Systematics of Grammitid ferns (Polypodiaceae): using a combined approach to resolve the circumscription of *Melopmene*, and portions of the polyphyletic genera *Lellingeria* and *Terpsichore*.

By

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ABSTRACT

Systematics of Grammitid ferns (Polypodiaceae): using a combined approach to resolve the circumscription of *Melopmene*, and portions of the polyphyletic genera *Lellingeria* and *Terpsichore*.

by

Michael Sundue

Advisor: Robbin C. Moran, Ph.D.

Recent phyogenetic analyses of grammitid ferns (Polypodiaceae) demonstrated that many genera recognized within this clade are not monophyletic. Focus here is upon circumscription of genera within one clade identified in previous analyses that includes the monophyletic *Melpomene*, plus portions of two polyphyletic genera, *Lellingeria* and *Terpsichore*. Morphology of grammitid ferns is reviewed and used to compile a matrix of 111 qualitative characters for 150 terminals. Phylogenetic analysis of the morphological matrix offer no support for a monophyletic *Terpsichore* as orginally circumscribed, but otherwise have limited value due to the lack of resolution in the consensus tree.

Phylogenetic analyses using chloroplast markers atpB, rbcL, and trnLF, along with 111 qualitative morphological characters resolve this ingroup as monopyletic and sister to a clade that includes Ceradenia, *Enterosora*, and *Zygophlebia*. *Melpomene* is monophyletic, but is nested within *Lellingeria* in most trees. Ingroup species of *Terpsichore* form three well supported monophyletic groups that together are paraphyletic with regards to *Melpomene* plus *Lellingeria*. Two clades of species currently combined in *Terpsichore* are recognized as new genera. One of these clades, sometimes referred to as the *Terpsichore anfractuosa* clade, is described as the new genus *Ascogrammitis*. Sixteen species of *Ascogrammitis* are recognized, including five new ones, and new combinations are made for the previously recognized species. A key is provided to distinguish the species, and illustrations are provided for 12 species. The genus occurs primarily in neotropical cloud forests, with the greatest diversity in the Andes.

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INTRODUCTION

Grammitid ferns constitute a monophyletic (Schneider & al., 2004) group of over 750 species (Parris, 2007) that is nested within the Polypodiaceae. Distributed primarily in tropical montane forests of the world, grammitids are distinguished by green spores with a trilete mark and sporangial stalks that are a single cell wide in the middle (Parris, 1990). One of the long-standing questions in the study of these ferns has been the number of clades recognized as genera. Prior to phylogenetic analysis, some pteridologists have recognized only one (Tryon & Tryon, 1982) and others up to 18 (Parris, 2003). The first phylogenetic study of grammitids (Ranker & al., 2004) found that out of twelve genera for which more than one species was included in the analysis, only three were recovered as monophyletic. Ranker & al. cited convergent evolution and the use of homoplastic characters by taxonomists to account for the problems in generic circumscription. Although these results have spawned some recent nomenclatural changes (e.g., Labiak & Matos, 2007; Parris, 2007), to date, a phylogenetic approach to resolving taxonomic problems established by Ranker & al. (2004) has not been undertaken (but see Lehnert, in press).

Research presented here is focused on resolving the generic circumscriptions within one clade identified in Ranker & al. (2004). This clade, which they called clade Va + Vb, includes the monophyletic genus *Melpomene*, plus portions of two polyphyletic genera, *Lellingeria* and *Terpsichore*. Together, these three genera constitute some of the most species-rich and widely recognized groups of grammitids in the Americas. Members of this ingroup can be distinguished from all other grammitids by a reliable combination of morphogical characters, including ventral root insertion, hydathodes, simple setae, hairs that are usually 1-furcate, sorus position, and glabrous sporangia. This clade includes the type species of *Lellingeria* and *Melpomene* but not that of *Terpsichore*. Therefore, establishing generic concepts here will resolve the circumscription of these two genera and establish relationships for the unplaced *Terpsichore* species. The following questions are addressed: Are clades Va + Vb monopyletic? Do *Melpomene*, and the portions of *Lellingeria* and *Terpsichore* that reside in our ingroup constitute separate monophyletic lineages that should be recognized as genera? And moreover, what morphological characteristics define these clades?

To this end, phylogenetic analyses were conducted combining DNA plastid sequence data with an extensive morphological matrix in order to address the circumscription of grammitid genera. The study is presented in three chapters. In the first chapter, a morphological character study is performed and analyzed. These data are used to test the monophyly of *Terpsichore* sensu Smith (1993). The second chapter combines the morphological data of the first chapter with chloroplast

DNA sequence data. It builds upon previous work of Ranker & al. (2004) by increasing taxon sampling within our study group, adding additional plastid data, and reexamining the characters used in our morphological matrix. The third chapter is a monograph describing one clade of species that were delineated in the second chapter, including descriptions of all sixteen species, maps, illustrations, and a key for identifaction. The clade is published as a new genus, *Ascogrammitis*.

A Morphological Cladistic Analysis of *Terpsichore* (Polypodiaceae)

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Abstract– Recent phylogenetic analyses of grammitid ferns (Polypodiaceae) have demonstrated that many genera recognized within this clade are not monophyletic. Here a morphological matrix is constructed of 111 qualitative characters for 150 terminals in order to re-examine the circumscription of grammitid genera using morphological criteria. This study focuses on *Terpsichore*, a neotropical genus of about 62 species that was among genera shown to be polyphyletic in other recent studies. The relationships of five infrageneric groups that were originally circumscribed for *Terpsichore* are also examined. The morphological data here offer no support for a monophyletic *Terpsichore*; the characters originally used to defined the genus are either plesiomorphic or homoplastic. Two of the five infrageneric groups of *Terpsichore* are resolved as monophyletic whereas the others are resolved as either paraphyletic or polyphyletic. Taxonomic solutions to these problems require a much more narrow circumscription of *Terpsichore*, but conclusions are difficult to draw because of a lack of resolution in the strict consensus tree. In addition to these analyses, new morphological and anatomical information is presented pertaining to grammitid morphology in general.

Keywords– morphology, character evolution, neotropical, *Acrospermum*, classification.

INTRODUCTION

Grammitid ferns constitute a monophyletic (Schneider et al. 2004) group of over 750 species (Parris 2007) that is nested within the Polypodiaceae. Distributed primarily in tropical montane forests of the world, grammitids are distinguished by green spores with a trilete mark and sporangial stalks that are a single cell wide in the middle (Parris 1990). One of the long-standing questions in the study of these ferns has been the number of genera that are recognized. Prior to phylogenetic analysis, some pteridologists recognized only one genus (Tryon and Tryon 1982) and others recognized up to 18 genera (Parris 2003).

The first phylogenetic study of grammitids (Ranker et al. 2004), based on three chloroplast genes and 86 morphological characters, found that only three out of 12 genera for which more than one species was included in the analysis were recovered as monophyletic. They also found that the inclusion of morphological data in their analyses resulted in the loss of resolution across the backbone of their trees and cited convergent evolution and the use of homoplastic characters by taxonomists to account for the problems in generic circumscription. In any case, it is important to assess which characters support monophyletic groups, and which provide support for monophyletic genera of grammitid ferns. To answer these questions I constructed a morphological matrix containing 111 qualitative characters that were scored for 150 taxa representing a broad sample of grammitid diversity. This matrix includes morphological characters pertaining to gametophytes, sporophytes, and spores, and also includes data from cytology, secondary compounds, and the host distribution of an epibiotic fungus. Taxon sampling was designed to allow the matrix to be combined with DNA sequence data to test relationships among some groups of neotropical grammitid ferns (Dissertation Chapter 2), but is employed here on its own to focus on a single genus, *Terpsichore*. Consequently, these analyses are not presented to provide a "better" estimate of evolutionary history, but test monophyly of *Terpsichore* by using morphological criteria and by increasing the number of taxa sampled compared to other studies (Ranker et al. 2004; Sundue et al. Chapter 2).

Terpsichore (Smith 1993) was the last genus published in a series of papers that split the neotropical species of grammitids into segregate genera based on morphological criteria (Bishop 1988; Bishop 1989; Smith et al. 1991; Smith and Moran 1992; Smith 1993). Characters used to define *Terpsichore* include weakly dorsiventral to radially symmetrical rhizomes, non-anastomosing and unbranched veins, hydathodes, setae present on the fronds, the lack of glandular paraphyses, concolorous rhizome scales that bear setae along the margin, and or the apex, and sometimes the surfaces as well (Smith 1993). At the time of publication, Smith included about 50 species in *Terpsichore*, which he placed into five informal infrageneric groups, which he suggested could be regarded as natural sections of the genus. Since then, 12 more species have been described or combined in *Terpsichore* (León and Smith 2003; Smith 1995; Sundue and Kessler 2008) bringing the total number of species to about 62 (but see Sundue et al. (Chapter 2); Sundue (Chapter 3)).

In the analysis of Ranker et al. (2004) *Terpsichore* was resolved as polyphyletic with species falling into four different parts of the tree. These separate groups partially corresponded to infrageneric groups informally recognized by Smith (1993). Species belonging to Smith's group one were resolved as a clade sister to all other grammitids, and species belonging to Smith's group five were nested in *Micropolypodium*. Most of the species from Smith's group two formed a clade together, along with species from his group four, along with species of two other genera, *Melpomene* and *Lellingeria*. These relationships had not previously been suggested and the implications for morphology have not been thoroughly examined. Consequently, I ask what the contribution of morphology is toward understanding the relationships within these ferns. Is *Terpsichore* resolved as monophyletic using morphological characters alone? Are Smith's infrageneric groups monophyletic? If *Terpishore* is resolved as polyphyletic, what characters support the new groupings?

MATERIALS AND METHODS

Phylogenetic methods. Matrices were constructed using Winclada (Nixon 1999–2002) (Appendix A). Maximum parsimony analyses were conducted in TNT (Goloboff et al. 2000, 2008) implementing the parsimony ratchet (Nixon, 1999) using 500 ratchets with 200 iterations per replicate, the up- and down-weights set to 5% each, followed by TBR-max branch swapping, holding 100,000 trees. Large amounts of missing data led to the deactivation of ten characters: 1, 5, 10, 40, 48, 50, 81, 102, 104, 108. Six additional characters, 13, 51, 58, 65, 67, 81, were parsimony non-informative and deactivated as well. The final matrix consisted of 97 parsimony informative characters. Character optimizations were reconstructed using Winclada (Nixon 1999-2002). Optimizations discussed are optimized unambiguously unless stated otherwise.

Taxon sampling. This matrix consists of 140 species of which 59 are members of *Terpsichore*. Outgroups include 16 genera of grammitid ferns as well as three genera of polypodioid ferns. Eleven of the outgroup genera include at least two species. Some species are represented by more than one terminal in order to represent the diversity within that species, thus in total the study uses 150 terminals, including 67 from *Terpsichore* including its type *T. asplenifolia* (L.) A. R. Sm. In particular, the geographically widespread and morphologically variable species *T. anfractuosa* (Kunze ex Klotzsch) B. León & A. R. Sm. is represented by eight terminals that serve to represent morphologically distinct populations. Among ingroup taxa, sampling is heaviest among species of *Terpsichore* from Smith's groups two and four, which are closely related in the results of Ranker et al. (2004), which contain the majority of species in *Terpsichore*, and which I am also addressing as the focus of a taxonomic study. Among outgroup taxa, sampling is heaviest among *Melpomene* and *Lellingeria* because these genera were found to be closely related to members of Smith's infrageneric group 2 in other studies (Ranker et al. 2004; Sundue et al. Chapter 2). In particular, members of the *Lellingeria myosuroides* group sensu Smith et al. (1991) is sampled heavily because those species were influential in tree topology in the aforementioned studies.

In early studies, it became apparent that *Terpsichore delicatula* (M. Martens & Galeotti) A. R. Sm. and *T. subscabra* (Klotzsch) B. León & A. R. Sm. (Smith's group 3) act as wildcard taxa in this matrix, and float between clades causing polytomies. Consequently, two separate analyses were conducted, the first including all of the taxa, the second excluding *T. delicatula* and *T. subscabra*.

