

Serpocaulon (Polypodiaceae), a new genus segregated from *Polypodium*

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We describe the neotropical fern genus *Serpocaulon* (Polypodiaceae), segregated from *Polypodium*, and make new combinations for the forty known species. *Serpocaulon* has been recognized previously as a putatively natural group by several authors, based on morphological evidence, but never accorded generic rank. The monophyly of *Serpocaulon* is strongly supported in chloroplast DNA-based phylogenetic analyses, using the genes *rbcL*, *rps4*, *rps4-trnS* intergenic spacer, and *trnL-F* intergenic spacer on 29 samples from 22 species. *Serpocaulon* is readily separated from other subclades within Polypodiaceae, and especially from *Polypodium*, which is less closely related to *Serpocaulon* than are several other genera. *Serpocaulon* differs from other New World polypods in the combination of usually long-creeping, sparingly branched rhizomes with clathrate (sometimes strongly so), usually peltately attached scales; regularly anastomosing (goniophleboid) veins with individual areoles chevron-shaped and each with a single, free, included excurrent veinlet; and non-paraphysate sori in one to 10 rows between costae and pinna margins. In *Polypodium*, the rhizome scales are not clathrate, ± concolorous, and invaginated at the base, with somewhat overlapping basal lobes, and rhizomes are generally shorter-creeping and more frequently branched, the veins are free or forming a single row of areoles, and the sori uniseriate on each side of the costae. Most species of true *Polypodium* are north-temperate, Mexican, or Mesoamerican in distribution, while *Serpocaulon* is entirely neotropical or subtropical, with the greatest number of species in South America. There appears to be no convenient infrageneric division of the species within *Serpocaulon*, although the most widespread species, *S. triseriale*, is somewhat isolated at the base of the clade. Species with the thinnest rhizomes also have the fewest scales, and generally grow at high elevations. Species having the scaliest rhizomes, with scales spreading and strongly overlapping, form a weakly supported subclade, as do species with multiseriate rows of areoles between costae and pinna margins.

KEYWORDS: ferns, phylogeny, Polypodiaceae, *rbcL*, *rps4*, *rps4-trnS* IGS, *Serpocaulon*, *trnL-F* IGS.

INTRODUCTION

The classical Linnaean genus *Polypodium*, as adopted in most recent floras and taxonomic treatises, comprises about 125–150 species, most of them New World. Sometimes, additional genera are subsumed within *Polypodium*, e.g., *Microgramma*, *Phlebodium*, and *Pleopeltis* in the New World, and *Goniophlebium* in the Old World (as by Hennipman & al. in Kubitzki, 1990), in which case *Polypodium* exceeds 250 species. Within a broadly defined, morphologically extremely diverse *Polypodium* there are many problematic groups. Recent molecular evidence suggests that *Polypodium* s.l. is a polyphyletic assemblage, even if several segregate genera (e.g., *Microgramma*, *Pecluma*, and *Campyloneurum*) are excluded (as in most recent tropical floras, e.g., Try-

on & Stolze, 1993; Moran in Davidse & al., 1995; Mickel & Smith, 2004), and that generic boundaries in this complex of genera (*Polypodium* s.l.) require substantial revision (Schneider & al., 2004b).

Within *Polypodium* s.l. (as applied in floras and taxonomic compendia by most authors today), several groups have been considered as “natural”, informally recognized, and taxonomically treated. These include 1) *Polypodium* s.s., a group of largely north-temperate species allied to *P. vulgare* L. (Haufler & al., 1995; Haufler & Ranker, 1995), with a closely related subgroup, *P. plesiosorum* and allies (Tejero-Díez & Pacheco, 2004; Group 1, part, of Tryon & Tryon, 1982), in Mexico and Central America; 2) *P. subpetiolatum* and allies (revised by Maxon, 1903; Group 1, part, of Tryon & Tryon, 1982); 3) the *P. furfuraceum* and *P. plebeium* groups

(Maxon, 1916a; 21 spp.; Groups 4 and 6, parts, of Tryon & Tryon, 1982); 4) *P. polypodioides* (Maxon, 1916b; Weatherby, 1939; Group 4, part, of Tryon & Tryon, 1982); 5) *P. squamatum* and relatives (Maxon, 1916b; Weatherby, 1947; revised by de la Sota, 1966; 22 spp.; Group 5, part, of Tryon & Tryon, 1982); 6) the *P. thysanolepis* group (Wendt, 1980; Group 4, part, of Tryon & Tryon, 1982); and 7) *P. loriceum*, *P. fraxinifolium*, and allies, an entirely neotropical group of about 40 species with regularly anastomosing (goniophleboid) veins and often long-creeping, cordlike rhizomes bearing partially or entirely clathrate scales (most of Group 2 of Tryon & Tryon, 1982; species taxonomy, 23 spp., revised by Hensen, 1990). Because nearly all of the major subgroups of *Polypodium* s.l. occur in Mexico and Central America, and these areas are a center of diversity for several of the subgroups, many species have been treated in floristic contexts by Lellinger (1989), Moran (in Davidse & al., 1995), and by Mickel & Smith (2004). However, the species allied to *P. loriceum* and *P. fraxinifolium* are predominantly South American and are less well studied, except for work by Hensen (1990), which was followed in the main in the floristic account for Peru by Tryon & Stolze (1993).

Existing evidence (Schneider & al., 2004b) supports the placement of species in 3) through 6), as delineated above, in *Pleopeltis*. All of these groups contain species that bear scales on the abaxial lamina. A few scaly-bladed species of *Polypodium* have already been transferred to *Pleopeltis* (Windham, 1993), as precursor to their treatment in the *Flora of North America North of Mexico* (Andrews & Windham in *FNA* Ed. Comm., 1993); however, most scaly species remain in *Polypodium*, to be transferred to *Pleopeltis* elsewhere (Smith & al., in prep.). Species now placed in the segregate genera *Dicranoglossum*, *Neurodium*, *Microphlebodium*, and *Pseudocolysis* also appear to be closely allied to, and perhaps inseparable from, *Pleopeltis* s.l. In the present paper we address the species mentioned under 7) above, and these lack a name at generic rank. This new genus we here name *Serpocaulon*, alluding to the long-creeping, snakelike rhizomes found in nearly all species.

Many of the species of *Serpocaulon* were initially described in *Goniophlebium* (Blume) C. Presl (see Appendix 2, electronic supplement), a genus of about 25 species occurring from India, throughout southeast and eastern Asia, the Himalayan region, and Malesia to Australasia, Melanesia, Samoa, and Micronesia (Rödl-Linder, 1990). The name *Goniophlebium* is derived from the Greek *gonia*, meaning angle, and *phleps*, vein, referring to the characteristic venation pattern formed by regularly anastomosing veins that often form a succession of chevron-shaped areoles between the pinna midribs and margins. Although the paleotropical species of *Gonio-*

phlebium and the neotropical species of *Serpocaulon* have similar venation, and both genera bear clathrate rhizome scales, the similarities are convergent, as indicated by their positions in phylogenetic trees based on molecular data (see Schneider & al., 2004b). *Goniophlebium* s.s. falls within an almost exclusively monophyletic Old World clade (as far as known, the lone exception is a single disjunct species of *Platyterium* in the Andes; Schneider & al., 2004b), whereas *Serpocaulon* nests in a predominantly New World clade (with a few African outliers) containing the genera *Microgramma*, *Campyloneurum*, *Pleopeltis*, *Pechuma*, and *Polypodium* s.s., as well as the pantropical grammitid clade. Rödl-Linder (1990) and Lellinger (1993) also specifically excluded all New World species of *Polypodium* from *Goniophlebium* on the basis of several morphological characters, e.g., the absence of black sclerenchyma strands in the rhizomes, peltate-based rhizome scales, the absence of hairy or scaly paraphyses in the sori, and the folded perine around the spores.

In this paper, we restrict the application of *Polypodium* L. (Sp. pl. 2: 1082. 1753), with lectotype *P. vulgare* L. (chosen by John Smith, Hist. fil. 88. 1875), to a group of predominantly temperate (mainly north-temperate) species plus a less widespread, tropical and subtropical group of Mexican-Mesoamerican species. *Polypodium*, as defined in this narrow sense, then comprises about 15 species in temperate regions of America, Europe, Asia and Africa (Haufler & al., 1995; Haufler & Ranker, 1995) and perhaps another 15 species in Mexico and Mesoamerica. The species have deeply pinnatifid or weakly 1-pinnate blades, concolorous or sometimes slightly bicolorous, orange-tan to brown, non-clathrate rhizome scales, free or weakly anastomosing venation (each areole with a single, free, included veinlet), sori terminal on ends of free included veinlets, channeled stipes, filamentous or branched paraphyses, and more frequently branched rhizomes.

