Two phyllotactic patterns are found in New World *Pseudolycopodiella*. These separate the plants into two subgroups which are dealt with separately in many of the following analyses. In the first, rhizome leaves are isophyllous (Figure 2C, D). Leaves entirely encircle the rhizome, ventral leave are present, and there is little to no differentiation between leaves on the dorsal and lateral surfaces of the rhizome. When some differentiation is present, dorsal leaves grade into lateral ones. This is unlike the sharp differentiation seen in anisophyllous taxa. The isophyllous group includes *P. contexta, P. iuliformis, P. krameriana*, and *P. tatei*.

In the other pattern, rhizome leaves are anisophyllous (Figure 2A, B). Dorsal and lateral leaves are starkly differentiated in size and shape without gradation between them and ventral leaves are absent. The anisophyllous group includes *Pseudolycopodiella carnososa, P. caroliniana, P. meridionalis, P. mesetarum, P. paradoxa*, and *P. floridana*. This group can also be referred to as the *P. caroliniana* complex.
Figure 2. Comparison of anisophyllous and isophyllous rhizomes. A. Top-down view of anisophyllous rhizome, showing distinct dorsal and lateral leaves (J. Prado 422 NY). B. Undersurface of anisophyllous rhizome, showing the absence of ventral leaves (J. Prado 422 NY). C. Side on view of an isophyllous rhizome, showing ventral leaves and intergrading dorsal and lateral leaves (Plowman & Thomas 13626 MO). D. Undersurface of an isophyllous rhizome showing ventral leaves (Vareschi & Foldats 4622 US).
The results of the PCAs are shown in Figure 3, Figure 5, and Figure 7, with plots of the character loadings (eigenvectors) in Figure 4, Figure 6, and Figure 7. The results did not vary substantially depending on the use of lengths and widths, ratios, or both together, so only the results of the analysis using lengths and width are shown for each group of taxa analyzed.

In the analysis of the isophyllous taxa (Figure 3-Figure 4), the first three components account for 33.4%, 29%, and 11.6% of the variation in the data, respectively, for a total of 74%. Specimens of *Pseudolycopodiella contexta* form a cluster at the higher end of principal component (PC) 1. This PC has loadings for characters related to the peduncle, including peduncle height, peduncle leaf ranks, and peduncle leaf density. *Pseudolycopodiella iuliformis* and *P. krameriana* are concentrated in the center, with *P. krameriana* entirely overlapping with *P. iuliformis*. A cluster of *P. iuliformis* that are small in size are found at low values of PC1 and PC2. *Pseudolycopodiella tatei* is separated from the others along PC3, which has a strong negative loading for rhizome width and positive loadings for sporophyll width and dorsal leaf length.

In the analysis of all of the anisophyllous taxa (Figure 5-Figure 7), the first three PCs account for 41%, 15.2% and 9.24% of the variation in the data, respectively, for a total of 65.44%. There is extensive overlap among putative taxa, particularly toward the centers of the graphs. This is likely due to the large number of data points. All character loadings in PC1 are positive, meaning that this PC reflects the overall size of the plants, with larger plants scoring higher in PC1. The most distinct cluster, *Pseudolycopodiella carnosas*, tends to score high in PC1 and low in PC2 and PC3. PC2 has high positive loadings for dorsal and lateral leaf length. *Pseudolycopodiella paradoxa* forms a cluster at the lower ends of PC1 and PC2, indicating its small overall size and short leaves. *Pseudolycopodiella mesetarum* is separated from the others at the high end of PC3, which has high positive loadings for rhizome leaf ranks and dorsal leaf length and negative loadings for lateral leaf width and peduncle height.

A second PCA of anisophyllous specimens

Figure 7) with fewer taxa and specimens included was done to avoid the congestion of data points found in the previous PCA. The first two PCs account for 43.1% and 13.4% of the total variation in the data, for a total of 56.5%. As before, all the character loadings for the first PC are positive. In this analysis we see three clusters of data points, with some overlap in the center of the graph. Specimens of *Pseudolycopodiella caroliniana* are clustered toward the
negative end of PC1, reflecting their small size. *Pseudolycopodiella meridionalis* and *P. floridana* are grouped toward the positive side of PC1. They are separated from each other along PC2.

Figure 3. PCA score plots of the first three PCs of analysis on isophyllous taxa.
Figure 4. Character loading plots for PCA of isophyllous taxa.
Figure 5. PCA score plots for first three PCs of analysis on anisophyllous taxa.

Legend
- P. carnosoa
- P. caroliniana
- P. floridana
- P. meridionalis
- P. mesetarum
- P. paradoxa
Figure 6. Character loading plots for PCA of anisophyllous taxa.
Figure 7. PCA score plot and character loading plot for first two PCs for analysis of selected anisophyllous taxa.

Cluster Analysis

As with the PCAs, there was no substantial difference between analyses done with just lengths and widths, just ratios, or both together. Nor were there considerable differences in the results between different distance calculating methods. The figures presented and discussed here were all made using lengths and widths and by using Ward’s method to calculate distances, which produced the most aesthetically appealing dendrograms.

The cluster analysis of the isophyllous taxa (Figure 8) produced two major clusters. The first is composed almost entirely of *Pseudolycopodiella contexta*, with two *P. iuliformis* mixed in. Examination of the two *P. iuliformis* collections showed that they had unusually long, narrow leaves, similar to *P. contexta*. The second cluster includes the rest of *P. iuliformis*, with *P. krameriana* and *P. tatei*. The *P. tatei* collections are mostly clustered together, but are
nested within the *P. iuliformis* cluster. *Pseudolycopodiella krameriana* does not form a separate cluster. This may be because there are only two collections of this taxon included and because their measurements are very similar to those of *P. iuliformis*. This taxon is best identified using qualitative characters.

The cluster analysis of the anisophyllous taxa (Figure 9) produced two major clusters, each made up of smaller subclusters. The first cluster includes two subclusters; one of all collections of *Pseudolycopodiella paradoxa* and another with almost all *P. caroliniana*. A couple collections from other taxa are included in each subcluster. Both *P. paradoxa* and *P. caroliniana* are characteristically small and likely group together for this reason. The second major cluster includes the other four taxa. One subcluster in this group contains most of the *P. carnosana*. All collections of *P. mesetarum* are grouped into the same subcluster. Collections of *P. meridionalis* and *P. floridana* are intermixed with each other.

**Rhizome Shape**

In most collections the rhizome is terete or slightly flattened in cross-section. In some plants the rhizome is fleshy and conspicuously flattened dorsoventrally. Because of the infrequent occurrence of this trait and its consistent co-occurrence with certain other characters, it is unlikely to be an artifact of pressing. The rhizome widths in the flattened taxa are greater than in the terete taxa. (Figure 10, Table 2). Flattened rhizomes occur in the in the anisophyllous group in *P. carnosana* (Figure 11G) and in isophyllous group in *Pseudolycopodiella tatei* (Figure 12A). The adaptive significance of a flattened, fleshy rhizome is unclear. It may function to increase surface area for photosynthesis, to store water and/or nutrients, or to conduct gasses in a waterlogged environment. Cursory examination of dried, pressed rhizomes did not reveal any obviously aerenchymatous tissues.

**Rhizome Leaves**

Dorsal rhizome leaf shape varies from linear to highly reduced and stub-like. The most commonly seen condition in the anisophyllous plants is narrowly triangular to somewhat lanceolate, which is typical in *Pseudolycopodiella caroliniana*, *P. floridana*, and *P. meridionalis* (Figure 11E, C, F). Ovate dorsal leaves are characteristic of *P. paradoxa* (Figure 11D). *Pseudolycopodiella carnosana* has reduced dorsal leaves that can triangular or reduced to the point of being shriveled stubs of leaf tissue (Figure 11G). The dorsal leaves of *P. mesetarum* are long and narrow, being narrowly triangular to linear and are usually recurved (Figure 11, Figure 12A, B). In all anisophyllous taxa lateral leaves are splayed out horizontally and curved, with the leaf apex pointing away from growing shoot of the rhizome. The amount of curvature in the leaves varies from almost straight to sharply falcate. *Pseudolycopodiella paradoxa* and *P. carnosana* tend to have triangular or ovate lateral leaves, while lateral leaves are typically narrowly triangular and lanceolate in other anisophyllous taxa.
Figure 8. Cluster analysis of isophyllous taxa, calculated using Ward’s method. Grey = *P. contexta*, Purple = *P. iuliformis*, Green = *P. krameriana*, Pink = *P. tatei*.
Figure 10. Beanplot of rhizome widths. Large bar at the center of each figure indicates the mean. Smaller bars indicate individual observations; the longer the bar, the more observations at that value.
Table 2. Summary statistics for rhizome widths

<table>
<thead>
<tr>
<th>Taxon</th>
<th>n</th>
<th>Mean (in mm)</th>
<th>Standard Deviation</th>
<th>Min (in mm)</th>
<th>Max (in mm)</th>
</tr>
</thead>
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<td>19</td>
<td>3.05</td>
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<td>1.7</td>
<td>4.5</td>
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<tr>
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<td>0.19</td>
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</tbody>
</table>

In the isophyllous group, three of the four species, Pseudolycopodiella iuliformis, P. contexta, and P. krameriana have narrow triangular to linear rhizome leaves. In P. iuliformis (Figure 12C) the dorsal leaves are usually recurved and the laterally positioned leaves are conspicuously falcate, but unlike the leaves of the anisophyllous taxa, they do not spread horizontally, but instead curve upward and remain more or less appressed to the rhizome. Dorsal leaves are erect to slightly recurved in P. krameriana (Figure 12E). They are somewhat erect in P. contexta (Figure 12D), forming an acute angle with the rhizome. In both of these taxa the lateral leaves are more or less straight. The dorsal and lateral leaves of all three of the above taxa grade into each other. There is not the sharp differentiation as seen in the anisophyllous species. The ventral leaves in this group are small, reduced, often achlorophyllous versions of the upper leaves, although they can be very small and almost hair-like in P. krameriana. The fourth taxon, P. tatei (Figure 12A, B), has triangular to narrowly triangular dorsal leaves with often broadened bases. These leaves grade into its longer, falcate lateral leaves that splay out horizontally, similarly to the anisophyllous taxa. Its ventral leaves are highly reduced, appearing membranaceous and often filamentous.
**Peduncle and Peduncle Leaves**

Peduncle leaves are most distinctive in *Pseudolycopodiella krameriana* (Figure 13A) and *P. contexta* (Figure 13B). In all other taxa, the leaves are borne in sparse pseudowhors (Figure 13C) of 2-5, rarely 6 or 7, which leave much of the peduncle surface exposed. Their leaves are appressed or acutely spreading. The leaves are straight, except occasionally at the base or very top of the peduncle. In *P. contexta* and *P. krameriana* the pseudowhors are densely arranged, such that the leaves cover most of the peduncle. The leaves of *P. contexta* occur in pseudowhors of 6-9 and diverge from the peduncle approximately perpendicular and then curve upward, while those of *P. krameriana* are in pseudowhors of 4-8 and diverge at an angle between 45° and 90°. Also, most taxa have triangular to narrowly triangular peduncle leaves, whereas *P. contexta* and occasionally *P. iuliformis* have linear ones with a greater length to width ratio (Figure 14, Table 3).