Several of the genera in this study are currently under monographic revision, which has helped to identify numerous unpublished species and unidentified ‘problem’ specimens. We choose to include some of these here in order to better represent the diversity present within these lineages. Terminals representing delineated but unpublished species are marked as ‘ined.’ in trees. Terminals for specimens that probably represent new species but which are not well understood by us at the time of writing are indicated by listing the collector and collection number in the tree. Morphological characters for such terminals are scored entirely from the specimens cited.

Morphological Data. For each terminal in this study, 111 morphological and cytological characters were scored. Characters and states were scored primarily from original observations of herbarium specimens primarily at NY and UC using a dissecting or compound light microscope, and by performing free-hand sections. These were supplemented with observations recorded on herbarium labels or from field studies made by the first author. Characters were scored from as many specimens of the same species as possible, but given the rarity of many grammitid ferns, several species are scored from observations of one or a few collections. Some characters and character states were derived from monographic and floristic treatments of grammitid ferns (Bishop, 1977, 1978, 1988, 1989; Bishop and Smith 1992; Holttum, 1968; Parris 1983, 1990, 1997, 2007;

Smith 1992, 1993, 1995; Smith and Moran 1992; Smith et al. 1991) or more general texts covering fern morphology and anatomy (Gifford and Foster, 1989; Ogura, 1972; Tryon and Tryon, 1982). Several characters used in this study are based in part upon that of Ranker et al. (2004). In particular, characters 61–62, 70, 85, 87, 91–92, 98–99, 102, 104–107, 109–110 and their coding are essentially equal to those of Ranker et al. (2004) but with additional taxa scored. Otherwise, this matrix departs strongly from Ranker et al. (2004) by using more characters that have fewer states to describe features. Inapplicable characters are scored as missing data. For example, all characters describing rhizome scales are scored as missing if rhizome scales are absent from the species. All characters were scored as non-additive.

Characters 0–1— Habit

Character 0: Growth habit: (0) epiphytic, (1) epipetric, (2) terrestrial. These data were scored from notes recorded along with collection data.

Character 1: Position of fronds (0) erect, (1) arching, (2) pendant, (3) prostrate or appressed to the substrate. Habit of the fronds scored as relative to the substrate. These characters were scored from field observations or from notes recorded along with collection data. This character was deactivated due to missing data.

Characters 2–3 — Roots

Character 2: Root insertion: (0) radial, (1) ventral. The roots in ferns, except the first roots of the sporeling, are adventitious. In grammitid ferns they are not usually associated with either the node or the leaf base as they may be in other groups of ferns.

Character 3: Root proliferations: (0) absent, (1) present. Vegetative reproduction occurs sporadically in ferns by shoot meristems that originate from recent derivatives of the root apical cell (Peterson 1970). This character is scored either as (0) absent, or as (1) present when a sporophyte is observed emerging directly from the roots of other sporophyte.

Characters 4–10 — Rhizomes

Character 4: Rhizome symmetry: (0) radial, (1) dorsiventral.

Character 5: Stelar perforations: (0) absent, (1) present. Perforations are gaps in the dictyostele in addition to leaf gaps that are associated with leaves. This character was deactivated in some analyses due to missing data.

Character 6: Internode length: (0) short-creeping (petioles overlapping or closely spaced along the rhizome), (1) long-creeping (petioles spaced at least five times the width of the petiole).

Character 7: Branch buds on the rhizome or phyllopodium: (0) absent, (1) present. When present, branch buds in ferns are not necessarily axillary, and are commonly internodal, or positioned upon the base of the petiole or phyllopodium. Wardlaw (1943) used the term detached meristems to describe these branch buds found out of position relative to those of seed plants.

Character 8: Phyllopodia: (0) absent, (1) present. Phyllopodia are scored as present when there is a clear demarcation between the tissue of the rhizome and the petiole that is usually evident by a difference in diameter, color, and texture.

Character 9: Rhizome branching: (0) commonly branched or (1) commonly unbranched.

Character 10: Blackened cortical tissue around the vascular strands of the stele: (0) absent, (1) present. This character can be seen in cross section of the rhizomes as dark bands (either sclerenchymatous or non-sclerenchymatous) of cortical cells adjacent to the vascular bundles. This character was deactivated in some analyses due to missing data.

Characters 11–32 — Rhizome indumenta.

Character 11: Setae on rhizomes: (0) absent or (1) present. Setae are multicellular, uniseriate, terete, and reddish to castaneous.

Character 12: Hairs on rhizomes: (0) absent or (1) present. Hairs are uni- or multicellular, and either simple or ansiotomously branched.

Character 13: Terminal glandular cell of rhizome hairs: (0) white and waxy, or (1) hyaline. This character was non-informative in the matrix and deactivated.

Character 14: Rhizome scales: (0) absent, (1) present.

Character 15: Rhizome scale attachment — (0) basifixed, (2) peltate. Pseudopeltately attached scales are scored here as basifixed as they differ from basifixed scales only by the presence of basal auricles, the presence of which is scored in Character 19.

Character 16: Rhizome scale cell shape — (0) flattened or semiturgid, or (1) turgid. Turgid cells retain a cavity that can be seen in broken or sectioned scales.

Character 17: Rhizome scale cell wall induration — (0) indurated or (1) non-indurated. Indurated cell walls were distinguished by being hard, thick, and dark.

Character 18: Rhizome scales, cell lumen occlusion — (0) not occluded, (1) occluded. Cells with occluded lumens appeared as hard, thick, and opaque.

Character 19: Rhizome scale, base shape — (0) non-auriculate, (1) auriculate.

Character 20: Rhizome scale shape — (0) ovate (length not exceeding two times the width), (1) lanceolate (length exceeding two times the width).

Character 21: Rhizome scales concolorous vs. clathrate — (0) concolorous, the cell lumen the same color as the cell wall, (1) clathrate the cell wall is a color distinctly different (usually darker) from the lumen. The character is scored regardless of cell induration which can cause clathrate scales to appear uniformly black under reflected light. The clathrate condition can be more accurately determined using transmitted light.

Character 22: Rhizome scale color – (0) orange to castaneous, (1) dark reddish to blackish, (2) light reddish-brown, or (3) tan.

Character 23: Rhizome scale iridescence — Rhizome scales are scored as either (0) non-iridescent, or (1) iridescent if the surface refracts light.

Character 24: Rhizome scale luster — (0) dull, (1) semi-glossy, or (2) glossy.

Character 25: Rhizome scale marginal indument — (0) absent or (1) present. This character is scored independently of Character 31.

Character 26: Rhizome scale marginal indument distribution — (0) distributed evenly along the margin, or (1) restricted to the apex of the scale.

Character 27: Rhizome scale indument type — (0) unicellular, and egandular setae, (1) simple glandular hairs which are either unicellular or mulitcellular.

Character 28: Rhizome scale seta color – (0) orange to castaneous, (1) clear to whitish, (2) reddish, or (3) tan.

Character 29: Rhizome scale margins — (0) entire or (1) denticulate. This character is considered inaplicable for taxa that have indument along their margin.

Character 30: Rhizome scale abaxial and adaxial surface— (0) glabrous or (1) provided with indument. Because the indument is the same as that scored for character 26, the type of indument is not scored again.

Character 31: Rhizome scale apical gland-like cells: (0) absent or (1) present. Species of *Melpomene* frequently exhibit singular or multiple gland-like cells at the apex of the rhizome scales (Smith and Moran 1992). It is unknown whether these cells are secretory; "glands" is used here only in descriptive sense referring to a swollen cell. Observations made in this study reveal that many grammitid ferns have an apical or sub-apical gland-like cell, but these are very small and easily overlooked. These usually consist of a single and often swollen oblique cell. Based on position and similarity, I consider all apical or sub-apical gland-like cells to be homologous. Some species in *Ceradenia* and *Andenophorus* bear apical gland-like cells that have the same characteristics of the glandular cells in the branched hairs of their fronds (e.g., white, waxy glands in *Ceradenia*, and red translucent glands in *Adenophorus*), but these were autapomorphic in this analysis and were therefore were not scored.

Character 32: Rhizome scales, number of apical and sub-apical gland-like cells— (0) one, (1) two or more.

Characters 33–35 — Fronds

Character 33: Frond growth — (0) determinate, (1) indeterminate. Some species exhibit delayed maturation but are in fact determinate in their growth. Fronds are only considered to have indeterminate growth when mature frond apices are never seen and fronds consistently terminate in small crosiers.

Character 34: Dimorphy of sterile and fertile fronds — (0) monomorphic, (1) hemidimorphic, (2) dimorphic. Morphological variation between sterile and fertile fronds is common among ferns. Fronds are considered monomorphic when the only difference between sterile and fertile fronds is the development of the receptacle and sporangia. Fronds are considered hemidimorphic when the fertile portion of a fertile frond is morphologically different from the sterile portion of a fertile frond, and dimorphic when the entire fertile frond, including its sterile portion, is morphologically different from that of a sterile frond. This latter condition was not observed in any taxa in this study.

Character 35: Morphological expression of hemidimorphic fronds — (0) fertile portions of fronds more densely setose, (1) fertile portions of lamina less dissected than the sterile portions.

Characters 36–41 — Petioles

Character 36: Leaf articulation — (0) non-articulate or (1) articulate.

Character 37: Petiole shape in cross section — (0) terete, (1) flattened on the adaxial side. This character is scored exclusive of any laminar tissue forming a margin along the length of the petiole. That state is scored in character 41.

Character 38: Petiole cortex, primary cell type: (0) parenchyma, (1) sclerenchyma.

Character 39: Epidermis of petiole — Petioles were scored as having their outermost layers of cells (0) sclerenchymatous, or (1) parenchymatous. When a parenchymatous epidermis is present, scraping the layer of cells off of the petiole will reveal the darker sclerenchymatous tissue beneath.

Character 40: Petioles, number of vascular bundles: (0) 1, (1) 2, (2) >3. The character was scored by sectioning petioles at the base, as steles typically fuse distally within petioles. This character was deactivated due to missing data.

Character 41: Petiole margins: (0) marginate throughout, (1) distally marginate, or (2) emarginate.

Characters 42–48 — Lamina morphology and anatomy

Character 42: — Lamina base shape: (0) tapered, (1) truncate.

Character 43: Lamina apex shape: (0) gradually reduced, (1) abruptly reduced to a conform terminal segment (i.e., one that resembles the lateral pinnae).

Character 44: Lamina dissection at base: (0) simple (undivided), (1) pinnatifid, (2) pinnatisect, (3) 1-pinnate.

Character 45: Pinna base shape — Pinnae are scored as either (0) even-sided, or (1) expanded when the base is either dilated, decurrent, or surcurrent. This character is not applicable for taxa with simple or shallowly pinnatifid leaves.

Character 46: Pinna apex shape — Pinna apices are score as (0) acute or (1) rounded. This character is not applicable for taxa with entire leaves.

Character 47: Lamina texture — The general texture of the lamina is scored as (0) chartaceous, (1) membranaceous, or (2) carnose.

Characters 48—51— Leaf structure and anatomy — Many grammitids have a well developed spongy mesophyll with stellate parenchyma and large air spaces. This is particularly well developed in *Enterosora*, which was described in part based on this characteristic (Bishop and Smith 1992), and occurs to a lesser degree in *Ceradenia* and *Cochlidium* as well. This character was scored as “blade tissue: (0) not spongiose, (1) spongiose” by Ranker et al. (2004). Leaf sections performed in this study suggest that the spongiose condition is a conglomerate of several characters that should be scored as separate characters. Here I score the presence or absence of a distinct palisade layer, the the relative length of cell arms in the stellate parenchyma, and the position of the leaf vasculature relative to these two layers.

Character 48: Leaf palisade parenchyma layer — (0) present, (1) absent. The palisade parenchyma layer is defined here as present when there is at least one layer of contiguous cells present beneath the epidermis on the inner abaxial side of the leaf. This character was deactivated due to missing data.

Character 49: Length of arm cells in leaf spongy parenchyma layer— (0) short-armed “peg cells,” (1) long-armed cells. Long-armed cells are those in which the arms are longer than the body of the cell.