Within *Serpocaulon*, eight (of about 40 total) species have been included previously (as *Polypodium*) in a phylogenetic study using the chloroplast DNA regions *rbcL*, *rps4*, and *rps4-trnS* intergenic spacer (Schneider & al., 2004b): *Polypodium adnatum* Kunze ex Klotzsch [voucher re-identified herein as *S. richardii* (Klotzsch) Domin], *P. fraxinifolium* Jacq., *P. funkii* Mett. (voucher re-identified as *S. ptilorhizon* (H. Christ) A. R. Sm.), but not used in the current study), *P. levigatum* Cav., *P. patentissimum* Mett. ex Kuhn, *P. ptilorhizon* H. Christ, *P. triseriale* Sw., and *P. wiesbaueri* Sodiro [= *P. eleutherophlebium* (Fée) Mett. in this paper]. In a maximum likelihood analysis (Schneider & al., 2004b), this clade is monophyletic, with clade confidence values of 1.00 (Bayesian posterior probability: PP) and non-parametric bootstrap support of 99%. In the Schneider & al.

analysis, this clade is weakly supported (Bayesian PP 0.52) as sister to the entire pantropical grammitid clade (Grammitidaceae, in many classifications), comprising about 750 species. In molecular analyses, *Serpocaulon* is well removed from other species groups currently treated in *Polypodium*, namely the scaly species (including *Pleopeltis* Humb. & Bonpl. ex Willd. s.s., *Marginaria* Bory, *Polypodium furfuraceum* and allies, *P. myriolepis* and allies, *P. guttatum* and allies, *Dicranoglossum* J. Sm., *Microphlebodium* L. D. Gómez (Gómez, 1985), *Pseudocolysis* L. D. Gómez (Gómez, 1977), and possibly several other segregate genera) as well as from the *Polypodium vulgare* group and from *Pecluma* M. G. Price. In the present study, we developed and analyzed new molecular data from 15 additional species, as well as incorporating examples from previously sequenced species, for a total of 22 species now examined—representing slightly more than half of the currently known species.

It is the objective of this paper to present the molecular and morphological evidence for characterizing *Serpocaulon*, formally name the new genus, and effect transfer of species belonging to it.

MATERIALS AND METHODS

Sequences of four chloroplast DNA regions, *rbcL*, *rps4*, *rps4-trnS* intergenic spacer, and *trnL-F* intergenic spacer, were generated using primers and protocols as described in previous studies (Haufler & Ranker, 1995; Schneider & al., 2002, 2004a, b; Haufler & al., 2003; Janssen & Schneider, 2005). With the exception of newly generated sequences for samples of *Serpocaulon* and *trnL-F* for *Microgramma percussa*, all sequences used in our current study were published in previous papers (Schneider & al., 2004a, b). The taxon dataset in the current paper is a subset of the one used by Schneider & al. (2004a), plus additional species of *Serpocaulon*. Appendix 1 provides the GenBank accession numbers for all samples of *Serpocaulon*, including previously published sequences. For information concerning sequences of taxa not belonging to *Serpocaulon*, except for *Microgramma percussa*, see Schneider & al. (2004a). All sequences were aligned manually using MacClade 4.0 (Maddison & Maddison, 2000). Ambiguously aligning regions were excluded from all analyses.

Phylogenetic analyses were performed using PAUP* 4.0b10 (Swofford, 2000). *Dictymia brownii* (Wikstr.) Copel. was chosen as the outgroup representing the loxogrammoid lineage, which has been shown to be the sister lineage of all other polygrammoid ferns (Schneider & al., 2004b). Maximum parsimony analyses were generated using the heuristic search mode with TBR branch

swapping, 1000 random addition sequence replicates, and MULTREES on. Bootstrap values were calculated with 10,000 bootstrap replicates using the heuristic search mode with TBR branch swapping and 100 random addition sequence replicates. The absence of incompatibilities among the four chloroplast DNA regions was controlled by visual comparison of the results of bootstrap analyses of each of the four cpDNA regions. Differences were judged to be inconsequential, and the four regions were combined in all analyses presented. Maximum likelihood analyses were carried out with models selected using the hierarchical likelihood test as implemented in Modeltest (Posada & Crandall, 1998). The same model, GTR + I + Γ , was selected using the AIC criterion in Modeltest. It was implemented with the following parameters: A = 0.2974, C = 0.1980, G = 0.2020, T = 0.2944, A-C = 1.2135, A-G = 3.4737, A-T = 0.4586, C=G = 1.0138, C-T = 4.3370, G-T = 1.000, I = 0.2371, and Γ = 0.999 in the files executed in PAUP* 4.0b10. Tree searches were performed using the heuristic mode with TBR branch swapping and 100 random addition sequence replications.

Bayesian inference of phylogeny was carried out with MrBayes 3.0 (Huelsenbeck & Ronquist, 2001) with the GTR + I + Γ model implemented for 4 chains with 10,000,000 generations, of which each 1000th generation was sampled. The burn-in phase was identified visually and excluded before inferring Bayesian posterior probabilities.

RESULTS

Maximum likelihood analysis of the combined dataset yielded an optimal tree with a $-\ln L = 0.20233.97$ (Fig. 1). Maximum parsimony analysis of the same dataset resulted in 348 most parsimonious trees with a length of 3023 steps, consistency index of 0.4408, homoplasy index of 0.5592, retention index of 0.7033, and a rescaled consistency index of 0.3899 (Fig. 2).

Serpocaulon was monophyletic in maximum likelihood (ML), maximum parsimony (MP), and Bayesian Inference of phylogeny (BY), with strong support in BY analysis (Fig. 1, PP = 1.00) and MP analysis (Fig. 2, BS = 99%). *Serpocaulon* was not closely related to other segregates of *Polypodium* such as *Goniophlebium*, *Pleopeltis*, *Pecluma*, and *Polypodium* s.s. *Serpocaulon triseriale* was strongly supported as sister to the remaining 21 species of *Serpocaulon* included in this study (Figs. 1, 2). In the ML analysis, *S. sessilifolium* (clade II in Figs. 1 and 2) was sister to the remaining 20 species. These 20 species clustered into two clades (clade III + IV in Fig. 1). One clade included the species *S. lasiopus* to *S. silvulae* (clade III in Fig. 1), whereas the other includ-

ed *S. eleutherophlebium* to *S. maritimum* (clade IV in Fig. 1). The latter clade had strong support in the BY analysis (PP = 1.00) and poor bootstrap support in the MP analysis (BS = 72%). The clade including *S. lasiopus* to *S. silvulae* was not monophyletic in the strict consensus tree of the 348 most parsimonious trees (clade III in Fig. 2), but it was present in 95% of these trees. In the

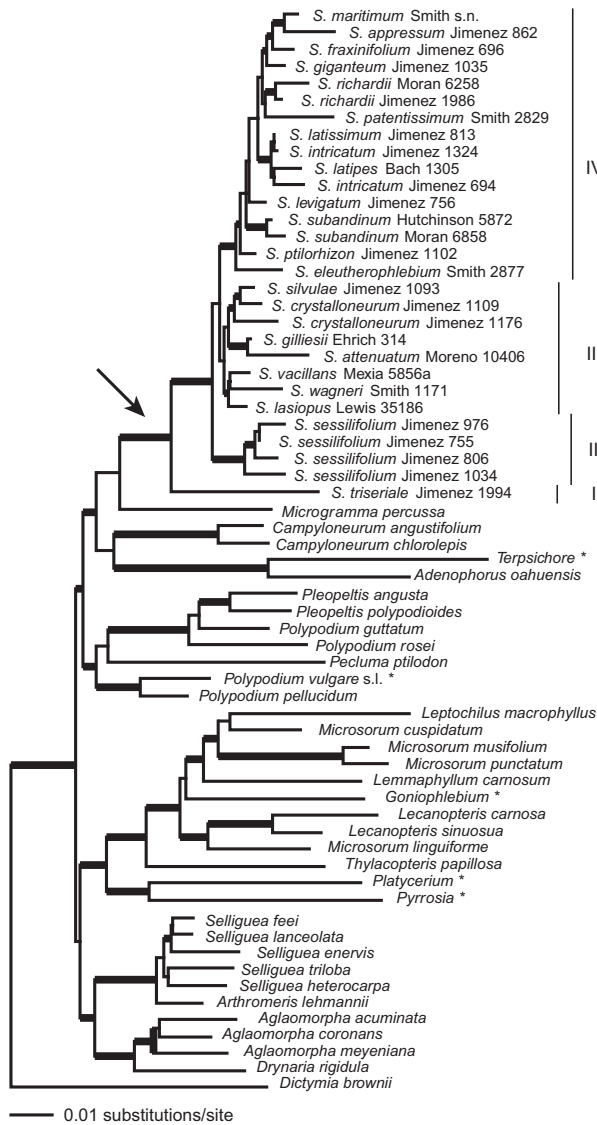


Fig. 1. Phylogram with the highest likelihood value found in the maximum likelihood analysis of the combined dataset. Thick lines indicate branches with Bayesian posterior probabilities of ≥ 0.95 . The arrow indicates the *Serpocaulon* clade. Vertical lines on the right indicate four clades within *Serpocaulon* discussed in the results. Asterisks indicate composite taxa that are based on sequences generated from two species of an unambiguously monophyletic genus or lineage (see Schneider & al., 2004a, for further information). All samples of *Serpocaulon* are given with species name and the corresponding voucher.

MP analysis, *S. sessilifolium* (clade II in Fig. 1) was sister to the clade comprising *S. eleutherophlebium* to *S. maritimum* (clade IV in Fig. 1).

All five species represented by more than one specimen formed clades, at least in the ML analysis. The four specimens of *S. sessilifolium* formed a strongly supported clade (BS = 100%, Bayesian PP = 1.00). Two specimens of *S. subandinum* were sister to each other with bootstrap support of 97% and PP = 1.00. Two specimens of *S. richardii* also formed a clade in the ML tree but this clade was found in only 74% of the MP trees. A Bayesian PP of 0.98 supported the monophyly of this species. Two specimens of *S. crystalloneuron* formed a clade with *S. silvulae* in the ML tree, with PP of 1.00, but only 95% of the most parsimonious trees possessed this clade. The two specimens of *S. intricatum* formed a clade with *S. latipes* and *S. latissimum* in both ML and MP trees. This result was supported by a Bayesian PP of 1.00 and a bootstrap value of 90%.