**Sporophylls and Strobilus**

Sporophylls in *Pseudolycopodiella* are made of an upper laminar portion, which makes up most of the sporophyll, and a basal membranaceous portion. The laminar portion varies from triangular to lanceolate in shape and has a leathery texture. The membranaceous portion sits below the point of insertion of the sporophyll stalk. It is thin and delicate, narrower than the adjacent laminar tissue, and truncate at its base. Sporophyll apices vary from acute to acuminate. In *P. contexta* and *P. krameriana* the apices are crinkled and have a crispy appearance. Sporophyll and apex shape tend to vary more within taxa than between them. The sporophyll margins are most commonly erose to varying degrees. They are almost entire in *P. krameriana*. In *P. carnosa* and *P. paradoxa* the margins tend to be serrulate, with tiny, more or less regular, teeth. Teeth are larger and more irregular in *P. iuliformis*. Sporophyll length is a useful character for identifying *P. caroliniana*, which characteristically has short sporophylls (Figure 15, Table 4).

**Spores**

Spore length is variable between species (Table 5, Figure 16). Increased spore size, and increased cell size in general, is a possible indicator of polyploidy. It is known from chromosome counts that there are both diploid and tetraploid populations of *Pseudolycopodiella* in the United States and a tetraploid population on Jamaica (Wagner 1992). The distribution of spore length measurements from North American collections is bimodal (Figure 17), which supports the use of spore size as an indicator of polyploidy. Most taxa have spores that are similar in size to the diploid *P. caroliniana*, meaning they are likely also diploids. An average spore size in the range of 35µm to 43µm appears to be typical of diploids. *Pseudolycopodiella floridana* is a tetraploid and has spores that are usually greater than 42µm long. *Pseudolycopodiella iuliformis* also has spores larger than most other taxa and may be a tetraploid. Spores for *P. krameriana* were not available.
Spore ornamentation in *Pseudolycopodiella* is of the rugulate type. There is some variation between taxa in the depth of the ridges and in the prominence of the equatorial flange (Figure 18).

Unusual and abortive spores are frequent in *Pseudolycopodiella*. Spore abortion is particularly common in *P. tatei*, where half or more of the spores are usually misshapen in some way. Flat spores (as in Figure 18J) have been observed in every taxon examined. Spore samples from some individuals were made up almost entirely of flattened spores. It is unclear what kind of developmental or environmental factors drive the formation of these spores.

*Character by character plots*

Plotting two characters against each other in scatterplots is a useful way to see gaps between putative taxa. This approach was especially useful in visualizing differences between *Pseudolycopodiella caroliniana* and *P. floridana*. These two taxa differ primarily in the size of the fertile shoot. Peduncle leaf length and strobilus width together can be used to discern between them (Figure 19). In

*Figure 20*, a plot of dorsal leaf length and width in the anisophyllous group, two general patterns in dorsal leaf shape are apparent. On the left side are *P. paradoxa* and *P. car nosa*, with short, broad leaves. To the right are the other taxa, with longer, narrow leaves. In the bottom right corner are collections with the highest length to width ratios, including all of *P. mesetarum*. For the isophyllous group, the characters of peduncle leaf density and rhizome width are powerful for separating out taxa.

*Figure 21*. The cluster in the bottom left has dense peduncle leaves and narrow rhizomes and includes *P. contexta*. The nebulosus area in the upper right contains collections with large, broad rhizomes. The bottom right has plants with sparse peduncle leaves and narrower rhizomes. The bulk of *P. iuliformis* and *P. krameriana* are in this cluster.
Hybrids and Intermediates

A small number of specimens were found that were intermediate between two otherwise distinct groups. While some of these may be anomalous members of one of the taxa, others are likely hybrids, particularly when they occur in an area where the ranges of two species overlap. Bruce (1976a), in discovering the existence of both diploids (n=35) and tetraploids (n=70) among North American *Pseudolycopodiella*, found triploids (reported as 2n=115, possibly a typo) in Louisiana, where he also found a tetraploid population. These triploids, which also had many aborted spores, were very likely hybrids between diploid and tetraploid plants. Hybrids are expected to occur where *P. caroliniana* and *P. floridana* co-occur and may be included in mixed collections. In this study, possible hybrids with abortive spores have been seen in New Jersey and South Carolina. Hybrids between *P. meridionalis* and *P. floridana* are also likely. High levels of spore abortion were observed in some Caribbean specimens, but it is uncertain if this is due to hybridization or some other cause.

In South America, *Pseudolycopodiella paradoxa* and *P. carnosa* co-occur in much of southern and central Brazil. They also overlap with *P. meridionalis*. Spore sizes suggest that all of these taxa are diploid. *Lycopodiella sensu stricto* has been found to have homoplid hybrids with intact, non-abortive spores (Bruce 1991), so *Pseudolycopodiella* hybrids may also have normal looking spores. Despite this limitation, possible hybrids involving *P. carnosa* are recognizable because of the broad, flattened rhizome of this parent. Intermediates between *P. carnosa* and *P. paradoxa*, with broadened rhizomes and the ovate leaves typical of *P. paradoxa*, were observed in central Brazil collections. These two species are otherwise distinct, and there does not appear to be continuous intergradation between them.
Figure 13. *Pseudolycopodiella* peduncles. A. *P. krameriana* (Kramer and Hekking 3040 GH) with narrowly triangular peduncle leaves, departing from peduncle at an acute angle and gently curving upward. B. *P. contexta* (*L. R. Marinho* 76 NY) with linear peduncle leaves in dense pseudowhorls, departing from the peduncle almost perpendicularly and abruptly curving upward. C. *P. meridionalis* (Christenhusz *et al.* 2535 AAU) narrowly triangular peduncle leaves in sparse pseudowhorls, slightly spreading, not conspicuously curved.
Figure 14. Beanplot of peduncle leaf length to width ratios for isophyllous taxa. Large bar at the center of each figure indicates the mean, smaller bars indicate single observations; the longer the bar, the more observations at that value.

Table 3. Summary statistics of peduncle leaf length to width ratios for isophyllous taxa.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>n</th>
<th>Mean</th>
<th>Standard Deviation</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. contexta</em></td>
<td>78</td>
<td>10.62</td>
<td>2.75</td>
<td>7.00</td>
<td>25.50</td>
</tr>
<tr>
<td><em>P. iuliformis</em></td>
<td>186</td>
<td>5.86</td>
<td>2.23</td>
<td>2.50</td>
<td>20.67</td>
</tr>
<tr>
<td><em>P. krameriana</em></td>
<td>12</td>
<td>5.68</td>
<td>0.91</td>
<td>4.11</td>
<td>7.00</td>
</tr>
<tr>
<td><em>P. tatei</em></td>
<td>40</td>
<td>5.07</td>
<td>1.34</td>
<td>3.10</td>
<td>9.88</td>
</tr>
</tbody>
</table>
Figure 15. Beanplot of sporophyll lengths. Large bar at the center of each figure indicates the mean. Smaller bars indicate individual observations; the longer the bar, the more observations at that value.
Table 4. Summary statistics for sporophyll length.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>n</th>
<th>Mean (in mm)</th>
<th>Standard Deviation</th>
<th>Min (in mm)</th>
<th>Max (in mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. carnosa</em></td>
<td>69</td>
<td>4.62</td>
<td>0.85</td>
<td>2.7</td>
<td>6.3</td>
</tr>
<tr>
<td><em>P. caroliniana</em></td>
<td>108</td>
<td>2.34</td>
<td>0.27</td>
<td>1.8</td>
<td>3.1</td>
</tr>
<tr>
<td><em>P. contexta</em></td>
<td>50</td>
<td>5.20</td>
<td>0.62</td>
<td>4.1</td>
<td>6.4</td>
</tr>
<tr>
<td><em>P. floridana</em></td>
<td>95</td>
<td>3.45</td>
<td>0.48</td>
<td>2.5</td>
<td>4.7</td>
</tr>
<tr>
<td><em>P. iuliformis</em></td>
<td>112</td>
<td>4.84</td>
<td>1.27</td>
<td>2.2</td>
<td>7.6</td>
</tr>
<tr>
<td><em>P. krameriana</em></td>
<td>6</td>
<td>4.80</td>
<td>0.64</td>
<td>4.0</td>
<td>5.8</td>
</tr>
<tr>
<td><em>P. meridionalis</em></td>
<td>242</td>
<td>3.67</td>
<td>0.59</td>
<td>2.3</td>
<td>5.6</td>
</tr>
<tr>
<td><em>P. mesetarum</em></td>
<td>46</td>
<td>3.12</td>
<td>0.57</td>
<td>2.4</td>
<td>4.8</td>
</tr>
<tr>
<td><em>P. paradoxa</em></td>
<td>87</td>
<td>3.21</td>
<td>0.48</td>
<td>2.4</td>
<td>4.5</td>
</tr>
<tr>
<td><em>P. tatei</em></td>
<td>23</td>
<td>5.30</td>
<td>0.63</td>
<td>4.4</td>
<td>7.2</td>
</tr>
</tbody>
</table>

Table 5. Summary statistics for spore lengths.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>n</th>
<th>Mean (in µm)</th>
<th>Standard Deviation</th>
<th>Min (in µm)</th>
<th>Max (in µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. carnosa</em></td>
<td>150</td>
<td>41.83</td>
<td>2.31</td>
<td>36.45</td>
<td>48.47</td>
</tr>
<tr>
<td><em>P. caroliniana</em></td>
<td>400</td>
<td>40.72</td>
<td>2.10</td>
<td>35.37</td>
<td>49.82</td>
</tr>
<tr>
<td><em>P. contexta</em></td>
<td>125</td>
<td>36.94</td>
<td>1.99</td>
<td>31.73</td>
<td>41.31</td>
</tr>
<tr>
<td><em>P. floridana</em></td>
<td>525</td>
<td>45.61</td>
<td>2.92</td>
<td>33.75</td>
<td>54.81</td>
</tr>
<tr>
<td><em>P. iuliformis</em></td>
<td>400</td>
<td>47.94</td>
<td>4.23</td>
<td>36.45</td>
<td>59.94</td>
</tr>
<tr>
<td><em>P. meridionalis</em></td>
<td>775</td>
<td>39.35</td>
<td>2.73</td>
<td>31.05</td>
<td>55.49</td>
</tr>
<tr>
<td><em>P. mesetarum</em></td>
<td>150</td>
<td>39.43</td>
<td>2.08</td>
<td>34.56</td>
<td>45.63</td>
</tr>
<tr>
<td><em>P. paradoxa</em></td>
<td>250</td>
<td>37.46</td>
<td>2.97</td>
<td>30.92</td>
<td>46.98</td>
</tr>
<tr>
<td><em>P. tatei</em></td>
<td>75</td>
<td>42.29</td>
<td>1.96</td>
<td>34.84</td>
<td>47.44</td>
</tr>
</tbody>
</table>
Figure 16. Beanplot of spore lengths. Large bar at the center of each figure indicates the mean. Smaller bars indicate individual observations; the longer the bar, the more observations at that value.
Figure 17. Histogram of average spore lengths (25 spores/collection) for North American collections, showing a bimodal distribution.
Figure 19. Scatterplot of strobilus width (including sporophylls) vs. peduncle leaf length. *Pseudolycopodiella floridana* is clustered in the upper right, with larger strobili and peduncle leaves, while *P. caroliniana*, with smaller strobili and peduncle leaves, is clustered in the bottom left.
Figure 20. Scatterplot of dorsal leaf length vs. dorsal leaf width for anisophyllous taxa.
Figure 21. Scatterplot of a reciprocal index of peduncle leaf density (higher value indicates less dense leaves, and vice versa) vs. rhizome width amongst isophyllous taxa.
Taxonomic Treatment


TYPE: _Lycopodium carolinianum_ L.