Character 50: Position of leaf vasculature relative to the palisade parenchyma — (0) at the abaxial surface of the palisade parenchyma, (1) below it. This character is not applicable for taxa that lack a palisade parenchyma layer. This character was deactivated due to missing data.

Character 51: Lamina margin black and sclerenchymatous — A blackened sclerenchymatous border is scored as either (0) absent or (1) present. This characters was non-informative in the matrix and deactivated.

Charactera 52–63 — Venation and vein tissue. Grammitid ferns typically have dark sclerenchymatous tissue surrounding their vascular tissue, at least along the midrib and pinna costae and often along the higher order veins. The dark color may be attributable to phlobaphenes.

The presence of sclerenchyma is scored by removing laminar parenchyma to reveal the veins and is scored regardless of whether the sclerenchyma is visible on the surface of the lamina. The visibility of vein sclerenchyma on the surface of the lamina is also scored, which is a measure of the amount of parenchyma surrounding the vein. In some cases, intermediate states render this character difficult to score precisely.

Character 52: Presence of sclerenchyma on veins — (0) present only along the pinna costa, (1) present on pinna costa as well as first order of veins, (2) present on pinna costa and first order veins but absent on second order veins, (3) present only on the proximal half of first order veins, or (4) absent entirely.

Character 53: Sclerenchyma of midrib visible abaxially — (0) not visible, (1) visible.

Character 54: Sclerenchyma of midrib visible adaxially — (0) not visible, (1) visible.

Character 55: Sclerenchyma of pinna costae visible abaxially — (0) not visible, (1) visible throughout its length, (3) visible only in the proximal portion.

Character 56: Sclerenchyma of pinna costae visible adaxially — (0) not visible, (1) visible.

Character 57: Sclerenchyma of veins visible abaxially — (0) not visible, (1) visible.

Character 58: Sclerenchyma of veins visible adaxially — (0) not visible, (1) visible. This character was not informative in the matrix and deactivated.

Character 59: Vein order — (0) two, (1) three, (2) four or more, or (3) none [veins beyond the pinna costa absent]. Scored here with the pinna costa considered as the first order vein.

Character 60: Secondary vein branching pattern — (0) dichotomous or (1) anisotomous. This character is not applicable for simple secondary veins.

Character 61: Vein fusion (anastomosation) — (0) absent or (1) present (at least in sterile fronds). This character equal to character 51 of Ranker et al. (2004).

Character 62: Hydathodes — (0) absent, (1) present. Visible with 10 × magnification. This character equal to character 38 of Ranker et al. (2004).

Character 63: Cretaceous deposit of hydathodes — (0) absent, (1) present. This character is not applicable for taxa that lack hydathodes.

Characters 64–83 — Laminar indument .

Character 64: Laminar scales — (0) absent, (1) present. This character equal to character 60 of Ranker et al. (2004).

Character 65: Laminar scale coloration — (0) concolorous, (1) clathrate. This character equal to character 61 of Ranker et al. (2004). This character non-informative in the matrix and deactivated.

Character 66: Setae of fronds — (0) absent or (1) present. Setae are multicellular, uniseriate, terete, and reddish to castaneous. Setae are scored here regardless of position on the frond.

Character 67: Seta branching pattern — (0) simple, (1) bifurcate, (2) stellate, i.e., three or more branches emerge from a single origin. This character is not applicable for taxa that lack setae. This character not informative in the matrix and deactivated.

Character 68: Setae present upon petiole — (0) absent, (1) present. This character is not applicable for taxa that lack setae.

Character 69: Setae present upon adaxial midrib — (0) absent, (1) present. This character is not applicable for taxa that lack setae.

Character 70: Rachis setae of uniform length or consistently bimetric — (0) uniform in length, or (1) bimetric, with distinctly long and short hairs mixed.

Character 71: Setae present along margin of lamina — (0) absent, (1) present. This character is not applicable for taxa that lack setae.

Character 72: Distribution of setae present along lamina margin — (0) evenly spaced, (1) confined to the apex of the pinna or segment. This character is not applicable for taxa that lack marginal setae or lack setae entirely.

Character 73: Setae present upon the adaxial surface of the lamina — (0) absent, (1) present. This character is not applicable for taxa that lack setae.

Character 74: Setae present upon the abaxial surface of the lamina — (0) absent, (1) present. This character is not applicable for taxa that lack setae.

Character 75: Setae present upon the adaxial pinna costa — (0) absent, (1) present. This character is inapplicable for taxa that lack setae.

Character 76: Hairs of fronds — (0) absent, (1) present. Hairs are uni- or multicellular, simple, or ansiotomously-branched. Unlike setae, the positions of hairs upon the frond are not scored here because it is hypervariable and not informative with regards to the study group. When present, hairs are generally found along petioles and rachises, and rarely upon the abaxial surface of the lamina or along its margin.

Character 77: Branching pattern of hairs — (0) simple, (1) 1-furcate, (2) 2-furcate, or (3) 3-furcate. This character is not applicable for 1-celled hairs.

Character 78: Number of cells in hairs — (0) 2-celled, (1) 3-celled, (2) greater than 3-celled, or (3) unicellular.

Character 79: Shape of hair cells, or hair branch cells — (0) acicular, (1) setose, (2) capitate including globose or glandular, and (3) unmodified, meaning essentially isodiametric cells with no conspicuous attributes. Grammitid hairs exhibit various cell shapes. The shapes seen in unicellular hairs are often identical to the shapes seen in the terminating branches of the branched hairs, thus they are considered part of a homologous series and scored as a single character.

Character 80: Color of capitate or glandular cell in hairs — (0) white and opaque, or (1) translucent. This character is scored for swollen or globose, glandular cells, regardless of whether the gland is known to be secretory or not. This character is not applicable for taxa that do not have glandular cells in their hairs.

Character 81: Gland cell secretion — (0) secretory, (1) or non-secretory. This character is scored regardless of whether the secretion is waxy or a fluid. This character is not applicable for taxa that whose glandular cells are not secretory, and taxa that lack glands. This character was not informative and deactivated in the matrix.

Character 82: Color of hair branch cells, exclusive of glandular cells — (0) pale, or (1) reddish.

Character 83: Marginal trichomidia along lamina margin— (0) absent, (1) present. It is not clear whether these minute, reduced, blackish hairs of 1–2 cells are homologous to hairs or not.

Characters 84 –100 — Sorus and sporangia

Character 84: Soral receptacle — (0) flat, (1) convex.

Character 85: Sori distinct or confluent — (0) distinct, (1) confluent when they form a coenosorus. This is similar scoring to Ranker et al. (2004), who described the character as "Sorus number per leaf: (0) >2, (1) 2."

Character 86: Soral position relative to the margin of the lamina and the penultimate axis — (0) inframedial: nearest to the penultimate axis, (1) medial: midway between the penultimate axis and the margin, (2) intramarginal: closer to the margin that the penultimate axis. This character is not applicable for those that have more than a single series of sori between the margin and the penultimate axis. This character equal to character 70 of Ranker et al. (2004).

Character 87: Distribution of sori — (0) even throughout the frond, (1) confined to the distal portion of the frond. This character equal to character 65 of Ranker et al. (2004).

Character 88: Outline of mature sorus — (0) round, (1) elliptic: up to 2x as long as wide, (2) elongate: more than 2x longer than wide.

Character 89: Sorus position relative to surface of lamina — (0) complanate: upon the surface of the lamina, (1) immersed into the surface of the lamina.

Character 90: Angle of wall surrounding immersed sori — (0) sloping sides, or (1) vertical sides.

Character 91: Sori embossed on adaxial side of the lamina — (0) not embossed, (1) embossed. This character equal to character 68 of Ranker et al. (2004).

Character 92: Margin of the lamina infolded over sori — (0) no, (1) yes. This character equal to character 78 of Ranker et al. (2004).

Character 93: Tissue subtending receptacle — (0) derived entirely from the abaxial surface of the lamina, (1) in part by the margin of the blade as in *Prosaptia*, where the sorus is sunken in the leaf margin.

Character 94: Paraphyses — (0) absent or (1) present. Paraphyses are simple or branched mulitcellular hairs developing from the receptacle. Receptacular setae are scored separately.

Character 95: Cells of paraphyses — (0) uniform cells, (1) whitish, opaque glands, (2) translucent glands, (3) setose branches.

Character 96: Receptacular setae — (0) absent, (1) present. Setae present within the radius of the sorus are considered to be receptacular.

Character 97: Sporangial stalk width at mid-stalk — (0) 2–3 cells wide, or (1) 1 cell wide at mid-stalk.

Character 98: Episporangial indument — (0) absent, or (1) present. In this study, only episporangial setae were observed, thus the type of indument was not scored. This character equal to character 75 of Ranker et al. (2004).

Character 99: Position of episporangial indument — (0) the side wall of the capsule or (1) from the annulus. This character is not applicable for taxa that lack episporangial indument. This character equal to character 76 of Ranker et al. (2004).

Character 100: Aggregation of episporangial indument — (0) scattered or (1) aggregated.

This character is not applicable for taxa that lack episporangial indument. This character equal to character 77 of Ranker et al. (2004).

Characters 101 — 105 Spores

Character 101: Spore color — (0) yellow, (1) green.

Character 102: Spore number — (0) 64, (1) 32, (2) 16. This character equal to character 80 of Ranker et al. (2004).

Character 103: Spore laesurae — (0) linear or (1) triradiate. This character equal to character 81 of Ranker et al. (2004).

Character 104: Number of cells in newly shed spores — (0) one, (1) two, or (2) three to four. Chlorophytic green spores frequently exhibit intrasporic cell division by the time of dehiscence from the sporangium.

This character equal to character 82 of Ranker et al. (2004). Only cells in the spore stage are counted. When the spore wall is ruptured, or the group of cells take on an elliptic shape, the mass of cells is considered here to be in the gametophytic stage. The states for this character were scored from fresh material in the field, relatively fresh spores on herbarium sheets. This character was deactivated because it contained too much missing data.

Character 105: Exospore surface — (0) unadorned, or (1) obviously patterned. Grammitid spores are relatively unadorned, and do not lend themselves to complex character scoring. This character equal to character 84 of Ranker et al. (2004).

The surface is genrally tuberculate, sometimes bearing sphearical deposits, which is scored here as state 1. State 0 is scored in this analysis for the polypod ferns that occur among outgroup taxa.

Characters 106 — 107 Gametophytes

Character 106: Gametophyte form — (0) a cordate thallus, (2) elongate to filamentous thallus. This character equal to character 85 of Ranker et al. (2004).

Character 107: Rhizoid developed in first cell division of the spore — (0) no, (1) yes. This character equal to character 86 of Ranker et al. (2004).

Character 108 —Chromosomes

Character 108: Chromosome base number – (0) 37, (1) 35, (2) 33, (3) 32. This character equal to character 87 of Ranker et al. (2004).

Character 109 —Fungal relations

Character 109: The presence of mycelia and ascomes of the biotrophic and comensal bitunicate ascomycete genus *Acrospermum* — (0) absent, (1) present. Characters should reflect inheritable characteristics of the organism. The consistency to which *Acrospermum* can be found on some ferns, and its consistent absence on closely related ferns growing in the same forest, suggests that an inheritable characteristic exists. This character equal to character 47 of Ranker et al. (2004).

Character 110 — Secondary compounds.

Character 110: Aromatic when dry — (0) absent, (1) present. Species of *Melpomene* contain coumarins which emit a sweet and spicy odor upon drying. This character equal to character 48 of Ranker et al. (2004).