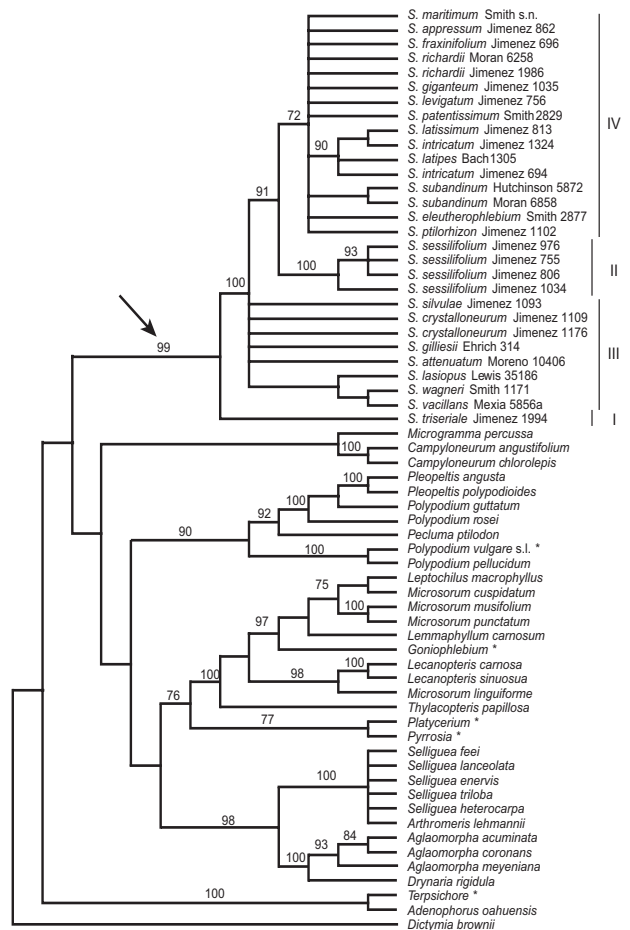


Fig. 2. Strict consensus tree of 348 most parsimonious trees obtained in a maximum parsimony analysis of the combined dataset. Bootstrap values $>70\%$ are given above branches. For further information see Fig. 1.

DISCUSSION

The monophyly of *Serpocaulon* is strongly supported in all analyses of the cpDNA sequence data, data that include slightly more than half of the currently accepted species. In all phylogenetic analyses, the lineage is clearly separated from other lineages traditionally assigned to *Polypodium* s.l. (Schneider & al., 2004a, b), and it is unambiguous whether a given species of *Polypodium* s.l. is included or not. *Serpocaulon* appears morphologically well-defined and has been recognized previously as a putative natural group by various authors (Tryon & Tryon, 1982, Group 2; Hensen, 1990), although Tryon and Tryon included three species that both we and Hensen exclude: *Polypodium decumanum* Willd. [= *Phlebodium decumanum* (Willd.) J. Sm.], *P. decurrens* Raddi [= *Campyloneurum decurrens* (Raddi) C. Presl], and *Polypodium kunzeanum* C. Chr.]. Lellinger's (1993) definition of *Polypodium* subg. *Polygoniophlebium* roughly coincides with our circumscription of *Serpocaulon*, except that we exclude *Polypodium plectolepidioides* Rosenst. and *P. rhachypterygium* Liebm. (which may be more closely related to *Pecluma*), as well as *P. plesiosorum* Kunze (which we retain in a redefined and smaller *Polypodium*; see Tejero-Díez & Pacheco, 2004); all three of these species were mentioned by Lellinger as belonging to subg. *Polygoniophlebium*.

Hensen (1990) attempted a revision of the *Polypodium loriceum* group (our genus *Serpocaulon*) based on morphological characters, and several new species have been described since (Kessler & Smith, 2005). Because Hensen's (1990) circumscription of the "loriceum" group is basically the same as ours, it is of interest to compare the results of his morphology-based cladistic analysis with our molecular results. With Hensen's dataset, homoplasy was acknowledged to be a major problem. A further problem was his selection of *Campyloneurum* as outgroup, because this genus may not be the closest relative of *Serpocaulon* (Schneider & al., 2004b). Hensen assessed 18 characters of the rhizomes, rhizome scales, fronds, indument, and spores, and his consensus cladogram shows two major lineages, one of which corresponds in part with a clade found in all analyses of our cpDNA dataset that was strongly supported in BY (PP = 1.00) but poorly supported in MP (BS = 72%) (Fig. 2, clade IV). This clade includes taxa with less scaly rhizomes, with many of the species having wholly or partly appressed scales. Hensen's "scaly" clade also included *S. sessilifolium*, which is either sister to the other major clade (Clade IV) of *Serpocaulon* (MP) or sister to clades III + IV (ML) based on our cpDNA evidence. Taking into account the basal position of *S. triseriale*, the cpDNA data suggest a trend from densely scaly

rhizomes towards less dense indument and decreasing size of the scales in this genus. In Hensen's analysis, *S. triseriale* was sister to a clade that included taxa with reduced indument density. This result may reflect the presence of many plesiomorphic features in this putatively earliest diverging species of *Serpocaulon*.

We see other resemblances of putatively related species in the Hensen cladogram and our molecular tree. These include 1) a Hensen-clade containing species with 1-pinnate blades and 3+ rows of areoles and sori between costae and pinna margins (containing *S. appressum*, *S. fraxinifolium*, *S. richardii*, and two other species not sampled by us, *S. adnatum* and *S. caceresii*—a subset of our clade IV in the ML analysis (Fig. 1); and 2) a clade containing most of the species with densely scaly rhizomes (comprising *S. crystalloneuron*, *S. gilliesii*, *S. lasiopus*, *S. vacillans*, and *S. wagneri*)—basically, our clade III in the ML analysis (Fig. 1). Thus, the genealogical composition of both Hensen's morphology-based tree and our molecular tree show similarities, although some of the results are difficult to compare because sampling in the two studies differed, and we have also adopted different circumscription of certain species.

Currently, evidence suggests some trends in the morphological evolution of *Serpocaulon*. Densely scaly rhizomes appear to be plesiomorphic, with a trend toward reduction in the number and size of scales on the rhizomes. Narrowing of the rhizome diameter also seems to be correlated with scale reduction. Species with the thinnest rhizomes (smallest diameter) and fewest scales form a grade at the base of our clade IV in the ML analysis (Fig. 1): *S. eleutherophlebium*, *S. ptilorhizon*, *S. subandinum*, and *S. levigatum*; however, *S. patentissimum*, with the fewest rhizome scales and thinnest rhizomes, is not clearly part of this clade. Not only is scale number reduced in these species, but the rhizome scales are often tightly appressed, or spreading only at the scale tips; the ultimate reduction is seen in *S. patentissimum*, *S. levigatum*, and *S. ptilorhizon*, where the rhizomes are subglabrous; these species tend to grow at high elevations. Species having dense, persistent, spreading, and strongly overlapping scales fall toward the base of the tree in both ML and MP analyses (Figs. 1–2): *S. attenuatum*, *S. crystalloneuron*, *S. gilliesii*, *S. lasiopus*, *S. sessilifolium*, *S. triseriale*, and *S. wagneri*. Several of these grow at low elevations, and all except *S. triseriale* have a single row of sori on each side of the costa.

Another trend within *Serpocaulon* appears to be increasing pinnation (ultimately to completely free, non-adnate pinnae) in the clade comprising *S. maritimum*, *S. fraxinifolium*, *S. appressum*, *S. giganteum*, and *S. richardii*. Several other unsampled species are expected to fall within this clade, e.g., *S. caceresii* and *S. adnatum*. Those species showing increased pinnation (free non-adnate

pinnae) also show a greater number of rows of areoles (and sori) between the costae and pinna margins.

Serpocaulon is related to several genera with an exclusively or nearly exclusively neotropical distribution. We refrain from drawing conclusions about the closest relative until denser sampling of the putative closest lineages, such as *Microgramma* and the grammitids, can be performed. In Schneider & al. (2004b), *Serpocaulon* was found to be sister to grammitids, but these relationships were poorly supported. Further evidence is needed to confirm this hypothesis or to confirm alternative hypotheses such as close relationships between *Microgramma* and *Serpocaulon* or between *Campyloneurum* and *Serpocaulon*. Further sampling must also precede exploration of the radiation of *Serpocaulon* in the Neotropics and possible correlations between the origin of Andean habitats and the diversification of the genus in that area, home of nearly three-fourths of the species in the genus. We note that the basalmost species in the genus, *S. triseriale*, has the largest distribution of any species in *Serpocaulon*, covering nearly the entire distribution of the genus latitudinally (but not elevationally). Biogeographical and ecological trends can be only generally stated using existing data: (1) *Serpocaulon* shows the greatest diversity in South America; (2) species occurring at lowest elevations in the genus, usually below 500 m, appear to be members of the basalmost branches of the tree (*S. attenuatum*, primarily Amazonian; *S. triseriale*, mostly 100–1500 m; and *S. wagneri*, mostly 0–1000 m); and (3) those species having thinnest rhizomes and fewest scales are entirely or predominantly middle- to high-Andean, in comparison to many of the other species of *Serpocaulon*, which are more widespread, in montane forests, or mainly at low to middle elevations.

Although the current sampling is insufficient to draw conclusions about the relationships among the species of *Serpocaulon* as well as the monophyly of some species, this summary illustrates that the sampling is adequate to outline some issues that need to be considered in future studies and in any exhaustive revision of the genus. A denser taxon sampling with additional molecular markers must be obtained before these issues are explored in detail.

TAXONOMIC TREATMENT

Serpocaulon A. R. Sm., **gen. nov.** – Type: *Serpocaulon loriceum* (L.) A. R. Sm. [= *Polypodium loriceum* L.]. Figs. 3, 4.