Sporophytes terrestrial, herbaceous; roots dichotomously branched, emerging periodically from the underside of prostrate shoots; prostrate shoots indeterminate, iso- or aniso-dichotomously branched in the horizontal plane; leaves of prostrate shoots spirally arranged, simple, entire, sessile, isophyllous or anisophyllous; upright shoots arising dorsally from prostrate shoots, not or rarely branched, fertile; leaves of upright shoots narrowly triangular to acicular, margins entire, usually in sparse, alternating pseudowhorls; strobili solitary, terminal, terete, conspicuously differentiated from upright and prostrate shoots; sporophylls lanceolate to triangular, with narrowed, membranaceous basal portion, subpeltate, with membranaceous wing on stalk, imbricate, borne in alternating whorls of 2-6, basal mucilage canals present, veinal canals absent; sporangia reniform, short-stalked, borne on sporophyll stalks; sporangial cell’s side walls straight, thin, with semiannular to nodular lignified thickenings; spores tetrahedral-globose, trilete, rugulate; gametophytes surficial, photosynthetic, tuberous, lobed on the upper surface; x=35, others?.
Key to the New World species of *Pseudolycopodiella*

1. Ventral rhizome leaves present; rhizome leaves isophyllous, without strongly differentiated lateral and dorsal leaves....2

2. Peduncle leaves uniformly incurved throughout.....3
   
   3. Peduncle leaves linear to acicular, >7 times longer than wide, departing approximately perpendicular from the peduncle and curving abruptly upward; vegetative leaves dark green, even when dried.....*P. contexta*
   
   3. Peduncle leaves narrowly triangular, <7 times longer than wide, departing from the peduncle at an acute angle, gradually curving upward; vegetative leaves yellow to yellow-green when dried.....*P. krameriana*

2. Peduncle leaves appressed to acutely spreading, not conspicuously incurved, except sometimes near the base or top of the peduncle.....4
   
   4. Rhizome flattened in cross section, fleshy; lateral rhizome leaves splayed, spreading horizontally; dorsal leaves often with broadened base, appressed to erect, not conspicuously recurved; ventral leaves highly reduced, membranaceous, filamentous, and hair-like.....*P. tatei*
   
   4. Rhizome terete not conspicuously fleshy; lateral rhizome leaves appressed, curving upward; dorsal leaves linear, erect, recurved; ventral leaves reduced, but not filamentous.....*P. iuliformis*

1. Ventral rhizome leaves absent, leaving underside of rhizome bare; rhizome leaves anisophyllous, dimorphic, with differentiated lateral and dorsal leaves......5

5. Rhizome broad, conspicuously flattened, fleshy; dorsal rhizome leaves reduced, to 3 mm long, triangular to stub-like.....*P. carnosa*

5. Rhizome terete, not conspicuously flattened or fleshy; dorsal rhizome leaves to 8 mm long, ovate to linear.....6

6. Dorsal rhizome leaves ovate; plants to 15 cm tall at maturity.....*P. paradoxa*

6. Dorsal leaves triangular, narrowly triangular, lanceolate, or linear; plants to 40 cm tall at maturity......7

7. Dorsal leaves linear to falcate, densely arranged in 4 or more obscure ranks, erect, often recurved; dorsal and lateral leaves strongly to weakly differentiated, often approaching conform; plants of high elevations, >2000 m.....*P. mesetarum*

7. Dorsal leaves of varying shapes, in 1-5 obscure ranks, appressed to erect, not recurved; dorsal and lateral leaves strongly dimorphic; plants of varying elevations, 0-2200 m......8

8. Peduncle leaves and sporophylls <3.0 mm long; peduncle <1.0 mm wide; strobili <6.0 mm wide.....*P. caroliniana*

8. Peduncle leaves and sporophylls >3.0 mm long; peduncle >1.0 mm wide; strobili >6.0 mm wide......9

9. Spores >42 µm in diameter; plants of North and Central America and the Caribbean; sporangia >1.2 mm wide.....*P. floridana*

9. Spores <43 µm in diameter; plants of Central and South America and the Caribbean; sporangia usually <1.2 mm wide.....*P. meridionalis*
**Pseudolycopodiella carnosa** (Silveira) Holub


Terrestrial herb, prostrate shoots closely appressed, flattened, with fleshy cortex, 1.7—[3.1]—4.5 mm broad excluding leaves; leaves of prostrate shoot dimorphic; lateral leaves spreading, triangular to ovate, falcate, 2.0—[4.2]—6.5 (-10) mm long, 1.0—[2.2]—3.3 mm broad, weakly imbricate, 2-ranked; dorsal leaves triangular to stub-like, smaller, 0.3—[1.5]—3.1 mm long, 0.5—[0.9]—1.7 mm wide, in 1—3 obscure ranks, not imbricate; ventral leaves absent; upright shoots 0.8—[1.6]—2.1 mm in diameter excluding leaves, to 29 cm high excluding the strobilus; upright shoot leaves narrowly triangular, 2.0—[4.0]—5.5 mm long by 0.5—[0.9]—1.5 mm wide, in sparse pseudowhorls of 4—6, appressed to acutely spreading; strobili to 15 cm long, 7—[9.9]—13.5 mm including spreading sporophylls; sporophylls ovate to lanceolate, appressed to reflexed, 3.0—[4.7]—6.0 mm long, excluding narrowed basal portion, 1.2—[1.7]—2.2 (-2.8) mm broad at widest point, tip acuminate, margins erose to serrulate, in alternating whorls of 4—6; sporangia 1.1—1.9 mm wide; spores 37—[42]—46 µm; chromosome number unknown.

**Distribution and Habitat**

This species is known from central South America. It has been recorded in the Brazilian states of Santa Catarina, Paraná, São Paulo, Minas Gerais, Goiás, Mato Grosso, Bahia, Amazonas, and the Federal District, in the Santa Cruz Department of Bolivia, the Caazapa and Caaguazu Departments of Paraguay, and along the Apa River on the Paraguay-Brazil border. It grows in wet soils that may be periodically inundated, or occasionally on rocks, in cerrado, savannas, marshes, and fields with grasses, Cyperaceae, Eriocaulaceae, and *Mauritia flexuosa* (Arecales), from 150-1400m.
Comments

This species is best characterized by its broad, flattened, fleshy rhizome and reduced dorsal leaves. The dorsal leaves vary from triangular to highly reduced, small, stub-like protrusions of leaf tissues. Most of the rhizome surface is exposed due to the widely separated nature of the leaves. The lateral leaves are often larger and broader than in other taxa.

*Pseudolycopodiella carnosa* co-occurs with *P. paradoxa*, *P. meridionalis*, and *P. tatei*. Two of these species, *P. paradoxa* and *P. meridionalis*, have rhizomes that are more or less terete and not only slightly fleshy. They have more densely arranged dorsal leaves that are ovate or scale-like in *P. paradoxa* and narrowly triangular to lanceolate in *P. meridionalis*. *Pseudolycopodiella tatei* shares the flattened, fleshy rhizome, but has ventral leaves, which *P. carnosa* lacks. It is also darker green than *P. carnosa*.

This species’ range overlaps completely with that of *Pseudolycopodiella paradoxa*. They can occur in the same habitats and are even found in mixed collections. Morphologically, the two species both have small dorsal leaves, a low length to width ratio for both dorsal and lateral leaves, and usually serrulate sporophyll margins. Morphological intermediates, which are likely hybrids, with a somewhat broadened, fleshy rhizome and ovate dorsal leaves also occur in the shared range. This all suggests that *P. carnosa* and *P. paradoxa* may be closely related.

Representative Examined Specimens

**BRAZIL.** Amazonas: Estrada de Estanho, road to Igarape Preto ca. 60 km SE of Transamazon Highway, 7/2/1979, Calderon et al. 2736 (NY, US). Bahia: Espigão Mestre, ca. 100 km WSW of Barreiras, 750 m, 3/7/1972, Anderson et al. 36813 (F, MO, NY, US); wet campo, Rio Plau, ca. 150 km SW of Barreiras, 850 m, 4/13/1966, Irwin et al. 14760 (F, NY, US). Federal District: Fazenda Agua Limpa (University of Brasilia field station), near Vargem Bonita, c. 18 km SSW of Brasilia TV tower, 3/18/1976, Ratter and da Fonseca 2810 (MO, NY). Goiás: Chapada dos Veadeiros, campo and cerrado on outcrops, ca. 22 km N of Alto do Paraíso, 1250 m, 3/22/1971, Irwin et al. 32957 (F, MICH, NY, US). Mato Grosso: Barra do Garças, bacia do Rio Araguaia, base de Serra Azul, Estrada Barra do Garças a Nova Xavantina (BR 158) km 76-77, 15º20’S 52º10’W, 350-400 m, 10/13/1990, P. G. Windisch 5838 (AAU, F); Agua Boa, bacia do Rio Araguaia, Estrada Barra do Garças a Canarana (BR 158), 14º00’S 52º10’W, 450 m, 10/14/1990, P. G. Windisch 5845 (AAU, F); Serra do Roncador, Barra do Garças, 235 km along new road NNE of village Xavantina, 25 km due S of Royal Society-Royal Geographic Society Base Camp, at “Lagoa do Sucuri”, 450 m, 8/31/1968, Eiten and Eiten 8474 (US); Alto Garça, limite com Pedra Preta, Estrada para Itiquira via Fazenda Ponte de Pedra, Serra da Saudade, ca. 21 km da BR 364, 16º50’S 53º55’W, 600-700 m, 6/18/1991, Windisch and Amorim 6289 (AAU). Minas Gerais: Serra do Espinhaço, lower cut-over slopes of Serra da Caraça, sandy slopes, near riacho, ca. 10 km W of Barão do Cocais, 1400 m, 1/22/1971, Irwin et al. 28866 (F, NY, US); Saramenho, Ouro Preto, 1/5/1951, A. Macedo 2877 (MO, US); Diamantina, Area de Proteção Ambiental Pau-de-Fruta, COPASA, 18º15’S29ºS 43º38’54”W, 2/14/2001, Stehmann et al. 2929 (AAU); Serra Cipo, 112 km N of Belo Horizonte, 1290 m, 7/11/1965, Glassman and Gomes Jr. 8088 (F); Serra do Espinhaço, ca. 2 km S of São João, da Chapada, 1200 m, 3/26/1970, Irwin et al. 28385 (F, NY,

**BOLIVIA.** **Santa Cruz:** Velasco Province, Parque Nacional Noel Kempff M. Los Fierros, La Meseta, campo rupestre, suelos limo arenosos con afloramiento de roca, 14°33′48.1″S 60°46′24.9″W, 650 m, 8/28/1995, *Guillén and Gonzales 4178* (NY).