RESULTS

After exclusion of non-informative and deactivated characters, the morphological matrix, contained 10,989 cells, with total missing values of 2,406 cells (14%), calculated as the sum of 599 (4%) cells of missing data, and 1807 (16%) cells of inapplicable characters. The parsimony analysis was run for matrices until 100,000 most parsimonious trees were found and memory overflowed. In the first analysis, which contained all of the taxa, the shortest trees were 791 steps long, had a CI of .16 and RI of .71, and 94 nodes collapse in the strict consensus tree of all equally most parsimonious trees (Fig. 1). *Terpsichore lehmanniana* (Smith's group 1) is sister to all remaining grammitids, which form a polytomy with little resolution in the strict consensus. Despite this lack of resolution, *Terpsichore* is demonstrated to be polyphyletic; one of the larger clades that is resolved contains representatives of *Tepsichore*, *Melpomene* A. R. Sm. & R. C. Moran, and *Lellingeria* A. R. Sm. & R. C. Moran. Many other genera sampled, such as *Lellingeria*, *Ctenopteris*, *Enterosora*, *Cochlidium*, and *Grammitis* were also not monophyletic. Trees from the second analysis (in which *T. delicatula* and *T. subscabra* were excluded) were 773 steps long, and had a CI of .16 and an RI of .71. In the second analysis, *Calymodon*, *Enterosora*, *Melpomene*, *Prosaptia* C. Presl, and *Zygophlebia* Bishop, were monophyletic (Fig. 2). The remaining genera were para- or polyphyletic. As in the first analysis, *T. lehmanniana*

(Hieron.) A. R. Sm. is resolved as sister to the remaining grammitids, which are more resolved than the first analysis and form a polytomy composed of six clades. The remaining species of *Terpsichore* are polyphyletic, and are found in two of the six clades in this polytomy. Clade A contains *T. anfractuosa* (Kunze ex Klotzsch) B. León & A. R. Sm. and related species (Smith's group 2 and species unplaced by Smith), the monophyletic genus *Melpomene*, and the *Lellingeria limula* group. The remaining species of *Terpsichore*, including the type, are part of clade B. A polytomy is formed within clade B of three clades labeled C, D, and E. Clades C and D are monophyletic groups of *Terpsichore*. Clade C includes the type of *Terpsichore*, *T. asplenifolia* (L.) A. R. Sm., in a paraphyletic grade with two other species from Smith's group 1. Nested here is a monophyletic group of five species representing Smith's group 3. Clade D includes the clade of *T. subtilis* (Kunze ex Klotzsch) A. R. Sm. and *T. cretata* (Maxon) A. R. Sm. (Smith's group 4) as sister to a clade that includes *T. taxifolia* (L.) A. R. Sm. and related species (Smith's group 2). Clade E contains two species of *Terpsichore*, *T. achilleifolia* (Kaulf.) A. R. Sm. and *T. longisetosa* (Hook.) A. R. Sm. (Smith's group 5), along with ten other grammitid genera. Of Smith's infrageneric groups of *Terpsichore*, only groups 4 and 5 are resolved as monophyletic.

DISCUSSION

Circumscription of Terpsichore. The following discussion refers only the second analysis, as the first analysis is too poorly resolved to offer additional insight. Numbers in parentheses refer to character numbers from the morphological matrix.

The morphological data set presented here offers no support for a monophyletic *Terpsichore* as defined by Smith (1993), and in this way is consistent with both Ranker et al. (2004) and Sundue et al. (Chapter 2). The characters originally used to define *Terpsichore* (Smith, 1993) are primarily plesiomorphic when optimized onto the shortest trees. This is the case for dorsiventral rhizomes (4), non-anastomosing (61) and unbranched veins (59), hydathodes (62), setae present on fronds (66), the lack of glandular paraphyses (94), and the presence of setae along the margins of rhizome scales (25), which are present in many or most grammitid ferns. Rhizome scale setae that are restricted to the apex of the scale (26), or present on the abaxial and adaxial scale surfaces (30), which were also used to define *Terpsichore,* act as synapomorphies uniting small groups of *Terpsichore*, but have too limited a distribution to unite the entire genus. Likewise, concolorous scales (21), which were cited as the condition for most species of *Terpsichore*, are actually absent in 13 species that are included here (those which reside in clade A), and do not unite the genus as a whole.

Terpsichore falls in five places in the strict consensus, and based on these results needs to be re-circumscribed more narrowly with the excluded taxa either being combined into other genera or in some cases established as new genera. The type of *Terpsichore* is placed in clade C, the relationships of which are supported with two alternative topologies in the shortest trees. In some trees, clade C is sister to clade D which is also composed of *Terpsichore* species. This sister group relationship is united by rounded pinna apices (46), and sori that are distributed evenly throughout the frond (87). Together these two clades would contain 44 of the *Terpsichore* species including the type in this study, and would be expected to include the majority of species of *Terpsichore* sensu Smith (1993) and therefore be a logical way of re-circumscribing the genus in light of this study. *Terpsichore* would then include most but not all of the species from Smith's informal groups 1, 2, 3, and 4. Complicating this solution is that in other most parsimonious trees, clade C is supported as sister to clade E by the absence of setae along the adaxial side of the pinna costae (75), and by hairs on the fronds that are composed of more than three cells (78). Clade E contains fourteen other genera, thus in this scenario *Terpsichore* would necessarily be restricted to clade C. By this definition, *Terpsichore* would contain all of the species in Smith's group 3, and some of the species from his group 1, and would be defined by rhizome scales with setose surfaces (30), rhizome scales lacking apical papillate glands (31), and the presence of episporangial setae (98).

Terpsichore lehmanniana, the two species of *Terpsichore* in clade E, and the 13 species of *Terpsichore* in clade A cannot be considered part of the genus in any scenario supported by the data. Whether to combine these taxa in existing genera, or create new genera will require additional sampling and is beyond the scope of this study.

While support is lacking for *Terpsichore* as originally defined, Smith's informal infrageneric groups are partially recognizable in the results. Groups number four and five in particular, are resolved as monophyletic, but the characters supporting them here are not identical to those originally described by Smith. Group four, in particular, including *T. cretata* and *T. subtilis*, was originally defined by having arching or pendant indeterminate fronds with reduced basal pinnae and provided with setae, blackish rhizome scales with either apical or marginal setae, glabrous sporangia, cretaceous hydathodes, and *Acrospermum* ascomes. Of these characters, only blackish rhizome scales (22) act as a synapomorphy uniting these two species. The other characters cited optimize at lower nodes in the tree. Cretaceous hydathodes (63) and *Acrospermum* ascomes (109) in particular support the sister relation between group four and clade D, a relationship that is also supported in Ranker et al. (2004) and Sundue et al. (Chapter 2).

Group five, of which *T. achilleifolia* and *T. longisetosa* are included in this study, is supported here by distally marginate petioles (41), even-sided pinna bases (45), presence of setae along adaxial pinna costae (75), sori distributed evenly throughout the frond (87), and presence of receptacular setae (96). Characters cited by Smith (1993) defining group five by comparison, are either plesiomorphic or optimize at a lower node in the analysis. In both Ranker et al. (2004) and Sundue et al. (Chapter 2), species from group five form a clade with *Micropolypodium*. Here they are both members of clade E, but do not form a clade together.

Smith's remaining infrageneric groups are resolved as para- or polyphyletic. Group two was not monophyletic in any study, the characters used to define it being either plesiomorphic or optimizing at deeper nodes in the shortest trees. Here, species from group two fall into two separate clades on the tree, A and D. In clade A, 14 species of *Terpsichore* form a clade along with the monophyletic genus *Melpomene*, and the species of *Lellingeria* that correspond to the infrageneric group of *L. myosuroides* as defined by Smith et al. (1991). These 14 *Terpsichore* species correspond to the monophyletic "*Terpsichore anfractuosa* group" of Sundue et al. (Chapter 2), and to the genus *Ascogrammitis* Sundue (Chapter 3). Although the close relation of the *Lellingeria myosuroides* group to *Melpomene* is supported in both Ranker et al. (2004) and Sundue et al. (Chapter 2), this clade composed of the *T. anfractusoa* clade plus *Melpomene* and the *Lellingeria myosuroides* clade is otherwise unique to this study; Ranker et al (2004) and Sundue et al. (Chapter 2) found *Lellingeria* pro parte in the place of the *Terpschore* species that reside here.

Clade D contains a monophyletic group of 30 species (32 terminals) that were either originally placed in Smith's group 2 or else circumscribed later, and which are supported in this analysis by supramedial sori (86) and by dark sclerenchyma of the veins (52) and pinna costae (55) visible on the abaxial side of the lamina. Two of the characters used by Smith (1993) to define the group, cretaceous hydathodes (63), and *Acrospermum* ascomes (Character 109), optimize at the next deeper node uniting this group with the two species from group 4. The other characters used by Smith to define this group are either plesiomorphic, optimize at a deeper node, or are of limited distribution. This clade corresponds to the monophyletic "*Terpsichore taxifolia* group" of Sundue et al. (Chapter 2). It was also resolved as monophyletic in Ranker et al. (2004), but contained only two species terminals in that study. These results lend support to both of those studies by demonstrating the monophyly of this clade with expanded sampling, and based entirely on morphological markers.

Most of the species from Smith's groups 1 and 3 group together to form clade C, except *Terpsichore lehmanniana* (group 1) which resides outside of clade C, and *Terpsichore subscabra* and *T. delicatula* (group 3) which are wildcard taxa and not placed with confidence in this study. While one possible placement for *T. subscabra* and *T. delicatula* is with clade C, multiple other topologies are just as well supported. This uncertainty does not come as a surprise; although Smith placed these two species within clade C, he noted two characteristics by which they differed from the other species: glabrous sporangia capsules and lack of clustered setae. Within clade C, species corresponding to group 3 form a monophyletic group which is nested inside a paraphyletic grade of species from group 1. Ranker et al. (2004) and Sundue et al. (2004) also found support for a monophyletic group 3 minus *T. subscabra* and *T. delicatula*, but in their results species from group 1 were placed at the base of the grammitids. None of the characters originally used to define group 3 act as synapomorphies here. Two of them, setose scale surfaces (30) and setose sporangial capsules (98) act as synapomorphies for clade C as a whole. Other characters originally cited for the group are plesiomorphic, such the lack of *Acrospermum* ascomes (Character 109), or homoplastic, such as cretaceous hydathodes (63). Synapomorphies for group 3 in this analysis are membranceous laminae (47) and adaxially setose pinna costae (75).

Morphological data. Obviously, the poor resolution in the strict consensus tree makes it difficult to arrive at firm conclusions on the evolution of most characters. Nevertheless, the results do provide a clear indication of minimum change for some characters. Here the opportunity is taken to discuss more general results from the morphological study that do not pertain directly to *Terpsichore*.

Grammitid ferns are widely cited as having petioles with a single vascular bundle (Parris, 1990), and this character state is often cited as a synapomorphy for grammitids as a whole (Ranker et al. 2004; Schneider 2004). One exception to this is *Luisma bivascularis* M. T. Murillo & A. R. Smith, a species in a monotypic genus that was considered unique among all grammitids by having two vascular bundles in the petiole (Murillo and Smith 2003). Here, 30 additional species are demonstrated to have two vascular bundles in their petioles (character 40), and the presence of two bundles acts as a synapomorphy uniting the grammitid ferns as a group. It is also homoplastic in the analysis, and appears at least 20 times in the shortest trees, but some of this homoplasy may be due to incomplete sampling of the character. Two vascular bundles are also present in the earliest diverging species in Ranker et al. (2004) and Sundue et al. (Chapter 2); thus this character is likely the ancestral condition in the grammitid ferns.

The presence of gaps within the dictyostele that are not associated with leaves was considered to be unique to *Zygophlebia* and *Ceradenia* by Bishop (1989) and Rakotondrainibe & Deroin (2006), who applied the term “accessory stelar perforations” for these gaps. In contrast, Ogura (1972) reported that the perforated dictyostele is common throughout the Polypodiaceae and also occurs elsewhere. Observations made here (character 5; Fig. 4) concur with Ogura that perforated dictyosteles are in fact widespread and the ancestral condition in the grammitid ferns; there is no indication that this character will be useful in diagnosing genera of grammitid ferns. Of the 43 taxa examined, four did not have perforated dictyosteles, and this loss appeared three times on the shortest trees. Plants lacking perforations generally had small rhizomes, suggesting that the presence of perforations likely coincides with larger diameter steles and is related to the efficiency of design regarding hydraulic conductivity.

Architecture and branching patterns in ferns remain largely unstudied (but see Croxdale, 1976; Gruber, 1981; Troop and Mickel, 1968); this is the first study to incorporate branch buds and branching (Characters 7, 9) of ferns into a cladistic analysis.