Polypodium L. subg. *Polygoniophlebium* Lellinger, Amer. Fern J. 83: 37. 1993. – Type: *Polypodium fraxinifolium* Jacq. [= *Serpocaulon fraxinifolium* (Jacq.) A. R. Sm.]

A *Polypodio* sensu stricto venis ordinate anastomosantibus, areolis cheveroniformibus (similaribus *Goniophlebio* et *Thelypteridi* subg. *Meniscio*), 1–10-jugatis inter costas et margines pinnarum, omnis areolis venula singulari inclusa excurrenti libero, paleis rhizomatium clathratis, minimum centraliter vel basaliter, generaliter peltatis, rhizomatibus plerumque longirepentibus, parce ramosis, distributione neotropico differt; a *Pleopelti* sensu lato laminis pinnatisectis vel 1-pinnatis, paleis carentibus abaxialiter et adaxialiter in venis et interveniis differt; a *Pechuma* venis ordinate anastomosantibus differt.

Epiphytic or epipetric, infrequently terrestrial. Rhizomes usually very long-creeping, short-creeping in a few species, sparingly branched, the phyllopodia (0.5)5–20 times the rhizome width apart, sometimes glaucous, root proliferations absent; black sclerenchyma strands absent; vascular bundles sometimes with sclerenchyma sheaths; scales round, oblong, lanceolate, or lanceolate-attenuate and with a filiform tip, bicolorous, part of each scale clathrate with the side walls dark brown or black, sometimes the lumina also blackish so that the scales appear completely black, generally peltately attached (or with strongly overlapping lobes at a deeply cordate base), surfaces glabrous (lacking rhizoidal surface indument), margins entire or toothed. Stipes stramineous to light brownish, nearly terete proximally, flattened to channeled distally. Blades pinnatifid to pinnate, rarely simple (*S. levigatum*) or shallowly pinnatifid, monomorphic, stipitate, articulate on short phyllopodia; laminae glabrous, hairy, with scales absent, or scattered clathrate scales present along the costae and a few on the rachises; veins regularly anastomosing (goniophleboid), areoles chevron-shaped and each with a single, free, included vein. Sori round or nearly so, in one to 10 rows between costae and margins, exindusiate, each sorus terminal on a free included vein; paraphyses absent or present and short, 2–3-celled, glandular, not easily seen; sporangia glabrous. Spores light yellowish to whitish, bilateral, exine verrucate, perispore relatively thin or occasionally thickened, generally tuberculate, occasionally winged; $x = 37$.

Distribution: ca. 40 species, several recently described (Kessler & Smith, 2005), and several more needing description. Preponderantly S. American, but with 14 species extending or restricted to the Antilles, Central America, and southern Mexico (*S. antillense*, *S. attenuatum*, *S. dissimile*, *S. eleutherophlebium*, *S. falcaria*, *S. fraxinifolium*, *S. giganteum*, *S. levigatum*, *S. loriceum*, *S. loriciforme*, *S. maritimum*, *S. ptilorhizon*, *S. triseriale*, *S. wagneri*). The only species restricted to the Antilles or to North America north of Colombia are *S. antillense* and *S. falcaria*, while 26 species are confined to South America.

Serpocaulon differs from *Polypodium* in having regularly anastomosing (goniophleboid) veins with individ-

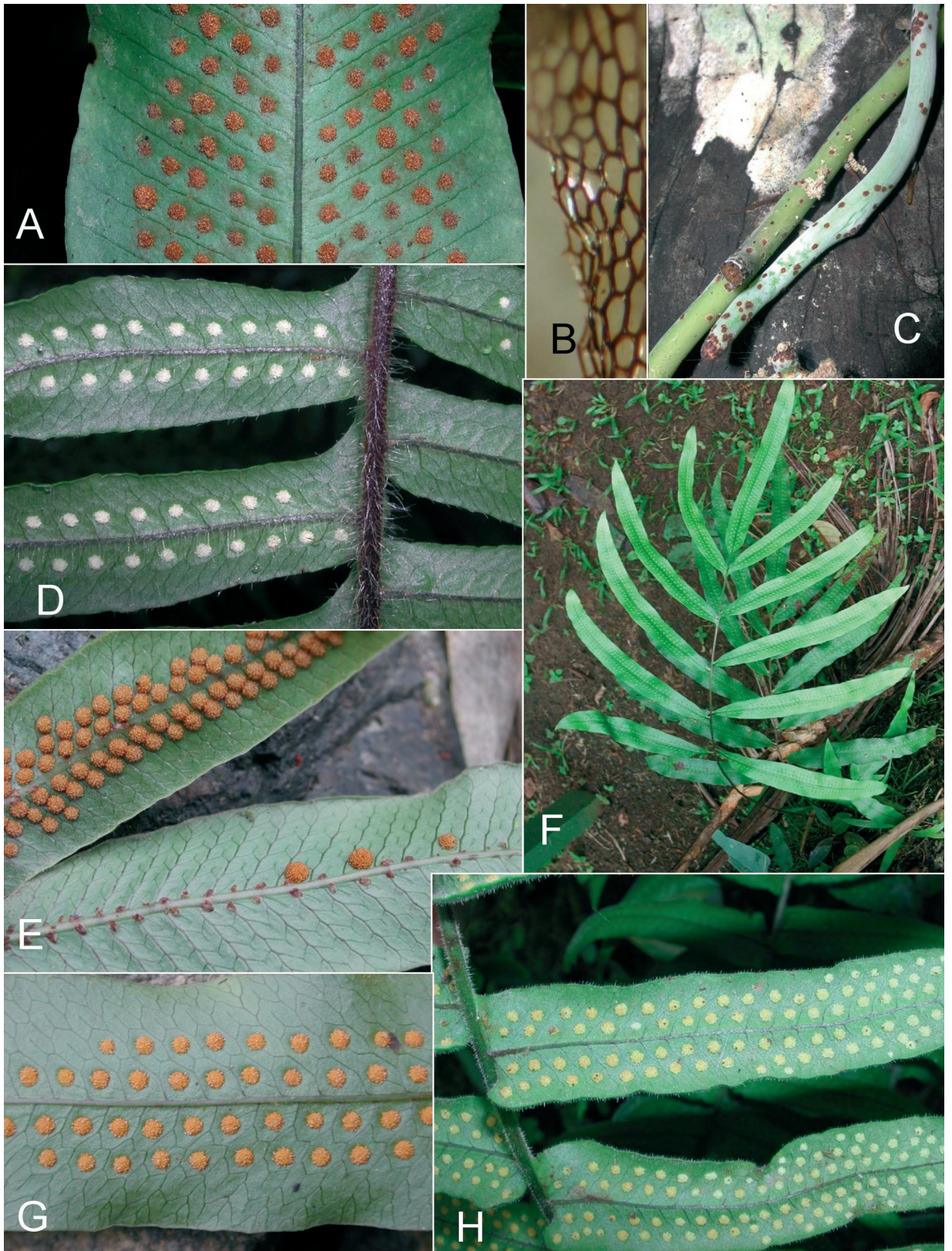


Fig. 3. *Serpocaulon* species. A, *S. caceresii*, portion of pinna, with multiseriate sori; B, *S. dissimile*, portion of clathrate scale; C, *S. fraxinifolium*, glaucous rhizomes, with sparse round scales; D, *S. dasyleuron*, portion of pinnatisect blade, with uniseriate sori; E, *S. levigatum*, portions of simple blades; F, *S. triseriale*, fronds, with 1-pinnate blades; G, *S. fraxinifolium*, portion of pinna; H, *S. dissimile*, portion of pinnae. Photo credits: R. C. Moran, <http://www.plantsystematics.org/>