Figure 22. *Pseudolycopodiella cariosa* (P. G. Windisch 5845). A. General habit, with rhizome and fertile shoot (AAU). B. Rhizome (F).
Figure 23. Distribution map of *Pseudolycopodiella carnosoa*.

*Pseudolycopodiella caroliniana* (L.) Holub


TYPE: USA. Carolina, Dilleni, Hist. Musc., t. 61, fig. 5., EPITYPE: USA, North Carolina, Bladen County, sandy ditch, 1.4 mi north of junction NC 210 and 53 on NC 210, 10/19/1957, H. E. Ahles 37456 (epitype: GH!; isoeptype: NY!; here designated).

Terrestrial herb; prostrate shoots closely appressed, terete to slightly flattened, without fleshy cortex, 0.5—[0.7]—1.3 mm broad excluding leaves; leaves of prostrate shoot dimorphic; lateral leaves spreading, narrowly triangular to lanceolate, falcate, 2.6—[4.3]—6.5 mm long, 0.6—[1.4]—2.0 mm broad, weakly imbricate, 2-ranked; dorsal leaves narrowly triangular, 2.0—[3.4]—4.7 (-6.4) mm long, 0.4—[0.8]—1.0 mm wide, in 1—3 obscure ranks, imbricate; ventral leaves absent; upright shoots 0.6 —[0.8]—1.0 (-1.4) mm in diameter excluding leaves, to 28 cm high excluding the strobilus; upright shoot leaves narrowly triangular, 1.8—[2.6]—3.0 (-3.9) mm
long by 0.5—[0.6]—1.2 mm wide, in sparse pseudowhorls of 3—4, appressed to acutely spreading; strobili to 9 cm long, (3.2—) 3.8—[5.0]—6.0 (-6.7) mm wide including spreading sporophylls; sporophylls ovate, appressed to spreading, 1.9—[2.4]—3.1 mm long, excluding narrowed basal portion, 0.9—[1.4]—1.9 mm broad at widest point, tip acute, margins erose to dentate, in alternating whorls of 3—4; sporangia 0.9—1.3 mm wide; spores 35—[40.5]—46 µm; n=35.

**Distribution and Habitat**

This species has been recorded from the eastern United States, primarily within the coastal plain, from upstate New York south to Florida and west to Texas. It grows in wet, usually sandy, soils in bogs, swamps, savannas, moist woodlands, and roadside ditches, from 0-150 m. Common associates include grasses, sedges, cedars, *Pinus*, *Drosera*, *Sarracenia*, and *Sphagnum*.

**Comments**

The name *Pseudolycopodiella caroliniana* was historically used very broadly and included plants from the Americas, Africa, and Asia. Many of the other anisophyllous taxa treated here have been considered varieties or subspecies of *P. caroliniana*. Here I am taking as stricter view of the taxon that limits it to the diploids of the eastern United States. Bruce (1976) found that North American *Pseudolycopodiella* includes both diploid and tetraploid individuals. The holotype drawing and specimen that it is based upon (*Dillenius CXLII* (OXF)) more closely match the morphology of the diploid, so the name *P. caroliniana* should be associated with that cytotype. In the interest of stabilizing the use of the name, and because the holotype drawing is somewhat ambiguous, an epitype for *P. caroliniana* is designated here. The epitype, *H. E. Ales 37456* (GH), is from the Carolinas, fits the usual diploid morphology, and has spores that are within the diploid size range.

This species is distinguished by its narrow, compact strobili (<6.0 mm), narrow peduncle (<1.0 mm), and short peduncle leaves and sporophylls (both <3.0 mm). The co-occurring tetraploid *Pseudolycopodiella floridana* has broader strobili (>6.0 mm) and peduncles (>1.0 mm) and longer peduncle leaves and sporophylls (both >3.0 mm). The species *P. paradoxa* is also small in stature, but has ovate dorsal leaves that are three or less times longer than broad, while *P. caroliniana* has narrowly triangular or lanceolate dorsal leaves that are greater than three times longer than broad.

**Representative Specimens Examined**

UNITED STATES. Alabama: Sand, clay, gravel of seep at s.w. side of Fayette by Ala. 159, 8/12/1975, *R. Kral 56413* (GA, GH); Covington County, south of Parker Springs in Parker Springs Bog, growing in wet swales along trail and in open pineland, 7/25/2003, *R. J. Hickey #03-01* (MU); Baldwin Co., roadside ditch along US96 near Mobile Bay, east side of road 1.65 m s of jct. Baldwin Co. 32, 7/25/1974, *Bruce and Gilman 74051* (GA); Creek banks, Mobile County, September, *W. C. Dukes s.n.* (MO). Florida: Open, springy slope along Road 201 (Beaver Pond Road), 4.1 mi e. of Fla. 285, 9.1 mi n. of Fla. 20 intersection in Niceville, S4, T1N, R21W, 8/23/1966, *D. B. Ward 5960* (FLAS); Roadside ditch 5 mi. south of Orange Dale, 10/8/1941,
West and West s.n. (FLAS); Flatwoods west of Polk City, 6/15/1931, J. B. McFarlin 5814 (MICH); Dunedin, 4/19/1900, S. M. Tracy 6628 (F, MO, NY, US); Boggy pinelands, east of Sebring, 3/21/1948, R. Garrett 111 (FLAS); Low pinelands near Wetumpka, Gadsden County, 11/25/1923, Small et al. 10986 (NY); Escambia Co., wet meadow in pine-lands 9 miles west of Pensacola, 7/25/1950, Webster and Wilbur 3576 (GH, MICH); 15 mi. E. of Orlando, common on moist sandy peat of grass sedge bog, 8/12/1957, R. Kral 5431 (GH, NY). 

Georgia: Between Moniac and St. George on GA hwy 94, low roadside along low slash pine forests, 8/31/1978, Bruce et al. 78015 (MICH); Sand flats between Savannah and Bonaventure, 8/31/1913, B. M. Duggar s.n. (MO); Sandy bog just southwest of Americus, 8/29/1900, 350 ft., R. M. Harper 529 (NY, US); Open wet ditch 11.4 mi. E of Tom’s Creek on US 94, 11/9/1963, J. Norsworthy 181 (US). 


Maryland: Powder Mill Swamp, Branchville, Prince George’s County, 9/30/1899, W. R. Maxon 343 (MICH). 

Massachusetts: Hampshire County, low, sandy area, Plain Road, Hatfield, 8/28/1976, H. E. Ahles 82397 (GA, NCU). 

Mississippi: Seepage area along lower face and base of sandy clay bank, 4mi. s. of Enterprise, 7/23/1955, J. D. Ray, Jr. 5108 (GH, NY); 7.5 miles south of Nescosie, Hancock County, 8/27/1940, L. G. Bremerr Jr. s.n. (MO); 1 mi. e. Leakeville along Miss 65, sandy clay of clearing in pine-black gum bottom, 9/4/1965, R. Kral 35885 (GA). 

New Jersey: Near pine barrens, Toms River, 9/18/1897, L. H. Lighthipe s.n. (MICH); Cedar swamp, Egg Harbor, 8/30/1882, Parker s.n. (NY); Sandy bog, Hampton Gate, 10/7/1934, J. J. Copeland s.n. (NY); Closter, J. F. Austin s.n. (US); Sandy and peaty bog, along Oswego River, near Sim Place, 8/11/1939, Long 53811 (GA). 

New York: Warren County, About ¾ mile south of State Route 9L at Harris Bay, south end of Lake George, Dunham Bay Marsh, 10/13/1996, M. Covey s.n. (NY); Long Island, Ronkonkoma, 9/27/1919, W. C. Ferguson s.n. (US); Ronkonkoma, 7/18/1921, W. C. Ferguson 475 (NY); Ronkonkoma, 11/11/1921, W. C. Ferguson 1183 (NY). 

North Carolina: Sandhills Game Land, Bones Fork north of Nursery Lane, 9/5/2009, B. A. Sorrie 12425 (NCU); Shallowly excavated area in wire-grass savanna, along NC Ft. 306, 2.5 miles northwest of Grantsboro, 7/21/1948, R. K. Godfrey 48331 (FLAS, GH); Moist Pineland several miles south of Holly Ridge, 9/6/1948, Thorne and Muenscher 8970 (F); Cut-over pine savannah along NC 211, about 8 miles northwest of Supply, Leonard and Hackney 3452 (NCU); Onslow Co., Weyerhauser Land, ditch along NC 53 4.9 miles north of county line with Pender Co., 8/6/1972, Bruce et al. 72028 (GA). 

Pennsylvania: E. A. Rau 174 (MO); Bethlehem, Aug. 1878, E. A. Rau s.n. (MO). 

South Carolina: Shealy’s Pond, South side Boiling Springs Rd., 1.7 mi W of Rte. 6, Edmund, 10/17/1987, S. R. Hill 18958 (GH, NY); Borrow pit in flatwoods on co. rd. S-27-169, 0.9 mile south of jct. with US 601, north of Hardeeville, 10/3/1967, Bozeman and Radford 11589 (FLAS, MICH); boggy area in quarry, 1.4 miles east of Edmund, vicinity of Kaolin Mines, 5/26/1960, Ahles and Haesloop 53515 (NCU). 

Texas: Savanna, 2 miles north of Kirbyville, 6/9/1946, Correll and Correll 12525 (GH, MICH, MO, MU, NY); ca. 0.4 mi NW of Cherokee Lake, and 0.3 mi SW of headwaters of Hines Branch, ca. 1.4 mi Ne of FM3, Hilltop Lakes Resort, 31°05'00"N 96°11'55"S, 425 ft, 6/6/1989, Orzell and Bridges 10343 (NY). 

Figure 25. Distribution map of *Pseudolycopodiella caroliniana*.

*Pseudolycopodiella contexta* (Mart.) Holub


Terrestrial herb with prostrate shoots creeping on the ground; prostrate shoots terete, without fleshy cortex, 1.0—[1.5]—1.9 mm broad excluding leaves; leaves of prostrate shoot isophyllous, lateral and dorsal leaves uniform, spirally arranged, many-ranked, linear to acicular, quadrangular, pointing toward the shoot apex, 2.0—[3.6]—5.3 mm long, 0.2—[0.4]—0.6 mm broad; ventral leaves present, reduced; upright shoots 1.2 —[1.5]—2.0 mm in diameter excluding leaves, 4.0—[4.80]—6.5 including leaves, to 50 cm high, densely leafy; upright shoot leaves linear to acicular, (3.0-)4.5—[5.4]—7.0 mm long by 0.2—[0.4]—0.6 mm wide, with medial ridge, tip long tapering, acuminate, crinkled, in dense pseudowhorls of 6—9, diverging approximately perpendicularly from shoot, curving upward; strobili to 8 cm long, 8.2—[9.9]—11.5 mm wide including spreading sporphylls; sporophylls lanceolate, spreading, 4.2—[5.2]—6.5 mm long, excluding narrowed basal portion, 0.7—[1.2]—1.6 mm broad at widest point, tip acuminate, crinkled, margins erose to minutely serrulate, in alternating whorls of 3—6; sporangia 0.9—1.5 mm wide; spores 32—[37]—40 µm; chromosome number unknown.