Branch buds were found on 50 taxa, and appear 10 times in the shortest trees. In the strict consensus they (Character 7) act as a synapomorphy for two large groups, Clade D and the clade that includes *Ceradenia*, *Enterosora* and *Zygophlebia*. They also unite smaller groups such as the species corresponding to the *Lellingeria myosuroides* group, and portions of both *Melpomene* and *Lellingeria* pro parte. Despite being widespread in the grammitid ferns, these meristems rarely develop into actual rhizome branches.

Regularly branched rhizomes (Character 9) were found only on nine grammitid taxa, and appear seven times in the tree. Interestingly, branched rhizomes appear to correlate with the habit of the plants; eight of the nine species exhibiting branched rhizomes are terrestrial or epipetric

(Character 0). Thus, while grammitid ferns regularly produce branch buds along their rhizomes, these buds only rarely develop into branches, and more often than not such branching occurs in terrestrial or epipetric species.

A well developed spongy mesophyll with stellate parenchyma and large air spaces was previously thought to be unique to *Enterosora* (Bishop and Smith, 1992; Ranker et al. 2004). Here, spongiose mesophyll is demonstrated to have evolved three times, in *Enterosora*, *Oregrammitis hookeri* (Brackenr.) Parris, and two species of *Lellingeria*. Evolution of the spongiose mesophyll involves at least three independent morphological characters, the presence or absence of a palisade layer (Character 48), the development of long-armed parenchyma cells (Character 49), and the relative postion of the vasculature to the palisade layer (Character 50) if it is present. While all three of these characters were included here, only the development of long-armed parenchyma cells could be scored completely; anatomical work required to score the other two characters was beyond the scope of this study. Nevertheless, based on the information gathered, it is apparent that these three characters vary independently and not all spongiose laminae are constructed in the same way. For example, both *Lellingeria subsessilis* and *L.* sp. aff. *humilis* have long-armed parenchyma cells, but they differ by the presence of a palisade layer, which is absent in *L.* sp. aff. *humilis*, thus using multiple separate characters better describes the evolution of spongiose tissue. Why stellate parenchyma should develop in epiphytic plants at all remains a mystery. This type of anatomy is common in emergent aquatics such as *Juncus* (Ogden, 1974), where it is thought to be an adaptation associated with CO_2 gas exchange (Evert, 2008), but is not common elsewhere.

Conclusions. Morphological data sucessfully recover some but not all of the groups found by traditional taxonomy. Clades C and D together contain most of the species combined in *Terpsichore*, and these two clades are sister in some of the shortest trees, supporting a monophyletic concept of the genus that is not radically different from the original. The recovery in part of Smith's infrageneric groups also shows some agreement between cladistic methodology and traditional taxonomy. Surprisingly though, in few cases do the characters originally cited by Smith act as synapomorphies for these groups. In most cases, these groups are supported by characters other than those cited by Smith. This may be explained in part by the fact that traditional taxonomy often relies on gestalt characters that are not included in descriptions and which can not easily be coded as characters in a matrix. Taxon sampling may also be responsible for some cases of paraphyly and polyphyly. In particular, denser sampling of Smith's group 1 may demonstrate monophyly instead of paraphyly with regard to group 3, which is nested inside of it in the results. Overall though, the polyphyly of *Terpsichore* seems to have resulted from it being defined by characters that are plesiomorphic, homoplastic, or of limited distribution of the genus.

Results presented here are perhaps more congruent with results based on DNA sequence data. In addition to the polyphyly of *Terpsichore*, Ranker et al. (2004) and Sundue et al. (Chapter 2) find similar groupings of Smith's infrageneric groups. For example, the species from Smith's group 2 that fall into clades A and D, are the same groups that form the *Terpsichore anfractuosa* and *Terpsichore taxifolia* groups of Sundue et al. (Chapter 2). The grouping of Smith's group 4 with the other species in clade D also occurs in Sundue et al. (Chapter 2). This is true of some other groups in the tree outside of *Terpsichore* as well such as the grouping of *Zygophlebia* with *Enterosora* and *Ceradenia*, and the grouping of *Melpomene* with the *Lellingeria myosuroides* group.

Clearly, morphology is extremely valuable for circumscribing clades of grammitid ferns and determining relationships between them. Morphology provides clear hypotheses that can be tested by the inclusion of additional data and or taxa. Unfortunately, in this case, morphology offers enough competing hypotheses that their consensus does not answer all of our questions. Additional morphological data such as and denser taxon sampling of some groups might improve these results as would the inclusion of a different type of data such as DNA sequences.

Appendix A. Morphological characters scored for this study; A = 0, 1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

	012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Ceradenia aulaeifolia	02101?0111000-101100100021010-01010?001102003110?0?021111001100-0-10110100001223---1001000-00011010--101?111?00
Calymmodon gracilis	00000?0001?00-10010A100011102001000-001100002112?0?001000--0?0100-10110101111111--0000110?-010??010--1010111?00
Calymmodon luerssenianus	0?000?0?01?00-1001001020?????????00-00????012100?0?0???????0-0??0-101101011-------??000110-0100-010--101?111?00
Campyloneurum angustifolium	0210111011100-100101001000---000-00-1101210?0--000?0400000021110110---------0-----?0101000-0000-000--0000000000
Ceradenia aulaeifolia	02101?0111000-101100100021010-01010-001102003110?0?021111001100-0-10110100001223--?1001000-00011010--101?111?00
Ceradenia fucoides	02000?010100100------------------00-001100001100?0?000000000-00-0-101000-000122201?0002010-00011010--101?111?00
Ceradenia intonsa	02101?0111000-101100100021001-01000?001012102102?0?011000001100-0-10110101111A23--?1002000-00012010--101?111?00
Ceradenia jungermannioides	00100?0101000-0----------------0-00-001?0???0--0?0?00??????1100-0-101101011?101201??001000-000?-?10--1010111000
Ceradenia kalberyeri	02101?0111000-101100100021000-01000-001012102102?0?011100001100-0-101100-0101D23--?1001000-00010010--1011111?00
Ceradenia pilipes	02000?0101000-0011001000210A0-01000-001102002100?0?031100001100-0-101000-000122H01?1001100-00011010--101?111?00
Ceradenia sp. aff. kalbreyeri Vasco 701	02101?0??1000-101100100021000-0??00-001002102102?0?01110?001100-0-101?00-?0?10A201?0002011000011010--101?111?00
Ceradenia sp. ined. Sundue 1238	02101?0111000-1011001000210A1-01100-001012103102?0?011100001100-0-1011010000122I11?1001010-00011010--101?111?00
Ceradenia sp. Moran 7520	02101?0??1?00-10110010002?????01?00-0010?2102102?0?0?000000-100-0-101-010-1-------??002010-00011010--101?111?00
Ceradenia spixiana	02101?0111000-1011001000210A1-01000-001002102102?0?020?0?0-1100-0-101?010?1?122????0001000-0001J010--1011111000
Chrysogrammitis musgraveana	0?001???01?00-100--000201101?????00-00????002????0?0???????210000-10--------1-----??00-100-000--?10--101?111?00
Cochlidium punctatum	0?000?0?01000-1?010A100000---10??01100110?0?0--2?0?0400----3-0100-0---------1013--2001012100000-?10--1111111?00
Cochlidium rostratum	0?000?0?01000-11010A100000---100-01100110?0?0--2?0?0400----3-00-0-0---------0-----?00101211000???10--1010111300
Cochlidium seminudum	00000?0?01?00-100100100000---000-00-00110?0?0--2?0?0410----3-00-0-0---------10F3--20010120-0000-?10--101?111?00
Ctenopteris heterophylla	B?001???01?00-100--0102010---0---00-00????001????0?0???????110100-10????????1-----??00-100-000--?10--101?111?00
Ctenopteris lasiostipes	0?001???01?00-100--0111010---0---00-00????003????0?0???????110100-10????????1-----??00-100-000--?10--101?111?00
Ctenopteris nutans	0?001???11?00-100--013101100-----00-10????002????0?0???????110000-10????????1-----??00-100-000--?10--101?111?00
Ctenopteris repandula	C?000???01?00-100--0103010---0---00-00????002????0?0???????110100-10????????1-----??00-100-000--?10--101?111?00
Ctenopteris rhodocarpa	0?001???11?00-100--011101100-----00-10????002????0?0???????110000-10????????1-----??00-100-000--?10--101?111?00
Enterosora barbatula	02101?0?10?00-10?1001030?1013-0??00-?0???20?0--2?1?0?0000??21A0-0-10110101111?221-00001011000012010--101?111?00
Enterosora enterosoroides	02101?0111000-100100103010---100-00-0010020?0--201?050000001100-0-10100100001122100000101110000-010--1011111000
Enterosora percrassa	0210110?11000-101100103011013-11000-0011120?0--211?000000001110-0-1?1101011?0-----?000101110000-010--1011111000
Enterosora trichosora	02101?0111000-101100103010---10?-00-0011020?0--211?010000001100-0-101101011?10221-?000102100000-110--101?111?00
Enterosora trifurcata - Costa Rica	02101?0111000-101100103011010011100-0010120011A211?0100000011A0-0-101100-0001223--??00102100000-010--101?111000
Enterosora trifurcata - Ecuador	02101?0111000-101100103010---011100-0010120011A211?0100000011A0-0-101100-0001223--??00102100000-010--101?111000
Grammitis billardieri	A?10100001100-100100103000---001000-0011010?0--0?0?021000001100-0-101000-0001H20--1000011101000-010--101?111000
Grammitis ciliata	D?000?0?01?00-100100103010---00--00-00????0-0--0?0?0???00??0-00-0-0---------1???????002000-0000-010--1010111?00
Grammitis deplanchei	0010110011000-101100100010---100-00-0011000?0--2?0?010000001000-0-0---------0-----??002110-0000-011111010111?00
Grammitis forbesiana	0?001?0?01?00-100100103010---00--00-00????0-0--0?0?0???????0-00-0-1---------0-----??000000-0000-01111101?111?00
Grammitis knutsfordiana	00001?1001?00-110100100110---000-00-0011020?0--0?0?011100001100-0-10110101100-----?0000110-0000-111011010111?00
Grammitis melanoloma	0?000?0?01?00-100100103010---0??00-00????0?0--0?0?1???????1000-0-0---------0-----??000100-0000-?10--101?111000
Grammitis parva	0?000?0?01?00-100100103010---00--00-00????0-0--0?0?0???????1000-0-1---------1-----??000100-0000--1101101?111?00
Grammitis poeppigiana	20001?0100000-100100100010---000-00-001100??0--200?0400----1000-0-0---------1223--10000110-0000-0100-1011111000
Grammitis pseudociliata	0?001?0?01?00-100100103010---00--00-00????0-0--0?0?0???????0-00-0-10????????1-----??0001A0-0000--10--1011111000
Lelligeria barbensis	02?0??0??1-?--1-0---1110-1001----00-0-----00210-???0-1111??0-0100-0---------1110--??00------000--10--101?111?00
Lelligeria hellwigii	00100?0101?00-1100000111111020010011001102002100?0?0411----3-?100-0---------1110--00000110-0000--10--101?111?00
Lelligeria myosuroides	00100?0101000-1000010111111021010011001102002100?0?001010--3-?100-0---------1110--10000110-0000--10--101?111?00
Lelligeria prionodes	00100?0101?00-1101000111111020010011001102002100?0?001010--3-?100-0---------1110--00000110-0000--10--101?111?00

Appendix A cont. Morphological characters scored for this study; A = 0, 1; B = 0, 1, 2, 3, C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2, G = 0, 3, H = 2, 3; I = 1, 2, 3; J = 1, 3.