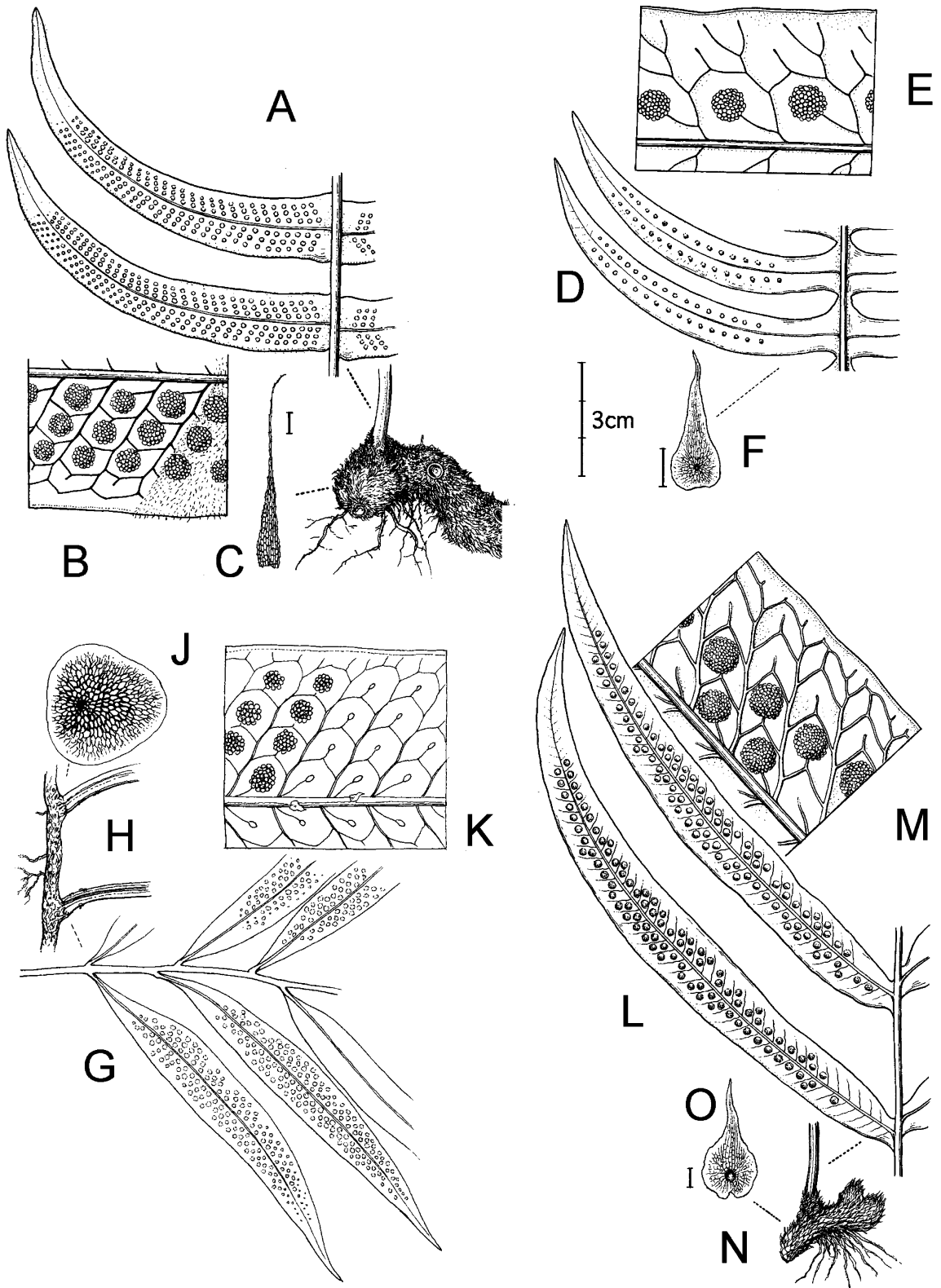


Fig. 4. *Serpocaulon* species. A–C, *S. dissimile* (Hallberg 1281, NY). A, pinnae and rhizome; B, pinna detail; C, rhizome scale. D–F, *S. falcaria* (Mickel 1527, NY). D, pinnae; E, pinna detail; F, rhizome scale. G–K, *S. fraxinifolium* (Türckheim 642, NY). G, pinnae; H, rhizome; J, rhizome scale; K, pinna detail. L–O, *S. triseriale* (Hallberg 1284, NY). L, pinnae; M, pinna detail; N, rhizome; O, rhizome scale. 3 cm bar scale applies to A, D, G, and L; smaller, unlabeled bar scales are 1 mm and apply to rhizome scales. Reproduced with permission from Mickel & Smith (2004).

ual areoles chevron-shaped and each with a single, free, included veinlet; sori are in one to 10 rows between costae and margins (Figs. 3–4). *Polypodium* has veins free, casually anastomosing, or (especially in Mexican and Mesoamerican species) with areoles forming a single row between costae and pinna margins, and species have only a single row of sori on each side of the costae. Additionally, the rhizome (and costal scales, if present) in *Serpocaulon* are clathrate (Fig. 3B), sometimes strongly so, at least in the central or basal part of the scales, although in some species, the lumina are also rather blackish or obscure; rhizome scales are also usually peltately attached at their base, or with a deeply cordiform base with strongly overlapping lobes (e.g., in *S. sessilifolium*). In *Polypodium*, the rhizome scales are \pm concolorous and invaginated at the base, with somewhat overlapping basal lobes. Rhizomes of *Serpocaulon* are generally much longer-creeping and less frequently branched than in *Polypodium* (Figs. 3C, 4A, H, N). *Polypodium* s.s. is largely north-temperate, Mexican, and Mesoamerican, while *Serpocaulon* is tropical or subtropical in distribution, with most species in South America.

From *Pleopeltis*, *Serpocaulon* differs in the absence of scales on veins and tissue between veins and generally easily visible venation. Many species of *Serpocaulon* have glandular or acicular hairs (Figs. 3D, 4B), which are lacking in most species of *Pleopeltis*. *Pechuma* differs from *Serpocaulon* in having free or sporadically anastomosing veins, a single row of sori on each side of the costae, often reduced proximal pinnae, non-clathrate, often comose rhizome scales, generally short-creeping rhizomes, and pinnatisect blades with usually more than 30 pairs of pinnae per blade and pinnae usually dilated at the base. *Phlebodium* differs from *Serpocaulon* in the shorter-creeping, generally much scallier rhizomes, non-clathrate, reddish to orangish, concolorous, spreading scales, the vein areoles more irregularly arranged, and by the sori served by two excurrent veinlets that are joined at their tips; *Phlebodium* is only remotely related to *Serpocaulon* in phylogenetic analyses (Schneider & al., 2004b).

Serpocaulon comprises several somewhat ill-defined and informal morphological groups: (1) the *S. loriceum* group (*S. dasyleuron*, *S. falcaria*, *S. intricatum*, *S. latipes*, *S. latissimum*, *S. loriceum*; Figs. 3D, 4D–F), with rhizomes glaucous or not, rhizome scales scattered (or rhizome nearly naked) to dense, clathrate, at least centrally, round to ovate to ovate-lanceolate, blades pinnatisect, or with strongly adnate and often surcurrent pinna; veins anastomosing in 1 (occasionally 2 or 3) row(s), scattered scales present on midribs abaxially, these dark and clathrate; (2) the *S. fraxinifolium* group (*S. adnatum*, *S. appressum*, *S. caceresii*, *S. fraxinifolium*, *S. giganteum*, *S. richardii*; Figs. 3A, C, G, 4G–K), with rhizomes not glaucous, scales scattered (or rhizomes nearly naked)

to dense, decidedly clathrate (at least centrally) and round to ovate to ovate-attenuate, blades 1-pinnate with pinnae sessile or adnate, not surcurrent, veins regularly anastomosing in (1–)2–10 series between midribs (costae) and pinna margins; (3) the *S. subandinum* group (*S. eleutherophlebium*, *S. funckii*, *S. levigatum*, *S. ptilorhizon*; Fig. 3E), with narrow, sparsely scaly, sometimes glaucous rhizomes, pinnatisect blades (simple in *S. levigatum*); and (4) the *S. lasiopus* group (*S. catharinae*, *S. crystalloneuron*, *S. dissimile*, *S. lasiopus*, *S. panorense*, and *S. wagneri*; Figs. 3B, 4A–C), with rhizomes densely scaly, scales usually spreading, blades pinnatisect or 1-pinnate with adnate pinnae.

Chromosome numbers reported for species of *Serpocaulon* are diploid, $2n = 37$ II (or $2n = 74$) for most species, a common number in Polypodiaceae: *Polypodium ptilorhizon* and *P. fraxinifolium* (Sorsa, 1966); *Polypodium chnoodes* (Walker, 1966); and *Polypodium loriceum* and *P. triseriale* (Smith & Mickel, 1977; Walker, 1985). The tetraploid condition, $2n = 74$ II, has also been reported for *P. triseriale* (Walker, 1966). $x = 37$ is by far the commonest base number in neotropical polypodioid ferns, and also occurs in *Polypodium* s.s.

The spores of *Serpocaulon* are typical of other polypods, light yellowish to whitish, ellipsoid or reniform and monolete, and with a generally tuberculate perispore (e.g., *Serpocaulon levigatum*, *S. latipes*, *S. maritimum*, *S. meniscifolium*, *S. subandinum*, and *S. triseriale*; Hensen, 1990) surrounding a low-verrucate exospore (e.g., *Serpocaulon latipes*, Tryon & Lugardon, 1991: 344; *S. wagneri*, Hensen 1990: fig. 62). The illustration of the spores of *S. sessilifolium* by both Hensen (1990) and by Tryon and Lugardon (1991: fig. 131.6) shows a perispore with loose folds (wings) that appears unlike most other members of the genus. *Serpocaulon wagneri* also has low perispore folds overlying a low-tuberculate pattern.

New combinations:

Serpocaulon adnatum (Kunze ex Klotzsch) A.R. Sm., **comb. nov.** \equiv *Polypodium adnatum* Kunze ex Klotzsch, *Linnaea* 20: 395. 1847. – Distribution: Colombia, Venezuela, and Guianas to Bolivia, Brazil.

Serpocaulon antillense (Maxon) A.R. Sm., **comb. nov.** \equiv *Polypodium antillense* Maxon, *Proc. Biol. Soc. Wash.* 43: 83. 1930. – Distribution: Cuba, Jamaica, Hispaniola, Guadeloupe, Martinique. Guayanian Venezuela?

Serpocaulon appressum (Copel.) A.R. Sm., **comb. nov.** \equiv *Polypodium appressum* Copel., *Univ. Calif. Publ. Bot.* 10: 305, pl. 66. 1941. – Distribution: Peru, Bolivia.

Serpocaulon attenuatum (Humb. & Bonpl. ex Willd.) A.R. Sm., **comb. nov.** \equiv *Polypodium attenuatum* Humb. & Bonpl. ex Willd., *Sp. pl.*, ed. 4, 5: 191.