**Distribution and Habitat**

*Pseudolycopodiella contexta* is found in northern South America, in the northwest portion of the Amazon in Brazil, Peru, Colombia, Venezuela, and Guyana. It grows in moist savanna, shrubland, and forested habitats, often associated with streams, from 100-1500m.

**Comments**

This is the most distinctive species of *Pseudolycopodiella*. This taxon is easily recognized by its dense, linear, incurved peduncle leaves that diverge almost perpendicularly from the peduncle. Because of its densely leafy peduncle it has been associated with *Lycopodiella alopecuroides*. *Pseudolycopodiella krameriana* also has incurved peduncle leaves, but they are broader, borne in more widely separated pseudowhorls, and depart from the peduncle at a smaller angle. When not fertile, *P. contexta* closely resembles *P. iuliformis*, but has straight rather than recurved or falcate rhizome leaves and tends to occur at lower elevations. This species is also unusual in that it retains a deep green color to its sterile leaves decades after drying and seems to be more tolerant of shaded conditions than other *Pseudolycopodiella*.

**Representative Specimens Examined**

Indigena La Sabana, 1°15’N 70°51’W, 200 m, 4/26/1993, Madrinan et al. 1161 (GH, MO); Rio Apaporis, Cachivera del Jirijirimo y alrededores, 250 m, 6/11/1951, Schultes and Cabrera 12379 (GH).

VENEZUELA. Amazonas: Cerro Duida, frequent on cano banks, Culaebra Peak, 1500 m, 4/22-24/1949, Maguire and Maguire Jr. 29101 (NY, US); Rio Negro, at base of Cerro Cucuy, 3/2/1944, J. T. Baldwin 3237 (US); Rio Guainia, locally abundant in high forest, 4 km north of Maroa, 130 m, 10/7/1957, Maguire and Maguire Jr. 41748 (MO, NY, US); Depto. Atabapo, acidic forest on slope of Huachamacari, 3°39’N 65°42’W, 850 m, 3/6/1985, R. L. Liesner (MO); Slope of Cerro Aracamuni, Aracamuni, Quebrade camp, 1°24’N 65°38’W, 600 m, 10/20/1987, Liesner and Delascio 22201 (MO); Rio Guainia, frequent in sabanite on right bank of Cano Pimichin 1 km. above Pimichin, 120-140 m, 11/24/1953, Maguire et al. 36391 (NY); Cerro Marahuaca, slope rainforest, 1000 m, 5/3/1949, Maguire and Maguire Jr. 29199 (NY, US); Cerro Huachamacari, E slope, forested, 03°49’N 65°42’W, 600-700 m, 11/3/1988, R. Liesner 25751 (NY). Bolivar: Dist. Piar, Amaruay-Tepui, summit, center of western side, 5°55’N 62°15’W, 1030 m, 5/27/1986, Liesner et al. 21152 (NY); Cumbre de Cerro Guaquinima, a lo largo del Rio Szczerbanari (Rio Carapo), 5°44’4”N 63°41’8”W, 750 m, 1/20-25/1977, Steyermark et al. 113367 (GH, MO).


PERU. Loreto: Ca. 2 km SW from village Yuto at Nanay River, 40 km from Iquitos, 03°56’S 73°30’W, 12/27/1991, Tuomisto et al. 3564 (AAU); Rio Nanay, Cesario Mishana, 1-2 hr walk from river, 9/4-6/1974, Foster and Foster 4102 (AAU, NY, US); Vicinity of Iquitos, 120 m, 1977, J. Revilla 4340 (F, MO); Manfinfa on the upper Rio Nanay, June-July 1929, L. Williams 1106 (F, US).

Figure 26. *Pseudolycopodiella contexta* A. Peduncle and strobilus (*L. T. Marinho 76 NY*). B. Rhizome (*S.P. Churchill 16068 NY*). C. General habit (*Foster and Foster 4102 US*).
**Pseudolycopodiella floridana** K. Cook & Hickey, ined.


Terrestrial herb; prostrate shoots closely appressed, terete to slightly flattened, without fleshy cortex, 0.6—[1.0]—1.5 mm broad excluding leaves; leaves of prostrate shoot dimorphic, lateral leaves spreading, triangular to lanceolate, falcate, 3.3—[5.2]—8.3 mm long, 0.9—[1.6]—2.3 mm broad, weakly imbricate, 2-ranked; dorsal leaves narrowly triangular, 2.7—[4.1]—6.8 (-8.2) mm long, 0.6—[0.9]—1.4 mm wide, in 2—4 obscure ranks, imbricate; ventral leaves absent; upright shoots 1.0 —[1.2]—1.6 mm in diameter excluding leaves, to 32 cm high excluding the strobilus; upright shoot leaves narrowly triangular, 2.6—[3.6]—4.7 mm long by 0.4—[0.7]—1.3
mm wide, in sparse pseudowhorls of 4—5, appressed to acutely spreading; strobili to 13 cm long, 5.5—[7.2]—10.7 mm wide including spreading sporophylls; sporophylls ovate to lanceolate, appressed to spreading, 2.5—[3.5]—4.7 mm long, excluding narrowed basal portion, 1.0—[1.6]—2.3 mm broad at widest point, tip acute to acuminate, margins erose to serrate, in alternating whorls of 4—5; sporangia 1.2—1.7 mm wide; spores 42—[45.5]—52 µm; n=70.

Distribution and habitat

This species is found in the southeastern United States, the Greater Antilles, and Central America. It occurs in wet, open areas such as savannas and riversides, from 0-1550 m.

Comments

This species co-occurs with Pseudolycopodiella caroliniana in the southeastern states in the U.S. and with P. meridionalis in Central America and the Caribbean. It is morphologically nearly identical to both of these species and has historically been included in them, but it is a tetraploid while the other two species are diploids. It may be an autopolyploid derived from either of these two species or an allopolyploid hybrid between them.

It can be distinguished from P. caroliniana by its broader peduncle and strobilus and by its longer peduncle leaves and sporophylls. These are 3.0 mm or shorter in P. caroliniana and typically 3.0 mm or longer in P. floridana. In the areas where its range overlaps with P. meridionalis, P. floridana has broader sporangia, 1.2 mm or broader, whereas P. meridionalis has sporangia 1.2 mm or narrower. This character only differentiates the two where they co-occur. Some P. meridionalis in South America have sporangia wider than 1.2 mm.

Chromosome counts of tetraploids have been obtained from plants in Louisiana and from the sole known Pseudolycopodiella population on Jamaica (Wagner 1992). The holotype of this species was chosen from the Jamaican population.

Representative Examined Specimens

UNITED STATES. Alabama: Gateswood, 10/30/1903, S. M. Tracey 8642 (F, MO, NY); Spring Mill, common in swamp, 8/8/1897, B. F. Bush 111 (MO); Mobile Co., wet savannah and boggy open area along Hwy 188 (north side), about 0.5 mile west of its intersection with county road 59, generally about 7 miles east of Coden, 9/8/1973, M. G. Lelong 7277 (NCU); Washington Co., 4.6 mi S of tres. 17 and 56 jct. in Chatom, along W side of rte. 17, sunny, wet roadside, 8/3/1994, R. F. C. Naczi 4501 (MICH). Florida: Clay Co., T6S, R24E, S27, Ca.0.5-1 mi E of Rt. 21 on small sand road, occasional in cut over moist pinelands, 9/30/1983, Judd et al. 3408 (FLAS); Santa Rosa Co., frequent on wet sandy peat of hillside bog, 6 mi. E of Munson, 7/20/1956, Kral and Redfearn 2942 (GH); Liberty Co., infrequent, clearing of wet pine flatwoods, Apalachicola National orest, by forest road 181, by forest road 181, 3.8 mi NE of Sumatra, 9/19/1989, R. K. Godfrey 83572 (GH); 4 mi N of Dorcas, Okaloosa Co., 8/2/1954, E. S. Ford 3975 (GH); West of Lutz on Lake Fern Road, wet roadside ditch, Hillsborough Co., 8/23/1953, R. Garrett s.n. (FLAS); Okaloosa Co., about 4 miles east of Crestview and just west of the Shoal River, 7/25/1950, Webster and Wilbur 3590 (MICH, US); Sanderson, Baker Co., 10/18/1952, E. P. Kearsley s.n. (NY); 2 miles from Yulee on the south side Fernandino Rd, 8/28/1949, E. P. Kearsley s.n. (NY); In low area of flat grassland with occasional pines, on e. side of Fla. 87, 1 mi. n. of Navarre,


**BELIZE.** Rio Privacion, Mountain Pine Ridge, 2/26/1931, *H. H. Bartlett* 11795 (MICH, US); All Pines, open places in swampy ground, 8/10/1930, *W. A. Schipp* 578 (F); Province Belize, found 1.5 miles east of Hattieville on the coastal pine savanna, 7/5/1972, *J. S. Huston* 0539 (MO).

**HONDURAS.** Vicinity of Puerto Lempira, 0-20 m, 1/30/1981, *G. R. Proctor* 38774 (GH); Puerto Lempira, orillas de la laguna Caratasca, 7/17-21/1977, *Nelson and Romero* 4227 (MO); Aguas, sabanas mojadas de gramineas cortas con bosquillos disperses de Pinus caribea, 15°30’N 84°20’W, 12/12-14/1972, *A. F. Clewell* 3587 (MO, NY).

**NICARAGUA.** Caño Manso Awalka Tingni, reached by “Geodesia” turn on road between Torre 7 and Bismuna Tara, ca. 11.9 SW of Bismuna Tara, 14°41’N 83°30’W, 20-40 m, *W> D. Stevens* 7708 (MO); Kornuk Creek near Bilwacarma, Puente Pozo Azul, 5-100 m, 5/14/1971, *J. T. Atwood* 4720 (MO).


**DOMINICAN REPUBLIC.** Ciénaga de la Culata, Costanza, in water, in swamps, 1550 m, 9/22/1969, *A. H. Liogier* 15990 (NY); Llano costero, Cuenca, on tembladera in laguna, 1/3/1929, *E. L. Ekman* s.n. (NY); Cordillera Central, El Valle, moist, highly acid savanna, 7/11/1930, *E. L. Ekman* 15656 (F, NY).


**JAMAICA.** Clarendon Parish, Mason River Savanna, 2.75 miles due northwest of Kellits P.O., 2300 ft, 12/21/1956, *G. R. Proctor* 15893 (MO).
Figure 28. *Pseudolycopodiella floridana*. A. General habit (Webster et al. 8122 MICH). B. Strobilus and peduncle (Webster et al. 8122 MICH). C. Rhizome (D. E. Boufford 11958).
Figure 29. Distribution map of *Pseudolycopodiella floridana*.