	11111111111
	11111111112222222222333333333344444444445555555555666666666677777777778888888888999999999900000000001
	012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lellingeria apiculata	01101?0001000-100100111011001-11000-001102103100?0?001100000-0100-0---------11F0--?1001100-0000--10--1011111?00
Lellingeria hirsuta	0110110001000-100100111001001-01000-001102113100?0?001111??0-0100-0---------1030--00001?00-0000-010--101?111?00
Lellingeria humilis	11101?0001100-100100011001001-0??00-001102002100?0?031100000-0100-0---------12F0--?0001000-0100--10--101?111?00
Lellingeria limula	00100?0101000-100001011110---001?001001101002100?0?0?1100000-0100-0---------1110--?0010120-0000--10--101?111300
Lellingeria major	01101?0101100-101100111001001-01000-0?1112003100?0?0G1100000-0110-0---------1110--?0001100-0000--10--101?111?00
Lellingeria myosuroides	00100?0101000-1000010111111021010011001102002100?0?001010--3-?100-0---------1110--10000110-0000--10--101?111?00
Lellingeria oreophila	01101?0001100-101100112001001-01000-001102003100?0?031110000-0100-0---------12F0--?0001100-0000--10--101?111?00
Lellingeria pseudomitchellae	00000?0?01-?0-0------------------001001101001010?0?001000000-0100-10110111111101--00000100-00000-10--1011111?00
Lellingeria saffordii	00000?0001?00-1000011111111020010011001101002100?0?001010--3-?100-0---------1110--10000110-0000--10--101?111?00
Lellingeria schenckei	01000?0?010??-10000011101100?00??00-001100002001?0?001000000-0100-1011?110101100--00000100-00000010--1011111?00
Lellingeria sp. aff. hirsuta Sundue 1159	02101?0?01?00-101100111001001-01?00-001102012100?0?001110000-0110-0---------1110--?1001100-0000--10--101?111?00
Lellingeria sp. ined. aff. humilis sundue 1126	01101?0101000-101100111001001-01000-00110000111011?00A000000-0110-0---------1110--?0001000-0000--10--101?111?00
Lellingeria subsessilis	02101?0001000-101100111001001-01000-001101001100011001000000-0110-0---------1110--?1001001-1000--10--101?111?00
Lellingeria suprasculpta	02001?0001000-101000112000---00??00-001101001101?0?011010000-0100-0---------0-----?0000001-1000--10--101?111?00
Lellingeria suspensa	02001?0?01000-100100111120---001000-001101002100?0?011100000-0100-0---------11A3--?0001001-1000--10--101?111?00
Melpomene anazalea ined.	13101?1100?00-100101112110---001100-001101002112?0?001100000-0100-10110101111123--?0001000-0000-110--101?111?01
Melpomene firma	01101?0?01100-100111112120---001000-001101103000?0?001111000-0100-101100-01111DJ--?1000100-0000-110--111?111?01
Melpomene flabelliformis	E0101?1?00000-10010A112120---0011010001100002112?0?001100000-0100-100000-0001123--?1001100-0000-110--1210111001
Melpomene moniliformis	F0101?1100100-100101111120---001100-001000002112?0?001100000-0100-101100-0001D23--000011?0-0000-010--111?111001
Melpomene occidentalis ined.	0010110101100-100101112110---0010010001110003100?0?001111--0-0100-1000?0-0101123--01000110-0000-010--101?111?01
Melpomene personata ined.	01101?0001?00-100100112120---0010010001101102110-0?001100000-0100-10100101101123---0000000-0000-110--101?111?01
Melpomene pseudonutans	E1101?0?01100-100101112120---0011010001100002100100001100000-0100-100000-0101F23--01001100-0000-110--1011111001
Melpomene vernicosa	01101?0001100-100101112120---001100-001102102112?0?001100000-0100-101101101011FJ--00001100-0000-110--101?111?01
Microgramma percussa	0010111010100-100101111000---100-00-1101220?0--0?0?0500000021110110---------0-----?0101000-1001-000--0000000000
Microgramma squamulosa	0010111010100-100101111001001100-00-1101220?0--0?0?0500000021110110---------0-----?0101000-0001-000--0000000000
Micropolypodium hyalinum	02000?100101111011011000210A2-01000-001102002100?0?0400----0-0100-10110101101123--10000100-0000-010--1011111000
Micropolypodium taenifolium	02000?0001000-101100100021000-01000-001102002100?0?0410----0-0100-10110100101121--10000100-0000-010--1012111000
Micropolypodium zurquinum	02000?0001000-101100100020---001000-001102002100?0?0400----0-0100-10110101111F23--10000100-0000--10--101?111000
Oreogrammitis hookeri	01001?0101000-110100100110---000-00-0011020?0--0011010000001100-0-10110101101003--?0000000-0000--11011010111?00
Pecluma alfredii	0110110011000-100100002000---000-00-101012102100?0?001110--110100-0---------10F3--00002000-0000--00--0000000000
Polypodium glycyrrhiza	1110111?10000-100100100000---100-00-110122112100?0?00001000 11A10100---------1003--00100000-0000--00--0000000000
Prosaptia alata	0210110?11000-100001111001002-01000-101101001100?0?010000001000-0-10110100101110--10?0210111010-010--1010111000
Prosaptia contigua	0?10110?11000-100000111011002-01000-001101002100?0?001110--0-00-0-10110100101110--11?0210111010-010--1010111000
Prosaptia obliquata	0100110?11000-100000113011002-00-00-101101003100?0?010000001100-0-10110100101110--1000110111010-010--1010111000
Prosaptia pubipes	E?101?0011?00-100000111111002-00-00-001101002100?0?001111--0-00-0-10110100111110--10?0210111010-010--1010111000
Scleroglossum sulcatum	10000?0?01?00-110100100000---000-00-0011?20?0--2?0?0400----3-?0-0-0---------1A23--1001212100010-?10--101?111?00
Terpisichore costaricense	0210110001000-101100100021100001100-001102003100?0?011111100-0110-101100-0101111--10001000-0000-110--101?111?10
Terpsichore achilleifolia	A?000?0001?00-100100100000--0000-00-001101002000?0?01000000010100-101100-1111F23--10000000-0000-110--1011111000
Terpsichore alsopteris s.s. - Costa Rica	02101?0111000-101100100021100001000-001112003100?0?001111--0-0110-101110-0101113--10002000-0000-010--101?111?10
Terpsichore amphidasyon	0110110011000-101100100121101001000-001102003010?0?011111100-0110-10110101111113--?0001000-0000-110--101?111?10
Terpsichore anfractuosa Jimenez 1399 - Bolivia	00111?0001?00-100001011111002-010010001100002100?0?001010--0-0110-10110A10101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Kessler 13507 - Mexico	00111?0001?00-100001011110-0--010010001100002100?0?001010--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Kessler 13517 - Mexico	00111?0001?00-100101011110-0--010010001100002100?0?001010--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Lehnert 1035 - Ecuador	A0111?0001?00-1000010111111020010010001100002100?0?001100--0-0110-101100-0101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Lehnert 212 - Peru	20111?0001?00-100001011111001-010010001100002100?0?001010--0-0110-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Lehnert 315 - Peru	00111?0001?00-100001011110---0010010001100002100?0?001100--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Lehnert 499 - Bolivia	00111?0001?00-100001011111002-010010001100002100?0?001010--0-0110-10110A10101113--10000110-0000-110--101?111?10

Appendix A cont. Morphological characters scored for this study; A = 0, 1; B = 0, 1, 2, 3, C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2, G = 0, 3, H = 2, 3; I = 1, 2, 3; J = 1, 3.

	012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Terpsichore anfractuosa Moran 7567 - Ecuador	00111?0001?00-100001011111002-010010001100002100?0?001100--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore angustipes	02101?0?01?00-100001111001002-010010001101002110?0?001110--0-0110-101100-*11113--11000010-0000-010--101?111?10
Terpsichore athyrioides	0210100001000-100011111001002-01000-001111004100?0?0?1111000-0110-101100-0001113--10001010-0000-010--101?111?10
Terpsichore attenuatissima	02101?0111000-101100100021000-01000-001112003100?0?001111--0-0110-10111100101113--10002000-0000-010--101?111?10
Terpsichore attenuatissima	02101?0111000-101100100021000-01000-001112003100?0?001111--0-0110-10111100101113--10002000-0000-010--101?111?10
Terpsichore clathrata	02101?0101?00-100001111111002-0100100011?2?03100?0?001111--0-0100-101100-0101113--11000010-0000-110--101?111?10
Terpsichore clavigera ined.	0110110101000-100011111001002-01000-001111002100?0?001111--0-0100-101100-0001113--11000110-0000-010--101?111?10
Terpsichore colombiense ined.	0110110101000-100011111001002-010010001111003100?0?001111--0-0100-101100-0111113--11000110-0000-110--101-111?10
Terpsichore communis	0200000001010-101100100021000-1??10-00111200311100?001111--0-0100-1A110101111321--10000000-0000-01100101?111?00
Terpsichore cretata	02101?0101?00-101110101001100001000-0011000021111000311A0000-0110-10100101111120--A1000000-0000-110--101?111?10
Terpsichore cuencana	00101?0001?00-100001111001002-010010001101002100?0?0?1111000-0110-10110100101113--10000110-0000-110--101?111?10
Terpsichore cultrata	02000?0001000-101100100021001-00-10-001102003111?0?001111--0-0100-1D110101111321--10000000-0000-0110010A1111000
Terpsichore david smithii	00101?0001?00-10000111100100F-010010001101003000?0?001110000-0110-101100-0101113--11000110-0000-110--101?111?10
Terpsichore delicatula	0210100001000-101100100001010-11010-001102013001?0?001110--0-0100-10110101111A321101000000-0000-110--101?111?00
Terpsichore dilatata	01101?0001?00-100001111001002-010010001100002100?0?001111000-0110-101100-0111113--11000110-0000-110--1011111?10
Terpsichore hanekeana	02101?0011010-1011001000210A0-10-00-001102002110?0?001100--110100-10110101101123--10000000-0000-01100101?111000
Terpsichore lanigera	0210100001010-101100100021000-10000-00111200211100?001111--0-0100-1A110101111323--10000000-0000-011001010111000
Terpsichore lehmanniana	02100?0001000-100100003001003-10000-001102103101?0?01110000110100-101101011110F3--00000000-0000-01A00101?111000
Terpsichore leucosticta	0210110111?00-101100100021000-01000-001112003110?0?011111100-0110-10111100101003--10002000-0000-010--101?111?10
Terpsichore longicaulis	21101?1100?00-101101100021000-01000-001012003100?0?011111100-0110-101100-0001113--10002000-0000-010--101?111?10
Terpsichore longipilosa ined.	0110110011000-101100100021101001000-001102003000?0?011110100-0110-10110101111113--?0001100-0000-010--101?111?10
Terpsichore longisetosa	A?00110101?00-100100100011010?00-00-00110100400000?011110--0-0100-101100-1111323--10000000-0000-110--1?1?111?00
Terpsichore loxense ined.	01101?0001000-100001111001002-010010001100002100?0?001111000-0110-10110000111113--11000110-0000-110--1011111?10
Terpsichore loxense ined. Lehnert 1233	01101?0001000-100001111001002-010010001100002100?0?001111000-0110-10110000111113--11000110-0000-110--1011111?10
Terpsichore mollissima	02000?0?01?10-0------------------10-001102003111?0?001100--0-0100-1E110101110?21100002000-0000-01100101?111?00
Terpsichore nana	00101?0001?00-100011111001002-010010001101003100?0?001111000-0110-10110110101AF3--10000110-0000-010--101?111?10
Terpsichore pichinchae	0110110001000-100001111001002-01000-001101003100?0?001111--0-0110-10110101111113--10000010-0000-110--101?111?10
Terpsichore pichinchense	02101?0001?00-100001111011002-010010001101003111000001A00000-0110-10110101111123--10000110-0000-110--1011111?10
Terpsichore praeceps Jimeez 2173	1?101?0100?00-101100100021100001010-001102003111?0?001110--0-0110-10110101111113--10002000-0000-010--101?111?00
Terpsichore semihirsuta s.s. - Colombia	02101?0111000-101100000021000-01000-001102003100?0?011111100-0110-101110-0001003--10002000-0000-010--101?111?10
Terpsichore senilis	02000?0001010-101100000001001-10-10-001102003111?0?001100--0-0100-10110101101321--00000000-0000-01100100?111?00
Terpsichore sp. aff. alsopteris 1 - Bolivia	02101?0111000-101100100021000-01000-0011?2003100?0?001111--0-0110-10111100101113--10002000-0000-010--101?111?10
Terpsichore sp. aff. semihirsuta - Costa Rica	02101?0101?00-101100100021000-01000-001102003100?0?011111100-0110-101110-0001003--10002000-0000-010--101?111?10
Terpsichore sp. aff. semihirsuta 1 - Bolivia	0210110111000-101100100021000-01000-001102003000?0?011111100-0110-10111100001113--10002000-0000-010--101?111?10
Terpsichore sp. aff. semihirsuta 2 - Mexico	02101?0101?00-101100100021000-01000-001102003100?0?011111100-0110-10111100001113--10002000-0000-010--101?111?10
Terpsichore sp. aff. taxifolia - Colombia	01101?0101000-101100100021100001000-001102003100?0?011111100-0100-101100-0101113--?0001000-0000-110--101?111?10
Terpsichore sp. ined. aff. subtilis	02101?0101?00-101100100021000-010?0-001102002111?0?011111100-0110-10111101111113--1000??00-0000-?1?--101?111?10
Terpsichore sp. Sundue 1160	02101?0?01?00-101101100021000-01000-001102003100?0?011111100-0110-101100-1011003--10002000-0000-010--101?111?10
Terpsichore sp. Sundue 1167	02101?0?01?00-101110100021000-01000-001112003100?0?011111100-0110-10110100101113--1000???0-0000-?10--101?111?10
Terpsichore subscabra	0210110001000-101100100011010-01010-001102003001?0?001111--0-0100-0---------1AF21101000000-0000-010--101?111?00
Terpsichore subtilis	02101?0?01000-101110101021001-0??00-001102002111?0?01110000010110-1010010*111111--A0000000-0000-110--1011111?10
Terpsichore taxifolia - Brazil	0110110?01?00-101100000021101001000-001112003010?0?01?111100-0110-10110100001113--10001000-0000-010--101?111?10
Terpsichore taxifolia vel aff. - Colombia	0110110?01?00-101100000021101001000-001112003010?0?011111100-0110-10110100001113--10001000-0000-010--101?111?10
Terpsichore vascoi ined.	0210110101000-101100100021000-01000-001102003000?0?011111100-0110-10111100101003--10000000-0000-010--101?111?10
Terpsichore zeledoniana	0110110111000-101100100020---000-00-001112003100?0?011111100-0110-101110-0101003--10001000-0000-110--101?111?10
Xiphopteris conjunctisora	?200110001100-100101110110---000-00-001112002110?0?000000--0-0100-A00000-0*00-----??000100-0000-?10--1010111?00
Zygophlebia mathewsii	0210110111000-101100100020---001000-001112101102000010000001110-0-101101011112221-?0101010-00012010--101?111?00
Zygophlebia sectifrons	0210110111000-101100100020---001000-001112111102?0?000000001110-0-101000-00010221-?0101010-00012010--101?111?00