1810. – Distribution: Nicaragua to Panama, Venezuela, Guianas, Colombia to Bolivia, Brazil.
- Serpocaulon caceresii* (Sodirol) A.R. Sm., **comb. nov.** (Fig. 3A) ≡ *Polypodium caceresii* Sodirol, Crypt. vasc. quit. 360. 1893. – Distribution: Colombia to Bolivia and French Guiana, Brazil.
- Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm., **comb. nov.** ≡ *Polypodium catharinae* Langsd. & Fisch., Pl. voy. Russes monde 1, t. 9. 1810. – Distribution: Brazil.
- Serpocaulon chacapoyense* (Hook.) A.R. Sm., **comb. nov.** ≡ *Polypodium chacapoyense* Hook., Hooker's Icon. 1: t. 69. 1937. – Distribution: Peru.
- Serpocaulon concolorum* (M. Kessler & A.R. Sm.) A.R. Sm., **comb. nov.** ≡ *Polypodium concolorum* M. Kessler & A.R. Sm., Candollea 60: 277. 2005. – Distribution: Bolivia.
- Serpocaulon crystalloneuron* (Rosenst.) A.R. Sm., **comb. nov.** ≡ *Polypodium crystalloneuron* Rosenst., Repert. Spec. Nov. Regni Veg. 11: 57. 1912. – Distribution: Peru, Bolivia.
- Serpocaulon dasypleuron* (Kunze) A.R. Sm., **comb. nov.** (Fig. 3D) ≡ *Polypodium dasypleuron* Kunze, Linnaea 9: 43. 1834. – Distribution: Colombia to Bolivia.
- Serpocaulon dissimile* (L.) A.R. Sm., **comb. nov.** (Figs. 3B, 3H, 4A–C) ≡ *Polypodium dissimile* L., Syst. Nat., ed. 10. 2: 1325. 1759. – Distribution: S. Mexico to Ecuador, Antilles, Trinidad.
- Serpocaulon eleutherophlebium* (Fée) A.R. Sm., **comb. nov.** ≡ *Goniophlebium eleutherophlebium* Fée, Mém. foug. 5: 255. 1852. – Distribution: Costa Rica, Panama, Colombia, Venezuela, Ecuador.
- Serpocaulon falcaria* (Kunze) A.R. Sm., **comb. nov.** (Fig. 4D–F) ≡ *Polypodium falcaria* Kunze, Linnaea 18: 316. 1844 [1845]. – Distribution: S. Mexico to Honduras.
- Serpocaulon fraxinifolium* (Jacq.) A.R. Sm., **comb. nov.** (Figs. 3C, 3G, 4G–K) ≡ *Polypodium fraxinifolium* Jacq., Collectanea 3: 187. 1789. – Distribution: Mexico to Bolivia, Guianas, S. Brazil.
- Serpocaulon funckii* (Mett.) A.R. Sm., **comb. nov.** ≡ *Polypodium funckii* Mett., Abh. Senckenberg. Naturf. Ges. 2: 57. 1857. – Distribution: Venezuela and Colombia to Bolivia.
- Serpocaulon giganteum* (Desv.) A.R. Sm., **comb. nov.** ≡ *Polypodium giganteum* Desv., Mém. Soc. Linn. Paris 6: 236. 1827. – Distribution: Costa Rica to Bolivia, S. Brazil.
- Serpocaulon gilliesii* (C. Chr.) A.R. Sm., **comb. nov.** ≡ *Polypodium gilliesii* C. Chr., Index fil. 529. 1906. (a nom. nov. for *Polypodium pubescens* Hook. & Grev. (non L., 1759)). – Distribution: Peru, Bolivia, NW. Argentina.
- Serpocaulon intricatum* (M. Kessler & A.R. Sm.) A.R. Sm., **comb. nov.** ≡ *Polypodium intricatum* M. Kessler & A.R. Sm., Candollea 60: 278. 2005. – Distribution: Ecuador, Peru, Bolivia.
- Serpocaulon lasiopus* (Klotzsch) A.R. Sm., **comb. nov.** ≡ *Polypodium lasiopus* Klotzsch, Linnaea 20: 393. 1847. – Distribution: Venezuela, Ecuador, Peru, Bolivia.
- Serpocaulon latipes* (Langsd. & Fisch.) A.R. Sm., **comb. nov.** ≡ *Polypodium latipes* Langsd. & Fisch., Pl. voy. Russes monde (Icon. Fil.) 1: 10, t. 10. 1810. – Distribution: Bolivia, S. Brazil.
- Serpocaulon latissimum* (R.C. Moran & B. Øllg.) A.R. Sm., **comb. nov.** ≡ *Polypodium latissimum* R.C. Moran & B. Øllg., Nordic J. Bot. 15: 184. 1995. – Distribution: Ecuador, Bolivia.
- Serpocaulon levigatum* (Cav.) A.R. Sm., **comb. nov.** (Fig. 3E) ≡ *Polypodium levigatum* Cav., Descr. Pl. 244. 1801. – Distribution: Costa Rica, Guadeloupe, Colombia to Guianas and Bolivia.
- Serpocaulon loriceum* (L.) A.R. Sm., **comb. nov.** ≡ *Polypodium loriceum* L., Sp. Pl. 2: 1086. 1753. – Distribution: Nicaragua to Panama, Antilles, Trinidad, Colombia, Venezuela, Guianas.
- Serpocaulon loriciforme* (Rosenst.) A.R. Sm., **comb. nov.** ≡ *Polypodium loriciforme* Rosenst., Repert. Spec. Nov. Regni Veg. 22: 17. 1925. – Distribution: Costa Rica to Peru.
- Serpocaulon maritimum* (Hieron.) A.R. Sm., **comb. nov.** ≡ *Polypodium maritimum* Hieron., Bot. Jahrb. Syst. 34: 527. 1904. – Distribution: Nicaragua to Peru.
- Serpocaulon meniscifolium* (Langsd. & Fisch.) A.R. Sm., **comb. nov.** ≡ *Polypodium meniscifolium* Langsd. & Fisch., Pl. Voy. Russes Monde 11, pl. 11. 1810. – Distribution: S. Brazil.
- Serpocaulon mexiae* (Copel.) A.R. Sm., **comb. nov.** ≡ *Polypodium mexiae* Copel., Univ. Calif. Publ. Bot. 17: 233. 1941. – Distribution: Minas Gerais, Brazil.
- Serpocaulon nanegalense* (Sodirol) A.R. Sm., **comb. nov.** ≡ *Polypodium nanegalense* Sodirol, Recens. Crypt. vasc. quit. 65. 1883. – Distribution: Colombia, Ecuador.
- Serpocaulon panorense* (C. Chr.) A.R. Sm., **comb. nov.** ≡ *Polypodium panorense* C. Chr., Dansk Bot. Ark. 6(3): 97. 1929. – Distribution: Guyana (vide Hensen, 1990), Brazil.
- Serpocaulon patentissimum* (Mett. ex Kuhn) A.R. Sm., **comb. nov.** ≡ *Polypodium patentissimum* Mett. ex Kuhn, Linnaea 36: 134. 1869. – Distribution: Colombia, Ecuador.
- Serpocaulon polystichum* (Link) A.R. Sm., **comb. nov.** ≡ *Polypodium polystichum* Link, Hort. Reg. Bot. Berol. 2: 101. 1833. – Distribution: Ecuador to Bolivia.

- Serpocaulon ptilorhizon* (H. Christ) A.R. Sm., **comb. nov.** ≡ *Polypodium ptilorhizon* H. Christ, Bull. Herb. Boissier, sér. 2, 5: 6. 1905. – Distribution: Nicaragua to Bolivia.
- Serpocaulon richardii* (Klotzsch) A.R. Sm., **comb. nov.** ≡ *Polypodium richardii* Klotzsch, Linnaea 20: 394. 1847. – Distribution: Guianas, Venezuela, Colombia to Bolivia, Brazil.
- Serpocaulon semipinnatifidum* (Fée) A.R. Sm., **comb. nov.** ≡ *Goniophlebium semipinnatifidum* Fée, Mém. Foug. 5: 256. 1852. – Distribution: Colombia, Venezuela, Peru.
- Serpocaulon sessilifolium* (Desv.) A.R. Sm., **comb. nov.** ≡ *Polypodium sessilifolium* Desv., Mém. Soc. Linn. Paris 6: 238. 1827. – Distribution: Venezuela and Colombia to Bolivia.
- Serpocaulon silvulae* (M. Kessler & A.R. Sm.) A.R. Sm., **comb. nov.** ≡ *Polypodium silvulae* M. Kessler & A.R. Sm., Candollea 60: 280. 2005. – Distribution: Bolivia.
- Serpocaulon subandinum* (Sodiolo) A.R. Sm., **comb. nov.** ≡ *Polypodium subandinum* Sodiolo, Crypt. vasc. quit. 348. 1893. – Distribution: Ecuador and Peru.
- Serpocaulon triseriale* (Sw.) A.R. Sm., **comb. nov.** (Fig. 3F, 4L–O) ≡ *Polypodium triseriale* Sw., J. Bot. (Schrader) 1800(2): 126. 1801. – Distribution: S. Mexico to Bolivia, Guianas, Brazil, Paraguay; Antilles, Trinidad.
- Serpocaulon vacillans* (Link) A.R. Sm., **comb. nov.** ≡ *Polypodium vacillans* Link, Hort. berol. 2: 97. 1833. – Distribution: Bolivia, S. Brazil, Paraguay.
- Serpocaulon wagneri* (Mett.) A.R. Sm., **comb. nov.** ≡ *Polypodium wagneri* Mett., Ann. Sci. Nat. Bot., sér. 5, 2: 255. 1864. – Distribution: Costa Rica to Venezuela and Ecuador.

Excluded species:

Polypodium kunzeanum C. Chr. – Cited by Tryon and Stolze (1993) as a synonym of *P. sessilifolium* Desv., which we believe is not closely related. *Polypodium kunzeanum* (Costa Rica to Peru and Brazil) has much less regular venation, sometimes with two included and themselves anastomosing veins within an areole, cordate-based, non-adnate pinnae (the basalmost with lobes overlapping the rachis), and non-clathrate rhizome scales.

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Appendix 1. Voucher information and GenBank accession numbers given for samples of *Serpocaulon* used in this study.