**Pseudolycopodiella iuliformis** (Underw. & F. E. Lloyd) Holub


Terrestrial herb; prostrate shoots creeping on the ground, mossy rocks, or cliffs, terete, occasionally somewhat fleshy, 0.9—[1.5]—2.5 mm broad excluding leaves; leaves of prostrate shoot isophyllous, spirally arranged, many-ranked; laterally positioned leaves narrowly
triangular to falcate, curving upward, 2.0—[3.5]—5.5 mm long, 0.3—[0.6]—1.1 mm broad; dorsally positioned leaves narrowly triangular to linear, quadrangular, recurved, 2.2—[3.9]—6.0 mm long, 0.3—[0.6]—1.1 mm wide; ventral leaves present, reduced; upright shoots 0.7—[1.3]—1.9 mm in diameter excluding leaves, to 23 cm high excluding the strobilus; upright shoot leaves narrowly triangular, 1.9—[4.4]—6.5 mm long by 0.4—[0.8]—1.2 mm wide, in sparse pseudowhorls of 2—6, appressed to acutely spreading; strobili to 15 cm long, 3.0—[9.5]—15.5 mm wide including spreading sporphylls; sporphylls triangular to lanceolate, appressed to spreading, 2.2—[4.8]—7.0 mm long, excluding narrowed basal portion, 1.0—[1.8]—2.6 mm broad at widest point, tip acute to acuminate, margins serrulate, ciliate, or frayed, in alternating whorls of 2—5 (-6); sporangia 1.3—1.9 mm wide; spores 42—[48]—54 µm; chromosome number unknown.

Distribution and Habitat

This species is found at high elevation on the tepuis and mountains of the Amazonas and Bolivar states of Venezuela and adjacent areas in Brazil and Guyana. It grows on wet sandy soil, rocks, and occasionally cliffs. It occurs in savannas, stream sides, swamps, and Bonnetia woodlands, from 1000-2630 m.

Comments

This isophyllous species is distinguished by its linear, typically recurved dorsal leaves. It occurs in Venezuela with two other isophyllous species, Pseudolycopodiella contexta and P. tatei. It is different from P. contexta in that its peduncle leaves are straight and more or less appressed to the peduncle, whereas they are strongly incurved in P. contexta. It can be distinguished from P. tatei on the basis of its terete rhizome. Pseudolycopodiella tatei has a distinctly flattened one.

The morphology of this species is highly variable. Individuals vary especially in overall height, strobilus size, sporophyll length to width ratio, and in the general color and texture of the leaves. This variability may be attributable to phenotypic plasticity. The species occurs on a variety of substrates, including sandy soil, moss, and rock, which may impact how the plant grows. There may also be genetic differentiation between populations on different tepuis and mountains.

The large spores found in this taxon imply that it may be a tetraploid. If this is true, there are no obvious candidate diploid taxa that could have given rise to it. Alternatively, large spores may be an adaptation to reduce dispersal away from the species tepui habitat into the surrounding lower elevation regions.

Representative Examined Specimens

VENEZUELA. Amazonas: Rio Negro, Camp III, Neblina and Massif, NW Plateau (Arm) 13.5 km ENE of Cerro de La Neblina Base Camp, 00°54’N 66°04’W, 1750-1800 m, 2/16-18/1984, R. Liesner 16033 (MO); Frequent on wet shaded cliff, pass between Peak I and Peak II, north rim, Cerro Sipapo, 1800 m, 1/3/1949, Maguire and Politi 28128 (US); Cerro Marahuaca, Atuhua, Shiho, cumber, parte aislada al Sur-Oeste del Cerro, 03°35’N 65°20’W, 2450 m, 2/9-10/1982, Steyermark et al. 126358 (AAU); Cerro de la Neblina, Rio Yatua, occasional on moist banks of runlet near Cumbre Camp, 1700 m, 1/5/1954, Maguire et al. 37062 (US); Cerro de la Neblina,
Rio Yatua, occasional in high montane forest 3-4 km south of Camp 3, 900-1000 m, 12/24/1953, Maguire et al. 36884 (US); Cerro Marahuaca, cumber, extremo noreste, 03°50’S 65°28’W, 2580-2600 m, 3/30-4/1/1983, Steyermark and Delascio 129205 (AAU, MO); Cerro de la Neblina, Planicie de Zuloaga, Rio Titirco, 2300 m, 10/10-15/1970, J. A. Steyermark 103860 (MO, NY); Summit of Cerro Duida, Brocchinia Hills, on wet ground along stream bank above Vegas Falls, 1700-1980 m, 9/1/1944, J. A. Steyermark 58144 (US); Camp VII, Cerro de la Neblina, 5.1 km NE Pico Phelps, 21.5 km E Neblina Base Camp, up new trail from heliport to steep, east-facing escarpment of west wall of valley, 00°50’40"N 65°58’10"W, 2150 m, 2/7/1985, J. Beitel 85169 (F, MO); Cerro Aracamuni, summit, Popa camp, 01°26’N 65°47’W, 1550 m, 10/19/1987, Liesner and Delascio 22175 (MO); Cerro de la Neblina, ridge at divide between Brazil and Venezuela, 26 km ENE of Neblina Base Camp, 00°53’N 65°56’W, 2000 m, 4/15/1984, Plowman and Thomas 13626 (F, MO); Sierra Maigualida, NW sector, small valley along an upper tributary of Cano Iguana, 05°30’N 65°15’W, 2000 m, 2/28-3/3/1991, Berry et al. 4903 (MO); Lomas graniticas, cañon Piedra, 115 km al SE de Pto. Ayacucho, 04°54’N 66°54’W, 1500 m, Sept. 1989, Fernandez et al. 5952 (MO).
GUYANA. Cuyuni-Mazaruni: Waukauyengtipu, eastern summit, 05°49’N 61°1’W, 1570 m, 7/10/1997, Clarke et al. 5579 (US).

Figure 30. *Pseudolycopodiella iuliformis* (Plowman and Thomas 13626 MO). A. Strobilus. B. Rhizome, side view. C. General habit.
Figure 31. Distribution map of *P. iuliformis*.

**Pseudolycopodiella krameriana** (B. Øllg.) B. Øllg.


Terrestrial herb; prostrate shoots creeping, terete, sometimes somewhat fleshy, 1.5—[1.8]—3.0 mm broad excluding leaves; leaves of prostrate shoot isophyllous, dorsal and lateral leaves uniform, spirally arranged, many-ranked, narrowly triangular to linear, quadrangular, 2.0—[4.0]—8.0 mm long, 0.4—[0.7]—1.0 mm broad; ventral leaves present, reduced; upright shoots 1.0—[1.6]—1.8 mm in diameter excluding leaves, 3.0—[3.9]—5.0 mm in diameter including leaves, to 17 cm high excluding the strobilus; upright shoot leaves narrowly triangular,
3.0—[4.6]—6.0 mm long by 0.5—[0.8]—1.0 mm wide, with conspicuous medial ridge, in dense pseudowhorls of 4—8, diverging at an acute angle from the shoot, curving upwards; strobili to 9 cm long, 8.0—[10.0]—12.0 mm wide including spreading sporophylls; sporophylls ovate to lanceolate, spreading, 4.0—[4.8]—7.0 mm long, excluding narrowed basal portion, 1.0—[1.3]—2.0 mm broad at widest point, tip acuminate, margins entire to minutely erose, in alternating whorls of 4—8; sporangia 1.0—1.5 mm wide; spore size unknown; chromosome number unknown.

**Distribution and Habitat**

This species is endemic to savannas in Suriname, from 30-300 m.

**Comments**

This species is known from only a few collections from Suriname. It is distinguished by its incurved peduncle leaves that are broader and less densely arranged than those of *Pseudolycopodiella contexta*. It has been recorded occurring with both *P. meridionalis* and *P. tatei*. In addition to the distinct peduncle leaves, *P. krameriana* can be distinguished from these two species by its isophyllous, terete rhizome with narrowly triangular to linear leaves. *Pseudolycopodiella tatei*, in contrast, has a broad, flattened rhizome, and *P. meridionalis* is anisophyllous and lacks ventral leaves.

**Representative Examined Specimens**

Pseudolycopodiella meridionalis (Underw. & F. E. Lloyd) Holub


Terrestrial herb; prostrate shoots closely appressed, terete to slightly flattened, without fleshy cortex, 0.7—[1.1]—1.7 mm broad excluding leaves; leaves of prostrate shoot dimorphic; lateral leaves spreading, triangular to lanceolate, falcate, 2.5—[4.3]—7.0 mm long, 1.0—[1.7]—2.5 (-3.5) mm broad, weakly imbricate, 2-ranked; dorsal leaves triangular to linear, 2.0—[3.4]—5.5 mm long, 0.5—[0.9]—1.4 mm wide, in 1—5 (-6) obscure ranks, imbricate; ventral leaves
absent; upright shoots 0.7—[1.2]—1.7 mm in diameter excluding leaves, to 28 cm high excluding the strobilus; upright shoot leaves narrowly triangular, (1.5-) 2.5—[3.5]—6.5 mm long by 0.5—[0.7]—1.2 mm wide, in sparse pseudowhorls of 4—5, appressed to acutely spreading; strobili to 12 cm long, 5.2—[7.8]—11.0 mm wide including spreading sporphylls; sporophylls ovate to lanceolate, appressed to spreading, 2.3—[3.7]—5.6 mm long, excluding narrowed basal portion, 0.9—[1.5]—2.3 mm broad at widest point, tip acute to acuminate, margins erose to serrulate, in alternating whorls of 3—5; sporangia 0.9—1.6 mm wide; spores 35—[39]—44 µm; chromosome number unknown.

**Distribution and Habitat**

This species is very widespread, ranging from Cuba to the southern tip of Uruguay. It occurs in a variety of habitats, including fields, savannas, swamps, beaches, open cliffs, and in coastal restinga communities, from 0-2300 m.

**Comments**

This species was originally segregated from the North American *Pseudolycopodiella caroliniana* based upon its larger size. This size difference is particularly apparent in the strobili and sporophylls. The strobili of *P. caroliniana* are narrow and compact, whereas the strobili of *P. meridionalis* are broader and the longer sporophylls give them an almost spiny appearance at maturity. At the northern end of its range, *P. meridionalis* occurs with its tetraploid relative *P. floridana*. That species tends to have larger sporangia than *P. meridionalis*, at least in the area of overlap. *Pseudolycopodiella meridionalis* is distinct among other New World anisophyllous taxa by its terete to only slightly flattened rhizome and triangular to linear dorsal leaves.

*Pseudolycopodiella meridionalis* varies extensively, particularly in the size, shape and arrangement of its rhizome leaves, throughout its range and even within more restricted areas. For example, the small island of Dominica is home to leathery, densely leafy specimens as well as thin-textured ones with small, sparse leaves, and morphologically intermediate ones. A few other variants are worth noting. The plants of the coastal region in Bahia, Brazil tend to have exorbitantly large strobili, some of the largest seen in the genus. Collections from the southwestern Amazon region are sparse, but those from that area are generally slender plants with small dorsal leaves arranged in few ranks. Given the range of variation seen within this species, none of these are particularly distinct or warrant taxonomic recognition.

In the protologue, Underwood and Lloyd (1906) designated the two sheets of *Percy Wilson* 94 at NY as the type. To avoid any confusion that may result from having multiple specimens referred to as the type, one of the two specimens, the one with the barcode number 00126961, is here selected as the lectotype.

**Representative Examined Specimens**

GUATEMALA. Chimaltenango, Pacaya, 10/9/1938, J. R. Johnston 1347 (F).