Table 1. Length, ci and ri values calculated for the optimization of each character employed in this study. Missing values are either characters that were deactivated, or uninformative.

No.	Character	Length	ci	ri
0	Growth Habit	9	22	30
1	Position of fronds			
2	Root insertion	10	10	76
3	Root proliferations	1	100	100
4	Rhizome symmetry	13	7	61
5	Stelar perforations			
6	Internode length	6	16	50
7	Branch bud	12	8	77
8	Phyllopodia	10	10	76
9	Rhizome branching	8	12	36
10	Blackened cortical tissue			
11	Setae on rhizomes	4	25	40
12	Hairs on rhizomes			
13	Terminal glandular cell of rhizome hairs			
14	Rhizome scales	3	33	0
15	Rhizome scale attachment	3	33	60
16	Rhizome scale shape	9	11	87
17	Rhizome scale cell wall induration	7	14	80
18	Rhizome scale lumen occlusion	5	20	42
19	Rhizome scale base shape	10	10	77
20	Rhizome scale shape	10	10	57
21	Rhizome scale concolorous vs. clathrate	7	28	91
22	Rhizome scale color	20	15	77
23	Rhizome scale irridescence	8	12	75
24	Rhizome scale luster	19	10	79
25	Rhizome scale marginal indument	15	6	69
26	Rhizome scale marginal indument distribut	8	12	63
27	Rhizome scale indument type	3	33	60
28	Rhizome scale seta color	11	27	84
29	Rhizome scale margins	6	16	44
30	Rhizome scale abax. and adax. surfaces	6	16	50
31	Rhizome scale apical pappilate cells	8	12	75
32	No. of pappilate cells on scale apex	7	14	40
33	Frond growth	3	33	66
34	Dimorphy of fronds	9	11	72
35	Expression of dimorphy	2	50	87
36	Leaf articulation	3	33	77
37	Petiole shape in x-section	1	100	100
38	Petiole cortex	1	100	100
39	Epidermis of petiole	7	14	50
40	Petiole, no. vascular bundles			
41	Petiole margins	18	11	65
42	Lamina base shape	8	12	53
43	Lamina apex shape	6	16	0
44	Lamina dissection at base	28	14	71
45	Pinna base shape	9	11	46
46	Pinna apex shape	16	6	48
47	Lamina texture	15	13	65
48	Leaf palisade parenchyma			
49	Lenght of cell arms in parenchyma	3	33	75
50	Postion of leaf vasculature			
51	Lamina margin black	2	50	0
52	Sclerenchyma on veins	24	20	68
53	Sclerenchyma of midrib visible abax.	12	8	59
54	Sclerenchyma of midrib visible adax.	16	6	65
55	Sclerenchyma of pinna costae visible abax	18	11	70

Table 1 cont. Length, ci and ri values calculated for the optimization of each character employed in this study. Missing values are either characters that were deactivated, or uninformative.

No.	Character	Length	ci	ri
56	Sclerenchyma of pinna costae visible adax	14	7	71
57	Sclerenchyma of veins visible abax.	1	100	100
58	Sclerenchyma of veins visible adax.			
59	Vein order	13	23	77
60	Secondary vein branching pattern	2	50	75
61	Vein fusion	3	33	60
62	Hydathodes	4	25	92
63	Cretaceous deposit of hydathodes	6	16	90
64	Laminar scales	1	100	100
65	Laminar scale coloration	1	100	100
66	Setae of fronds	5	20	86
67	Seta branching pattern			
68	Setae on petioles	4	25	25
69	Setae on adax midrib	11	9	28
70	Rachis setae uniform or bimetric	4	25	78
71	Setae present along margin of lamina	16	6	55
72	Distribution of marginal setae	4	25	40
73	Setae on adaxial lamina	16	6	57
74	Setae on abaxial lamina	15	6	46
75	Setae on adaxial pinna costa	20	5	40
76	Hairs on fronds	9	11	27
77	Branching pattern of hairs	16	18	63
78	No. cell in hairs	12	25	81
79	Shape of hair cells or hair branch cells	15	20	66
80	Color of capitate or glandular hair cells	2	50	0
81	Gland cell secretion			
82	Color of hair branch cells, excl. of glandular cells			
83	Marginal trichomidia along lamina margin	10	10	57
84	Soral receptacle	3	33	71
85	Sori distinct of confluent	2	50	75
86	Soral position	21	9	73
87	Distribution of sori	16	6	77
88	Outline of mature sorus	15	13	74
89	Sorus postion relative to surface	7	14	66
90	Angle of wall in immersed sori	4	25	57
91	Sori embossed on adax. surface	5	20	55
92	Margin of lamina infolded over sori	2	50	50
93	Tissue subtending receptacle	2	50	80
94	Paraphyses	4	25	75
95	Cells of paraphyses	3	66	75
96	Receptacular setae	14	7	62
97	Sporangial stalk width	1	100	100
98	Episporangial indument	4	25	76
99	Postion of episporangial indument	2	50	0
100	Aggregation of episporangial indument	1	100	100
101	Spore color	1	100	100
102	Spore number	4	50	0
103	Spore laesurae	2	50	80
104	Number of cells in newly shed spores			
105	Exospore surface	1	100	100
106	Gametophyte form	1	100	100
107	Rhizome developed in first cell division	1	100	100
108	Chromosome base no.			
109	*Acrospermum*	5	20	92
110	Aromatic odor when dry	1	100	100

Fig. 1. Strict consensus of 100,000 trees from first analysis including all taxa, L = 1341, CI = 9, RI = 47.

Fig. 2. Strict consensus of 100,000 trees from second analysis excluding *T. delicatula* and *T. subscabra*, L = 841, CI = 15, RI = 68.

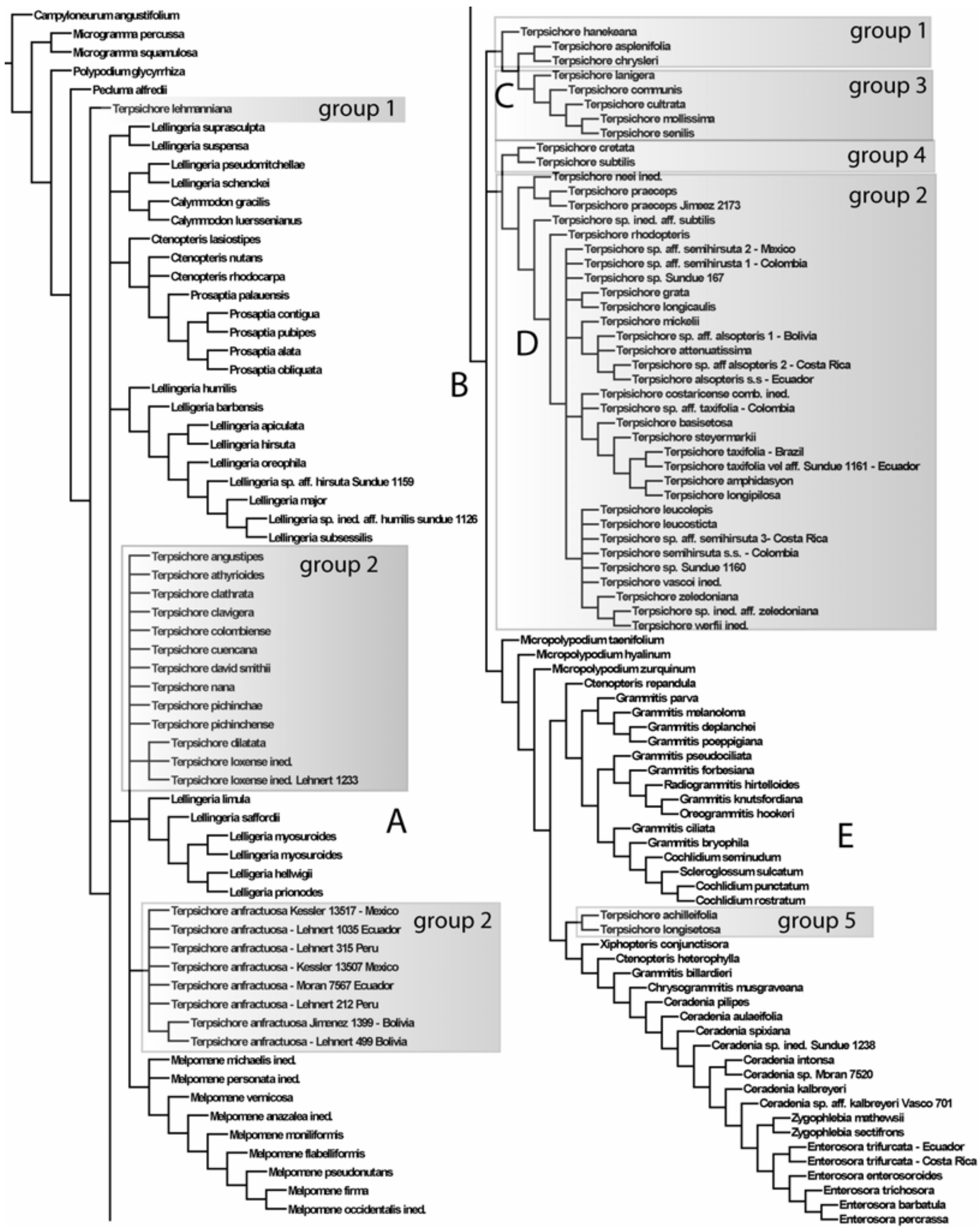

Fig. 3. Petiole of *Terpsichore atroviridis* showing two vascular bundles stained with phloroglucinol/HCL.