Species, origin, voucher, GenBank accession no. (*rbcl*, *rps4*, *trnLF*).

S. appressum, Bolivia, Jimenez 862 (LPB), DQ151905, DQ151930, DQ151957; *S. attenuatum*, Nicaragua, Moreno 10406 (UC), DQ151912, DQ151937, DQ151964; *S. crystalloneuron*, Bolivia, Jimenez 1109 (LPB), DQ151906, DQ151931, DQ151958; *S. crystalloneuron*, Bolivia, Jimenez 1176 (LPB), DQ151907, DQ151932, DQ151959; *S. dissimile*, Ecuador, Smith 2852 (UC), DQ151908, DQ151933, DQ151960; *S. eleutherophlebium*, Ecuador, Smith 2877 (UC), AY 362601, AY362673, DQ151983; *S. fraxinifolium*, Bolivia, Jimenez 696 (UC), DQ151909, DQ151934, DQ151961; *S. giganteum*, Bolivia, Jimenez 1035 (UC), DQ151910, DQ151935, DQ151962; *S. gilliesii*, Bolivia, Ehrlich 314 (UC), DQ151911, DQ151936, DQ151937; *S. intricatum*, Bolivia, Jimenez 694 (UC), DQ151919, DQ151944, DQ151967; *S. latipes (intricatum)*, Bolivia, Jimenez 1324 (LPB), DQ151915, DQ151940, DQ151971; *S. lasiopus*, Bolivia, Lewis 35186 (UC), DQ151913, DQ151938, DQ151965; *S. latipes*, Bolivia, Bach 1305 (LPB), DQ151914, DQ151939, DQ151966; *S. latissimum*, Bolivia, Jimenez 813 (UC), DQ151916, DQ151941, DQ151968; *S. levigatum*, Bolivia, Jimenez 756 (UC), DQ151917, DQ151942, DQ151969; *S. maritimum*, cult. Alford, Smith s.n. (UC), DQ151918, DQ151943, DQ151970; *S. patentissimum*, Ecuador, Smith 2829 (UC), AY362602, AY362674, -; *S. ptilorhizon*, Bolivia, Jimenez 1102 (UC), DQ151920, DQ151945, DQ151972; *S. richardii*, Bolivia, Jimenez 1986 (UC), DQ227291, DQ151929, DQ151956; *S. richardii*, Ecuador, Moran 6258 (NY), AY362593, AY362666, -; *S. sessilifolium*, Bolivia, Jimenez 755 (LPB), DQ151923, DQ151948, DQ151975; *S. sessilifolium*, Bolivia, Jimenez 806 (LPB), -, DQ151951, DQ151978; *S. sessilifolium*, Bolivia, Jimenez 976 (UC), DQ151924, DQ151949, DQ151976; *S. sessilifolium*, Bolivia, Jimenez 1034 (LPB), -, DQ151950, DQ151977; *S. subandinum*, Peru, Hutchison & Wright 5872 (UC), DQ151922, DQ151947, DQ151974; *S. subandinum*, Ecuador, Moran 6858 (NY), DQ151921, DQ151946, DQ151973; *S. silvulae*, Bolivia, Jimenez 1093 (LPB), DQ151925, DQ151952, DQ151979; *S. triseriale*, Bolivia, Jimenez 1994 (UC), DQ151926, DQ151953, DQ151980; *S. vacillans*, Brazil, Mexia 5856a (UC), DQ151927, DQ151954, DQ151981; *S. wagneri*, Venezuela, Smith 1171 (UC), DQ151928, DQ151955, DQ151982.

Appendix 2. Synonyms referable to species of *Serpocaulon* (basionyms only). Names included herein are largely on the basis of descriptions (original and other) and circumscriptions adopted by Lellinger (1989), Hensen (1990), and a few other sources, as well as provenance of the type and any original illustrations.

- Goniophlebium acuminatum* Fée, Mém., Foug. 11: 68, pl. 19. 1866. = *Serpocaulon sessilifolium* (Desv.) A.R. Sm. (fide Hensen, 1990).
Goniophlebium arcuatum Fée, Mém. Foug. 5: 255. 1852. = *Serpocaulon loriceum* (L.) A.R. Sm. (fide Hensen, 1990).
Goniophlebium chondrocheilon Fée, Mém. Foug. 8: 92. 1857. = *Serpocaulon eleutherophlebium* (Fée) A.R. Sm. (fide Hensen, 1990).
Goniophlebium deflexum T. Moore & Houlst., Gard. Mag. Bot. 3: 61. 1851. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Lellinger, 1989).
Goniophlebium demissum Fée, Crypt. Vasc. Brésil 2: 63. 1872. = *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
Goniophlebium elatum Fée, Mém. Foug. 5: 256. 1852. = *Serpocaulon dissimile* (L.) A.R. Sm. (fide Hensen, 1990).
Goniophlebium excelsior Fée, Crypt. Vasc. Brésil 1: 244, pl. 77. 1869. = *Serpocaulon meniscifolium* (Langsd. & Fisch.) A.R. Sm.
Goniophlebium gauthieri Fée, Crypt. Vasc. Brésil 1: 112, t. 34, f. 3. 1869. = *Serpocaulon meniscifolium* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
Goniophlebium grammitoides Fée, Crypt. Vasc. Brésil 1: 110, pl. 34. 1869. = *Serpocaulon vacillans* (Link) A.R. Sm.
Goniophlebium haenkei C. Presl, Tent. pterid. 186, pl. 7. 1836. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Hensen, 1990).
Goniophlebium intermedium Fée, Mém. Foug. 11: 69, t. 18, f. 3. 1866. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989).
Goniophlebium invertens Fée, Mém. Foug. 9: 25. 1857. = *Serpocaulon falcaria* (Kunze) A.R. Sm. (fide Hensen, 1990).
Goniophlebium pectinans Fée, Crypt. vasc. Brésil 1: 109, pl. 34. 1869. = *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
Goniophlebium pectinatum J. Sm., in Seemann, Bot. Voy. Herald 230. 1854. (nom. illeg., non *Goniophlebium pectinatum* (L.) J. Sm., 1841, which is *Pecluma pectinata* (L.) M. G. Price) = *Serpocaulon wagneri* (Mett.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Goniophlebium pictum Fée, Crypt. Vasc. Brésil 1: 244. 1869. = *Polypodium pictum* (Fée) Brade, Arq. Inst. Biol. Veg. 1: 228. 1935, non *P. pictum* (T. Moore) Baker = *Polypodium limbatum* Brade, Arq. Jard. Bot. Rio de Janeiro 11: 30. 1951. = *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
Polypodium adnatum Kunze ex Klotzsch var. *glaucescens* Mille, Revista Col. Nac. Vicente Rocafuerte 9: 208. 1927. = *Serpocaulon giganteum* (Desv.) A.R. Sm. (fide Lellinger, 1989).
Polypodium alboripunctatum Raddi, Opusc. Sci. 3: 287. 1819. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Polypodium andinum H. Karst., Fl. Columb. 1: 171, pl. 85. 1861 (non Hook., 1860). = *Serpocaulon sessilifolium* (Desv.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Polypodium argyrolepis Sodiro, Crypt. vasc. quit. 355. 1893. = *Serpocaulon lasiopus* (Klotzsch) A.R. Sm. (fide Hensen, 1990).
Polypodium articulatum Desv., Mém. Soc. Linn. Paris 6: 236. 1827 (non *P. articulatum* (Sw.) Juss. ex Poir., 1804, which is *Oleandra articulata* (Sw.) C. Presl) = *Serpocaulon caceresii* (Sodiro) A.R. Sm. (fide Hensen, 1990).
Polypodium beyerianum Rosenst., Repert. Spec. Nov. Regni Veg. 22: 17. 1925. = *Serpocaulon loriceum* (L.) A.R. Sm. (fide Lellinger, 1989; but for a different opinion, see Hensen, 1990, who placed it in synonymy under *Polypodium maritimum* Hieron.).
Polypodium brasiliense Poir., in Lam., Encycl. 5: 525. 1804. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990). = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989).
Polypodium brasiliense Poir. var. *pleiosorum* Rosenst. ex Hassl., Treb. Inst. Bot. Farm. Buenos Aires 45: 71. 1928. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989).
Polypodium campylopodum Klotzsch, Linnaea 20: 395. 1847. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Polypodium catharinae Langsd. & Fisch. forma *aurita* Rosenst., Hedwigia 46: 142. 1906. = *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm.
Polypodium catharinae Langsd. & Fisch. forma *bipinnatifida* Rosenst., Hedwigia 46: 142. 1906. = *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm.
Polypodium chartaceum Baker, J. Bot. 15: 166. 1877. = *Serpocaulon loriceum* (L.) A.R. Sm., s.l. (fide Lellinger, 1989).
Polypodium chnoodes Spreng., Neue Entd. 3: 6. 1822. = *Serpocaulon dissimile* (L.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Polypodium chnoodes Spreng. var. *minus* H. Christ, Bull. Herb. Boissier, sér. 2, 6: 49. 1906. = *Serpocaulon dissimile* (L.) A.R. Sm. (fide Lellinger, 1989).
Polypodium costaricense H. Christ, Bull. Herb. Boissier 4: 660. 1896. = *Serpocaulon wagneri* (Mett.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Polypodium cymatodes Kunze, Linnaea 23: 277, 317. 1850. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Lellinger, 1989).
Polypodium deflexum Houlst. & T. Moore, Gard. Mag. Bot. 3: 60. 1851. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Hensen, 1990).
Polypodium distans Raddi, Pl. Bras. Nov. Gen. 1: 21, pl. 31. 1825 (non Kaulf., 1824). = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Polypodium elatius Schrad., Gött. Gel. Anz. 1824: 868. 1824. = *Serpocaulon meniscifolium* (Langsd. & Fisch.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Polypodium elegans Cav. ex Sw., Syn. fil. 35. 1806 (non Poir., 1804). = *Serpocaulon loriceum* (L.) A.R. Sm., s.l. (fide Lellinger, 1989).
Polypodium fluminense Vell., Arq. Mus. Nac. Rio de Janeiro 5: 447. 1881. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Hensen, 1990).
Polypodium fraxinifolium Jacq. var. *fraxinellum* H. Christ, Bull. Herb. Boissier, sér. 2, 5: 5. 1905. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Lellinger, 1989).
Polypodium fraxinifolium Jacq. subsp. *articulatum* H. Christ, Bull. Herb. Boissier, sér. 2, 6: 49. 1906. = *Serpocaulon giganteum* (Desv.) A.R. Sm. (fide Lellinger, 1989).
Polypodium fraxinifolium Jacq. subsp. *luridum* H. Christ, Bull. Herb. Boissier, sér. 2, 6: 48. 1906. = *Serpocaulon giganteum* (Desv.) A.R. Sm. (fide Lellinger, 1989).
Polypodium gladiatum Kunze, Linnaea 9: 45. 1834 (non Vell., 1827) = *Polypodium ampliatum* Maxon, Contr. U.S. Natl. Herb. 10: 492. 1908. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
Polypodium glandulosissimum Brade, Arq. Inst. Biol. Veg. 1: 230. 1935. = *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).