HONDURAS. La Picucha peak, highest point in Agalta National park, windswept ridge with dwarfed and stunted vegetation no taller than 3 m and usually 1 m tall, 13 km NNW of Catacamas, 14°58'N 88°55'W, 2300 m, 6/2/1992, Thomas et al. 456 (AAU, MO).

CUBA. Wet sandy ground, pure woods, trail, Camp Toa to Camp La Barga, Oriente, 2/26/1910, J. A. Shafer 4161 (GH, NY).

HAITI. Massif du Nord, Le Bohme, slope of Morne Beaubrun, on denuded roadsides, on the road to Gros-Morne over Marie Congo, 850 m, 9/11/1925, E. L. Ekman 4875 (NY).


GUATEMALA. Basse Terre, Savane aux Ananas, 1000m, 12/8/1959, G. R. Proctor 20336 (GH); Basse-Terre, Massif le la Soufrière, partie NW, trace Victor Hughes, Savane aux Ananas, 1000m, 5/5/1974, G. R. Proctor 40303 (US).

DOMINICA. St. Patrick Parish, Valley of Desolation, creeping on bare cliff, 2800 ft, 12/9/1964, D. H. Nicolson 1954 (GH, US); Forming mats on exposed lava rocks on mountain-top, summit of Morne Trois Pitons, 1400 m, 2/26/1946, J. S. Beard 633 (GH); Laudat, high wet turf, Boiling Lake, 1903, F. E. Lloyd 316 (NY, US).


VENEZUELA. Amazonas: Sabana natural arbustiva de arena blanca, camino San Carlos de Rio Negro-Solano, 2/10-22/1989, Stergios et al. 13398 (NY, US); Depto. Atabapo, slope of Cerro Marahuaca, Rio Yameduaka arriba, riverbank, 03°38'N 65°28'W, 1225 m, 2/21/1985, R. L. Liesner 17806 (MO); Savannas near Sta. Cruz, a small village on the Rio Atabápo 1 km N of the confluence of the Rio Temeni and the Rio Atacavi, 11/17-18/1979, Thomas and Rogers 2682 (NY); Swampy savanna between first and second woodlands after crossing Esmeralda Ridge on way to Duida, 200 m, 8/22/1944, J. A. Steyermark 57798 (F, MO, NY, US). Anzoátegui: Morical San Pedro, 3 km norte del Mapire, 8/16/1982, R. A. Montes 1333-A (MO). Bolivar: Frequent in marshy areas of slopes of summit ridge, Serra do Sol, 2050-2200 m, 12/28/1954, Maguire and Maguire 40435 (NY); Dist. Piar, sabanas entre la Quebrada Equetubá y el Rio Churí, al E del Churí-tepui, en el Valle del Rio Karuay inferior, 05°18'N 61°55'W, 900 m, 11/18/1984, O. Huber 9799 (NY); Locally abundant in moist sand in savanna about 4 km east of Mission, 1300 m, 12/23/1952, Maguire and Wurdack 34008 (MICH, NY); Foraneo San Isidro, Kms 118-128, route 10 Bolivar, Sierra de Lema, 05°50'N 61°28'W, 1000-1400 m, 8/1/1993, Rivero and Diaz 2421 (AAU); Km 118 (old camp at km 125) along El Dorado – Sta. Elena road, , wet forest area on ascent to the Gran Sabana, 1100 m, 11/15/1978, Luteyn et al. 6247 (MO, NY, US); Gran Sabana, Cerro Akurima, Sta. Elena, Feb. 1946, F. Tamayo 2819 (US); Mount Roraima, Glycon Swamp and vicinity, southwest-facing slopes, 1830-1920 m, 9/25/1944, J. A. Steyermark 58636 (F); Dist.

GYANA. Cuyuni-Mazaruni: Savanna between Partang and Karowrieng Rivers, 3-4 km SW of Imbaimadai, 05°41′N 60°16′W, 570-580 m, 12/20/1989, G. Gillespie and J. Smart 2796 (NY); Boy Scout Lookout & Johnsons Lookout, 05°10′N 59°29′W, 466 m, 8/30/2006, Wurdack et al. 4199 (NY, US); Chinowening Village, Ayangann Archytatei forest, 05°32′N 60°0′W, 650-675 m, 10/15/1981, Maas et al. 10372 (NY).


SURINAME. Marowijnese: Via secta ab Moengo tapoe Grote Zwiebelzwamp, in floating vegetation in Zwiebelzwamp near km 18, 10/21/1948, Lanjouw and Lindeman 953 (US); Via secta ab Moengo tapoe ad Grote Zwiebelzwamp, creeping in savanna near km 10.9, 10/7/1948, Lanjouw and Lindeman 701 (NY). Para: Frequent, damp sand, Zanderij II, 6/3/1944, Maguire and Fanshawe 32111 (MO, NY, US); Zanderij National Park, near airstrip, savanna and Bonnetia-Clusia scrub islands, 05°10′N 59°29′W, 390 m, 1/24/1987, Pipoly and Gharbarran 9816 (NY, US); Kurupukari-Annai road, 28 miles from Kurupukari, Iwokrama International Rainforest Reserve, 04°20′N 58°50′W, 60 m, 9/30/1996, D. Clarke 2660 (NY, US).

FRENCH GUIANA. Cayenne: Route de l’Est, Km 8, sur butte de micashiste, 04°45′N 52°26′W, 50-150 m, 8/22/1986, Sastre and Bell 8022 (US); Commune Regina, Montagne Petet Tortue, near Regina, at km 90 along Route Nationale 2, forest on steep slopes, 04°45′N 52°43′W, 36-50 m, 2/26/2003, Christenhusz et al. 2535 (AAU); Route du Tour de l’Île de Cayenne, RN 2 au PK 13, 3/28/1986, G. Cremer 9419 (AAU). Saint-Laurent-du-Maroni: Savane Macoua, region littorale, le long d’une piste perpendiculaire à la RN 1 allant vers la mer, savane basse marecageuse, 05°59′N 53°33′W, 10 m, 5/26/1989, Hoff and Cremer 5575 (AAU, US).

BRAZIL. Amapá: Oeste do Acampamento da Sop do km. 105 este de Porto Grande, 10/19/1979, Austin et al. 7128 (F, GH, MICH, NY, US). Amazonas: Rio Cuieiras, igarape da Cachoeira, campina renosa, umida, aberte, 9/15/1964, W. Rodrigues 6045 (F). Bahia: Municipality of Ilhéus, road from Olivença to Una, 18 km S of Olivença, near sea level, 4/21/1981, Boom et al 724 (NY); On the coast road between Alcobaça and Prado 12 km N of Alcobaça, mixed restinga with high forest, 17°29′S 39°13′W, ca. sea level, 1/16/1977, R. M. Harley 18010 (MO, NY); 11 km S of Santa Cruz Cabrália, restinga by the sea with strand


Peru: Tambopata, mas arriba de Moho en la quebrada Juliaca e inicio al oeste de las pampas del Rio Heath en la frontera con Bolivia, 12°30'S 68°40'W, 200 m, 8/13/1988, Nuñez et al. 9812 (MO).


Figure 34. *Pseudokyropodiella meridionalis*.  A. General habit (*P. Wilson 94 NY*).  B. Peduncle and strobilus (*K. Lems s.n. US*).  C. Rhizome (*J. Prado 422 NY*).
Figure 35. Distribution map of *Pseudolycopodiella meridionalis*.

*Pseudolycopodiella mesetarum* (B. Øllg.) K. Cook & Hickey, ined.


TYPE: VENEZUELA. Amazonas, Atabapo, Cerro Marahuaca, Huha. Cumbre altiplanicie no arbolada, mas o menos plana, con piedras expuestas, rio abajo, 2580m, 3°40’N 65°60’W, 1/31/1982, Steyermark, J. A. et al. 125967 (holotype: AAU; isotypes: NY!, US!).

Terrestrial herb; prostrate shoots appressed, terete, without fleshy cortex, 1.0—[1.3]—2.0 mm broad excluding leaves; leaves of prostrate shoot dimorphic, sometimes only weakly so;
lateral leaves spreading, narrowly triangular, falcate, 3.0—[4.3]—6.5 mm long, 0.7—[1.2]—1.5 mm broad, weakly imbricate, 2-ranked; dorsal leaves linear to falcate, erect, recurved, 2.7—[4.0]—5.2 mm long, 0.5—[0.7]—1.0 mm wide, in 4—6 obscure ranks, imbricate; ventral leaves absent; upright shoots 0.9—[1.3]—1.6 mm in diameter excluding leaves, to 13 cm high excluding the strobilus; upright shoot leaves narrowly triangular, (1.5-) 2.7—[3.6]—5.2 mm long by 0.6—[0.8]—1.1 mm wide, in sparse pseudowhors of 4—5, appressed to acutely spreading; strobili to 5 cm long, 5.0—[7.0]—9.2 mm wide including spreading sporophylls; sporophylls ovate, appressed to spreading, 2.4—[3.3]—4.8 mm long, excluding narrowed basal portion, 1.0—[1.7]—2.3 mm broad at widest point, tip acute to acuminate, margins erose to serrulate in alternating whors of 4—5; sporangia 1.2—1.6 mm wide; spores 37—[39.5]—43 µm; chromosome number unknown.

Distribution and Habitat

"Pseudolycopodiella mesetarum" is found at high elevations on the tepuis and mountains of Venezuela and the adjacent areas of Guyana, and likely Brazil. A disjunct population appears to exist in the Peruvian Andes. It grows in open, rocky and sandy habitats, from 2000-2800 m.

Comments

This species is distinguished by its narrow rhizome leaves, dense, erect, and often recurved dorsal leaves, and high elevation habitat. Its dorsal and lateral leaves are often only weakly differentiated, being similar in size and shape, but the plants are never completely isophyllous as in the co-occurring "Pseudolycopodiella iuliformis." The degree of rhizome leaf differentiation can vary along the length of the shoot.

This species was originally described as a variety of "Lycopodiella caroliniana" from Venezuela (Øllgaard 2004). It was said to be intermediate between "L. iuliformis" and "L. caroliniana" var. "meridionalis." The postulated diploid status of "Pseudolycopodiella mesetarum" and "P. meridionalis" and the possible tetraploid status of "P. iuliformis" make hybridization an unlikely cause of this morphological intermediacy.

Two collections from the Peruvian Andes bear remarkable similarity to the Venezuelan material. They share the dense, erect, narrow dorsal leaves and high elevation habitat, but are a lighter green in color and have more differentiated dorsal and lateral leaves. They are tentatively being classified as disjunct members of "Pseudolycopodiella mesetarum." It is possible that they represent a distinct species, but current material is insufficient to support such a conclusion. These plants could also be forms of "P. meridionalis," although the "P. meridionalis" most nearby in Colombia and southeastern Peru do not resemble the Andean ones.