Appendix 2 (continued).

- Polypodium glaucophyllum* Kunze ex Klotzsch, *Linnaea* 20: 393. 1847. = *Serpocaulon levigatum* (Cav.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
- Polypodium glaucum* Raddi, *Pl. Bras. Nov. Gen.* 20, pl. 29. 1825 (non Thunb., 1784) ≡ *Chrysopteris raddiana* Fée, *Crypt. vasc. Brésil* 1: 120. 1869. = *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
- Polypodium harpeodes* Link., *Hort. berol.* 2: 97. 1833. = *Serpocaulon vacillans* (Link) A.R. Sm. (fide Hensen, 1990, who first synonymized *P. harpeodes* under *P. vacillans*).
- Polypodium hassleri* H. Christ in Hassler, *Bull. Herb. Boissier, sér. 2, 7*: 923. 1907. = *Serpocaulon vacillans* (Link) A.R. Sm.
- Polypodium hirsutulatum* Raddi, *Pl. bras. nov. gen.* 1: 21, pl. 29. 1825. = *Serpocaulon meniscifolium* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
- Polypodium kuhni* E. Fourn., *Bull. Soc. Bot. France* 19: 251. 1872. = *Serpocaulon attenuatum* (Humb. & Bonpl. ex Willd.) A.R. Sm.
- Polypodium laetum* Raddi, *Opusc. Sci.* 3: 287. 1819 (non Salisb., 1796) = *Serpocaulon latipes* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
- Polypodium longifolium* C. Presl, *Delic. prag.* 1: 167. 1822 (non Cav., 1802). ≡ *Polypodium preslianum* Spreng., *Syst. Veg.*, ed. 4, index. 1828. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
- Polypodium loriceum* L. forma *duplosorum* Domin, *Rozpr. Král. České Spolecn. Nauk, Tr. Mat.-Přir.* 2[Pterid. Dominica]: 130. 1929, as “*duplisora*”. = *Serpocaulon loriceum* (L.) A.R. Sm., s.l. (fide Lellinger, 1989).
- Polypodium loriceum* L. var. *heterolepis* Sodiro, *Anales Univ. Centr. Ecuador* 11(72): 28 (Crypt. vasc. quit. 352). 1894. = *Serpocaulon loriceum* (L.) A.R. Sm., s.l. (fide Lellinger, 1989).
- Polypodium loriceum* L. var. *obscurum* Rosenst., *Repert. Spec. Nov. Regni Veg.* 6: 308. 1909, as “*obscura*” = *Serpocaulon loriceum* (L.) A.R. Sm., s.l. (fide Lellinger, 1989).
- Polypodium loriceum* L. var. *oligomerum* H. Christ, *Bull. Soc. Roy. Bot. Belgique* 35, *Mém.* 221. 1896. = *Serpocaulon loriceum* (L.) A.R. Sm., s.l. (fide Lellinger, 1989).
- Polypodium loriceum* L. var. *squamuligera* Rosenst., *Repert. Spec. Nov. Regni Veg.* 6: 308. 1909. = *Serpocaulon loriceum* (L.) A.R. Sm., s.l. (fide Lellinger, 1989).
- Polypodium lucens* Schrad., *Gött. Gel. Anz.* 1824: 868. 1824. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
- Polypodium martii* Colla, *Herb. pedem.* 6: 230. 1836. = *Serpocaulon vacillans* (Link) A.R. Sm. (fide Hensen, 1990).
- Polypodium mindense* Sodiro, *Crypt. vasc. quit.* 348. 1893. = *Serpocaulon eleutherophlebium* (Fée) A.R. Sm. (fide Hensen, 1990).
- Polypodium mosenii* C. Chr., *Bot. Tidskr.* 25: 78. 1902. = *Serpocaulon meniscifolium* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
- Polypodium mutabile* Kunze, *Linnaea* 9: 46. 1834. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
- Polypodium neriofolium* Schkuhr, *24. Kl. Linn. Pfl.-Syst.* 1: 14, t. 15. 1804. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
- Polypodium neriofolium* Schkuhr var. *acuminatissimum* Kuntze, *Revis. gen. pl.* 2: 819. 1891. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; holotype NY!).
- Polypodium neriofolium* Schkuhr var. *heterophyllum* Kuntze, *Revis. gen. pl.* 2: 819. 1891. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; holotype NY!).
- Polypodium ornatum* Klotzsch, *Linnaea* 20: 396. 1847. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Hensen, 1990).
- Polypodium palma* Vell., *Arq. Mus. Nac. Rio de Janeiro* 5: 447. 1881. = *Serpocaulon meniscifolium* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
- Polypodium preslianum* var. *immersum* Rosenst., *Repert. Spec. Nov. Regni Veg.* 6: 314. 1909. (as “*immersa*”) = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989).
- Polypodium pseudofraterum* A.C. Sm., *Bull. Torrey Bot. Club* 58: 307. 1931. = *Serpocaulon sessilifolium* (Desv.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990; holotype NY!).
- Polypodium punctulatum* Hook., *Icon. pl.*, pl. 720. 1845 (non Poir., 1804). = *Serpocaulon subandinum* (Sodiro) A.R. Sm. (fide Hensen, 1990).
- Polypodium pycnosorum* Link, *Fil. spec.* 128. 1841. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Hensen, 1990).
- Polypodium ramosum* Loddiges ex Link, *Hort. berol.* 2: 97. 1833. = *Serpocaulon loriceum* (L.) A.R. Sm., s.l. (fide Lellinger, 1989).
- Polypodium remotum* Baker, *Ann. Bot. (Oxford)* 5: 470. 1891 (non Desv., 1827). ≡ *Polypodium uniseriale* C. Chr., *Index fil.* 527. 1906. = *Serpocaulon sessilifolium* (Desv.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
- Polypodium retrofractum* Desv., *Mém. Soc. Linn. Paris* 6: 237. 1827. = *Serpocaulon dissimile* (L.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
- Polypodium rhizocaulon* Willd., *Sp. pl.*, ed. 4, 5: 196. 1810. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Lellinger, 1989).
- Polypodium rimbachii* Sodiro, *Crypt. vasc. quit.* 356. 1893. = *Serpocaulon sessilifolium* (Desv.) A.R. Sm. (fide Hensen, 1990).
- Polypodium rupincolum* Brade, *Arq. Inst. Biol. Veg.* 1: 230. 1935. = *Serpocaulon catharinae* (Langsd. & Fisch.) A.R. Sm. (fide Hensen, 1990).
- Polypodium scutulatum* Sodiro, *Anales Univ. Centr. Ecuador* 22: 169. 1908. = *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (fide Hensen, 1990).
- Polypodium sessilifolium* Desv. var. *papallactense* Mille, *Revista Col. Nac. Vicente Rocafuerte* 9: 211. 1927. = *Serpocaulon sessilifolium* (Desv.) A.R. Sm. (fide Lellinger, 1989).
- Polypodium subalatum* Klotzsch, *Linnaea* 20: 394. 1847. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Hensen, 1990).
- Polypodium subviride* Lellinger, *Proc. Biol. Soc. Wash.* 98: 389, f. 17. 1985. = *Serpocaulon loriciforme* (Rosenst.) A.R. Sm.
- Polypodium surucuchense* Hook., *Icon. pl.* 1: t. 69. 1837. = *Serpocaulon sessilifolium* (Desv.) A.R. Sm. (fide Hensen, 1990).
- Polypodium vagans* Mett., *Ann. Sci. Nat., Bot.*, sér. 5, 2: 255. 1864. = *Serpocaulon eleutherophlebium* (Fée) A.R. Sm. (fide Hensen, 1990).
- Polypodium variolatum* Willd., *Sp. pl.*, ed. 4, 5: 192. 1810. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Lellinger, 1989; Hensen, 1990).
- Polypodium wiesbaueri* Sodiro, *Recens. Crypt. vasc. quit.* 65. 1883. = *Serpocaulon eleutherophlebium* (Fée) A.R. Sm. (fide Hensen, 1990).
- Polypodium xiphophoron* Kunze ex Mett., *Abh. Senckenberg. Naturf. Ges.* 2: 73. 1856. = *Serpocaulon triseriale* (Sw.) A.R. Sm. (fide Hensen, 1990).