Representative Specimens Examined

VENezUELA. AMAZONAS: Cerro Marahuaca, summit, SW side of center, open rocky plateaus and ravines, at base of boulder on slope, 03°39'N 65°26'W, 2660 m, 10/24/1988, R. Liesner 25285 (MO); Cerro Marahuaca, cumber, seccion noroccidental, 03°30'N 65°26'W, 2500 m, 2/16/1981, Steyermark et al. 124375 (MO, NY). Bolivar: Kukenan tepui, summit, large open rocky areas, boggy areas, small patches of shrubs, an small patches of forest, 05°13'N 60°18'W, 2550 m, 4/11/1988, R. Liesner 23135 (MO); Cumbre del Yuruni-tepui, al NNW del Cerro Kukenan, vegetacion herbaceo-arbustiva sobre planicies de arenisca en el sector centro-este.
del tepui, 05°19′N 60°51′W, 2300 m, 4/27/1984, O. Huber 9460 (AAU, NY); Summit of Mount Roraima, on northwest portion north and northwest of Summit Camp, sandy depression, 2620-2740 m, 9/27/1944, J. A. Steyermark 58808 (F, NY, US); Distrito Piar, Macizo del Chimanta, sector centro-noroeste del Chimanta-tepui, cabeceras orientales del Caño Chimanta, 05°18′N 62°09′W, 2000 m, 1/26-29/1983, Steyermark et al. 128145 (AAU, MO); Chimanta Massif, central section, Bonnetia swale along creek just east of west branch of headwaters of Rio Tirica, 2120 m, 2/11/1955, Steyermark and Wurdack 721 (F, NY); Cerro Roraima, cumber, parte noreste de Venezuela inmediata al sur del hito que marca los limites con Guyana, Brasil y Venezuela, 05°12′N 60°42′W, 2750-2800 m, 8/26-9/2/1976, Steyermark et al. 112557 (NY, US).

GUYANA. Mazaruni-Potaro: Roraima, summit, La Proa Camp, East of border, near Lake Gladys, mostly open rocky areas with ravines and lake, in grassy area, 05°15′36″N 60°13′W, 2800 m, 4/13/1988, R. Liesner 23244 (MO).

PERU. Amazonas: Provincia de Chachapoyas, Jalca zone 1-5 km west of Molinopampa, locally frequent in seepages, 2400-2450 m, 7/18/1962, J. J. Wurdack 1382 (NY, US). Pasco: Dist. Oxapampa, La Suiza Nueva, low montane forest, 10°33′4″S 75°27′22″W, 2210 m, 5/6/2005, van der Werff et al. 19732 (NY).
Figure 36. *Pseudolycopodiella mesetarum* (Steyermark et al. 125967 NY). A. Rhizome. B. General habit.
Figure 37. Distribution map of *Pseudolycopodiella mesetarum*.

*Pseudolycopodiella paradoxa* (Mart.) Holub


**TYPE:** BRAZIL. Martius, Icon. Pl. Crypt. t. 20, f. 2

Terrestrial herb; prostrate shoots closely appressed, terete to slightly flattened, without fleshy cortex, 0.6—[0.9]—1.1 mm broad excluding leaves; leaves of prostrate shoot dimorphic; lateral leaves spreading, deltate to triangular, falcate, 1.5—[2.8]—4.0 mm long, 1.1—[1.7]—2.2 mm broad, weakly imbricate, 2-ranked; dorsal leaves ovate, 1.2—[2.0]—3.0 (-3.6) mm long, 0.6—1.4 (-2.1) mm wide, in 2—4 obscure ranks, weakly imbricate; ventral leaves absent; upright shoots 0.5 —[0.9]—1.3 mm in diameter excluding leaves, to 10 cm high excluding the strobilus; upright shoot leaves narrowly triangular, 1.8—[2.5]—3.4 mm long by 0.4—[0.7]—1.0 mm wide, in sparse pseudowhors of 3—4, appressed to acutely spreading; strobili to 6 cm long, 4.7—[6.5]—8.7 mm wide including spreading sporophylls; sporophylls ovate, appressed to spreading, 2.4—[3.2]—4.1 mm long, excluding narrowed basal portion, 1.0—[1.6]—2.2 mm broad at widest point, tip acute, margins erose to serrulate, in alternating whors of 3—4; sporangia 1.1—1.9 mm wide; spores 33—[37.5]—44 µm; chromosome number unknown.

**Distribution and Habitat**

This species has a peculiar distribution. It is found in southern and central Brazil, Paraguay, and Bolivia in the southern end of its range. To the north it is known from Venezuela, the Antioquia department of Colombia, and from a single collection in Morazan department, El Salvador. It grows in open, wet, often sandy locations such as savannas and cerrado, from 500-1900 m.

**Comments**

This species is distinguished by its small ovate dorsal leaves that are almost scale-like in appearance and its overall small stature. Even the larger plants do not exceed 20 cm in height at maturity. Their lateral leaves are also small, usually less than 3.5 mm long. Both dorsal and lateral leaves are typically less than three times longer than broad. This taxon most closely resembles the small *P. caroliniana* of North America, but that taxon has narrowly triangular or lanceolate dorsal leaves rather than ovate ones. The habitat, distribution, and leaf size ratios of *P. paradoxa* most closely resemble *P. carnosa*, which can be distinguished from *P. paradoxa* by its broad, fleshy, flattened rhizome. These two species appear to hybridize and are likely closely related.

**Representative Examined Specimens**

EL SALVADOR. Morazan: Terrestrial on hummocks in swamp 3 km south of El Zancudo, 1900 m, 3/29/1979, *R. Suter* 1014 (F, NY).

COLOMBIA. Antioquia: Guatape, forest on slopes above river, Jan. 1977, *McAlpin and Kuhn* 77-16 (NY); Guatape, road to San Rafael ca 4 km E of Guatape-Santa Rita Road (Pinca Montepinar), 06°15’N 75°08’W, 1850 m, 10/22/1987, *Brant and Roldan* 1460 (MO); En selva humeda en las fuentes Termales de Santo Domingo, 1200 m, 5/7/1949, *Scolnik et al.* 19An516 (US).


![Figure 38. Pseudolykopodiella paradoxa. A. Rhizome (Heringer et al. 4211 MO). B. General habit (T. Lasser 1966 F).](image)
Figure 39. Distribution map of *Pseudolycopodiella paradoxa*

**Pseudolycopodiella tatei** (A. C. Smith) Holub


Terrestrial herb; prostrate shoots closely appressed, flattened, with fleshy cortex, 2.5—[3.5]—4.5 mm broad excluding leaves; leaves of prostrate shoot slightly dimorphic, spirally arranged, many-ranked; laterally positioned leaves spreading, falcate, 2.9—[4.1]—8.6 mm long, 0.6—[1.0]—1.5 mm broad; dorsally positioned leaves triangular to narrowly triangular, often broadened at the base, 1.3—[2.8]—7.5 mm long, 0.5—[1.0]—1.8 mm wide; ventral leaves present, highly reduced, membranaceous or filamentous; upright shoots 1.0—[1.4]—2.0 mm in diameter excluding leaves, to 18 cm high excluding the strobilus; upright shoot leaves narrowly triangular, 3.0—[4.0]—5.7 (-7.9) mm long by 0.5—[0.8]—1.3 mm wide, in pseudowhorls of 4—6, appressed to acutely spreading; strobil to 9cm long, 9.0—[11.2]—15.0 mm wide including spreading sporophyll; sporophylls lanceolate, appressed to spreading, 4.4—[5.3]—7.2 mm long, excluding narrowed basal portion, 1.0—[1.4]—2.2 mm broad at widest point, tip acuminate, margins almost entire to serrate, in alternating whorls of 4—6; sporangia 1.0—1.5 mm wide; spores (31-) 39—[42]—46 µm, frequently aborted; chromosome number unknown.

**Distribution and Habitat**

This species is found in the Guianas region of South America, in Venezuela, Guyana, and Suriname. It is also found farther south along the Bolivia-Brazil border. Windisch (1991) reported this taxon (as *Lycopodiella benjaminiana*) in Mato Grosso, Brazil. It occurs in open, wet habitats including savannas and swamps, from 300-1550 m.

**Comments**

This species is distinguished by its flattened, fleshy rhizome. Its dorsally, laterally, and ventrally positioned rhizome leaves tend to be somewhat differentiated. It has falcate, spreading lateral leaves and smaller dorsal ones, often with broadened bases. Although there is some differentiation, the dorsal and lateral leaves steadily grade into one another. There is not the sharp differentiation as is seen in the truly anisophyllous taxa, such as *Pseudolycopodiella caroliniana*. The ventral leaves are highly reduced, membranaceous, and often hair-like. The transition into ventral leaves is more abrupt than between lateral and dorsal ones.

*Pseudolycopodiella tatei* resembles and occurs with *P. iuliformis* and *P. krameriana*. These taxa may have a somewhat swollen rhizome, but they are not nearly as flattened as in *P. tatei*. In Brazil and Bolivia *P. tatei* occurs with *P. carnosae*, which also has a flattened rhizome, but *P. carnosae* lacks ventral leaves, is completely anisophyllous, and is a lighter green in color.

This species was described from a plant on Mount Roraima in Venezuela. Windisch (1991) later described *Lycopodiella benjaminiana* from Mato Grosso, Brazil. Material from this area and the illustration from Windisch’s description match the appearance of the *P. tatei*
holotype and other Venezuelan material, so *L. benjaminiana* is here treated as a synonym of *P. tatei*. The taxon *Lycopodium duidae* var. *guianense* from Suriname, which also has a flattened rhizome and somewhat differentiated leaves, is included here as well.

**Representative Examined Specimens**

**VENEZUELA.** Amazonas: Dpto. Atures, Valley of Rio Coro-Coro, W of Serrania de Yutaje, plateau on W side of valley, 5°41′N 66°08′30″W, 1000 m, 2/28/1987, Holst and Liesner 3221 (MO); Cumbre del cerro Autana, sabana y afloramientos expuestos, 04°52′N 67°27′W, 1230-1240 m, 9/20-22/1971, J. A. Steyermark 105154 (US). Bolivar: Auyantepui, sabana humeda de Bromeliaceas cerca Guayaraca, 1100 m, 4/10/1956, Vareschi and Foldats 4622 (US); Kavanayén, trail from Misión de Santa Teresita de Kavanayén to rio Pakairau, 1100-1200 m, 8/8/1970, Moore, Jr., et al. 9605 (GH); Mount Roraima, Emerald Swamp, southwest facing slopes, 1520 m, 9/25/1944, J. A. Steyermark 58610 (F).

**GUYANA.** Potaro-Siparuni: Pakaraima Mts., Upper Ireng River, 2 km E of Cipo settlement on N end of adjacent ridge, seepage bog on W aspect slope, 04°49′N 60°01′W, 750 m, 2/3/1993, T. W. Henkel 1158 (NY, US).

**SURINAME.** Sipaliwini: Kappel-savanna near the foot of Tafelberg, 300 m, 2/25/1961, Kramer and Hekking 3040 (GH, NY).

**BOLIVIA.** Santa Cruz: Velasco Province, Parque Nacional Noel Kempff M. Los Fierros, La Meseta, campo rupestre, suelos limo arenosos con afloramiento de roca, 14°33′48.1″S 60°46′24.9″W, 650 m, 8/28/1995, Guillén and Gonzales 4178 (NY).
Figure 40. *Pseudolycopodiella tatei* (Moore et al 9605 GH). A. Fertile shoot and rhizome. B. Rhizome.
Figure 41. Distribution map of *Pseudolycopodiella tatei*.
References