Fig. 4. Rhizome cross section of *Lellingeria major* showing dorsal perforations associated with leaves, and ventral perforations that are not associated with either leaves or roots.

CHAPTER 2

Systematics of grammitid ferns (Polypodiaceae): using morphology and plastid sequence data to resolve the circumscription of *Melpomene* and portions of the polyphyletic genera *Lellingeria* and *Terpsichore*.

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ABSTRACT:

Recent phylogenetic analyses of grammitid ferns (Polypodiaceae) have demonstrated that many genera recognized within this clade are not monophyletic. We focus on resolving the circumscriptions of some prominent neotropical genera by focusing on one clade identified in previous analyses that includes the monophyletic genus *Melpomene*, plus portions of two polyphyletic genera, *Lellingeria* and *Terpsichore*. Phylogenetic analyses using chloroplast markers *atpB*, *rbcL*, and *trnLF*, along with 111 morphological characters, resolve this ingroup as monophyletic and sister to a clade that includes *Ceradenia*, *Enterosora*, and *Zygophlebia*. Trees generated with morphological characters included in the analysis are used to circumscribe clades. *Melpomene* is clearly monophyletic, but is nested within *Lellingeria* in most trees. Ingroup species of *Terpsichore* form three well supported monophyletic groups that together are paraphyletic with regards to *Melpomene* plus *Lellingeria*. Two clades corresponding with species groups of *Terpsichore* are recognized as new genera.

KEYWORDS: morphology, character evolution, neotropical, *Acrospermum*, classification.

INTRODUCTION

Grammitid ferns constitute a monophyletic (Schneider & al., 2004) group of over 750 species (Parris, 2007) that is nested within the Polypodiaceae. Distributed primarily in tropical montane forests of the world, grammitids are distinguished by green spores with a trilete mark and sporangial stalks that are a single cell wide in the middle (Parris, 1990). One of the long-standing questions in the study of these ferns has been the number of clades recognized as genera. Prior to phylogenetic analysis, some pteridologists have recognized only one (Tryon & Tryon, 1982) and others up to 18 (Parris, 2003). The first phylogenetic study of grammitids (Ranker & al., 2004) found that out of twelve genera for which more than one species was included in the analysis, only three were recovered as monophyletic. Ranker & al. cited convergent evolution and the use of homoplastic characters by taxonomists to account for the problems in generic circumscription. Although these results have spawned some recent nomenclatural changes (e.g., Labiak & Matos, 2007; Parris, 2007), to date, a phylogenetic approach to resolving taxonomic problems established by Ranker & al. (2004) has not been undertaken (but see Lehnert, in press).

We focus here on resolving the generic circumscriptions within one clade identified in Ranker & al. (2004). This clade, which they called clade Va + Vb, includes the monophyletic genus *Melpomene*, plus portions of two polyphyletic genera, *Lellingeria* and *Terpsichore*. Together, these three genera constitute some of the most species-rich and widely recognized groups of grammitids in the Americas. Members of this ingroup can be distinguished from all other grammitids by a reliable combination of morphogical characters, including ventral root insertion, hydathodes, simple setae, hairs that are usually 1-furcate, sorus position, and glabrous sporangia. This clade includes the type species of *Lellingeria* and *Melpomene* but not that of *Terpsichore*. Therefore, establishing generic concepts here will resolve the circumscription of these two genera and establish relationships for the unplaced *Terpsichore* species. We address the following questions. Are clades Va + Vb monopyletic? Do *Melpomene*, and the portions of *Lellingeria* and *Terpsichore* that reside in our ingroup constitute separate monophyletic lineages that should be recognized as genera? Infrageneric species groups were circumscribed by Smith (1993) and Smith & al. (1991) for the genera *Terpsichore* and *Lellingeria* (Table 1), some of which are resolved as monophyletic in Ranker & al. (2004). With additional sampling, we can address which of these groups form clades, and identify the morphological characters that support them. What is the sister group to clade Va + Vb? Although not well supported in their analysis, Ranker & al. (2004) established the clade of *Ceradenia* plus *Enterosora* (clade VI) as a possible sister group for clade Va + Vb, these together constituting a large clade of primarily neotropical species defined by ventral root insertion.

To this end, we conducted phylogenetic analyses combining DNA plastid sequence data with an extensive morphological matrix in order to address the circumscription of grammitid genera. This study builds upon previous work of Ranker & al. (2004) by increasing taxon sampling within our study group, adding additional plastid data, and reexamining the characters used in our morphological matrix.

MATERIALS AND METHODS

Taxon sampling. — This study is based on 179 accessions, representing 128 ingroup taxa, and 24 taxa from the suspected sister group of the Va + Vb clade (clade VI of Ranker & al., 2004) (Appendix A). These were combined with a broad selection of grammitid taxa available to us that were previously published in Ranker & al. (2004), or Geiger & al. (2007). Together these constitute 14 genera of grammitid ferns, plus three genera of polypodioid ferns. Sampling is stronger among neotropical taxa, but contains enough paleotropical diversity to test our hypotheses.

Among ingroup taxa, sampling was heaviest within *Terpsichore* because it is morphologically heterogeneous and is the subject of a monograph by the first author. Our study includes samples from each of the groups delineated in Smith's (1993) informal classification of *Terpsichore* but does not include its type, *T. asplenifolia*, because this species in not related to the ingroup. Based on morphology (rhizome scales with setose surfaces as well as margins, geniculate petioles, setose sporangia capsules) we can determine the placement of *T. aspenifolia* in a clade (clade X of Ranker & al. 2004) unrelated to our ingroup. Table 1 summarizes ingroup sampling by listing the infrageneric groups of *Lellingeria* and *Terpsichore*, the number of samples included for each, and their ingroup status as informed by morphology in the light of Ranker & al. (2004).

In some cases multiple accessions of a single species were included in order to represent the range of variation within that species. The geographic provenance of a species is listed in the tree when multiple accessions of the same species differ considerably in their collection locality. In particular, the widespread and morphologically variable species *Terpsichore anfractuosa* is represented by ten accessions that serve to cover four morphologically distinct allopatric populations.

Several of the genera involved in this study are currently under monographic revision resulting in numerous unpublished species and unidentified 'problem' specimens. We choose to include some of these here in order to better represent the diversity present within these lineages. Terminals representing delineated but unpublished species are marked as 'ined.' in trees. Terminals for specimens that probably represent new species but which are not well understood by us at the time of writing are indicated by listing the collector and collection number in the tree. Morphological characters for such terminals are scored entirely from the specimens cited.

DNA extraction and amplification protocols. — This study utilizes sequences from three plastid loci: *atpB*, *rbcL,* and the *trnLF* intergenic spacer. Total genomic DNA was extracted from silica-dried tissue or herbarium specimens using either the CTAB method or using the DNeasy minikit (Qiagen) following the manufacturer's protocols. General laboratory protocols for amplifying *atpB*, *rbcL*, and *trnLF* were described in Ranker & al. (2004), Schuettpelz and Pryer (2007) (using primers ESRBCL1F, ESRBCL628F, ESRBCL654R, ESRBCL1361R), and Ranker & al. (2003), respectively. The resulting PCR products were sent to the High-Throughput Genomics Unit (HTGU), Department of Genome Sciences, Univ. of Washington, where they were purified using ExoSap-IT (USB Corporation). Cycle sequencing reactions were conducted using the amplification primers, and the BigDye terminator kit (Applied Biosystems, Foster City, California). Sequences were generated using an ABI 3100 or 3130 sequencer (Applied Biosystems, Foster City, California). Forward and reverse sequences obtained were edited and assembled using Sequencher 4.5 (Gene Codes Corporation, Ann Arbor, Michigan, USA). For some taxa we were unable to retrieve sequences from at least one of the 3 markers. In the combined data set these sequences were treated as missing data.

Morphological Data. — For each terminal in this study, 111 morphological and cytological characters were scored. Character states as they are scored are presented in chapter 1. All characters were scored as non-additive.

Sequence Alignment and Phylogenetic Analysis. — Sequences of individual markers were aligned using MUSCLE (Edgar, 2004). Morphological characters, data editing, tree viewing, and character optimizations were performed in Winclada (Nixon, 1999-2002). Indels of *trnLF* were coded using 2xRead.pl (Little, 2005), an application that generates a data matrix using the "simple gap coding" method of Simmons & Ochoterena (2000). Indels did not occur in the other two markers.

Maximum parsimony analyses were performed with TNT (Goloboff & al., 2001) implementing the parsimony ratchet (Nixon, 1999), using 1000 ratchets with 200 iterations per replicate, the up- and down-weights set to 5% each, followed by TBR-max branch swapping, holding 180,000 trees. Bootstrap support values were estimated from 1,000 replicates. Each replicate was performed with 10 ratchets holding 20 trees per replicate, keeping only the strict consensus. Each of the three plastid markers was analyzed independently and the combined plastid data set was analyzed both with and without the morphological data set. Optimizations are reconstructed as slow (DELTRAN) unless otherwise stated.

RESULTS

The three plastid genes, *atpB*, *rbcL*, and *trnLF*, had aligned lengths of 1266 bp, 1311 bp, and 608 bp, with 282 (22%), 285 (22%), and 233 (38%) parsimony-informative sites respectively. The *trnLF* indel coding provided an additional 130 characters, 65 (50%) of which were parsimony informative. The morphological matrix contained 19,869 cells, with total full ambiguity of 4,165 cells (20%), calculated as the sum of 1381 (6%) cells of missing data, and 2784 (14%) cells of inapplicable characters. Of the 111 morphological characters, six were not parsimony-informative, leaving the morphological matrix as 95% parsimony informative. Seven morphological characters (1, 10, 40, 48, 50, 104, 108) were deactivated because they were missing data from the majority of terminals. Thus, the 98 remaining morphological characters constituted 3% of the parsimony-informative characters in the combined matrix of plastid and morphological data.

Combined Plastid Data. — The parsimony analysis of the combined plastid data set (*atpB*, *rbcL*, *trnLF*, *trnLF* indels), was run until 180,000 most parsimonious trees were found and memory overflowed. The shortest trees are 3026 steps long, have a CI of .37, an RI of 0.79, and collapse at 56 nodes in the strict consensus tree. The strict consensus tree (Fig. 1) shows the ingroup resolved as monophyletic (100% BS support), supported as sister (92% BS) to the clade of *Ceradenia*, *Enterosora*, and *Zygophlebia* (100% BS). Among ingroup genera, only *Melpomene* is clearly monophyletic (100% BS). Ingroup members of *Terpsichore* are paraphyletic, and resolved as three distinct and well supported clades, here referred to as the *Terpsichore anfractuosa* clade (100% BS), the *Terpsichore taxifolia* clade (99% BS), and the *T. subscabra* clade (100%). The *Terpsichore anfractuosa* clade is sister to the remainder of the ingroup (96% BS), which in turn are supported as monophyletic themselves by 96% BS value. The *Terpsichore taxifolia* clade is sister to the remaining ingroup taxa including *Lellingeria*, *Melpomene*, and the *Terpsichore subscabra* clade. *Lellingeria* is monophyletic in some MP trees but paraphyletic in others. In the strict consensus tree, *Melpomene* forms a clade with the following: the *L. myosuroides* clade (100% BS), the species *L. hirsuta*, and a clade containing a broad sampling of *Lellingeria* species including its type (*L. apiculata*), here after referred to as *Lellingeria* pro parte (91% BS). Relationships within the clade, including monophyly or paraphyly of *Lellingeria* are not resolved.

Total Evidence. — Tree search of the combined data sets was run until 180,000 equally parsimonious trees were found and memory overflowed. The shortest length trees have 3956 steps, with a CI of 0.31, an RI of 0.77, and collapse at 39 nodes in the strict consensus. The relationships between clades returned by the combined data sets (Fig. 2) were similar to those generated by plastid data alone, but with a polytomy forming in the strict consensus tree between the *Terpsichore subscabra* clade, the *Terpsichore taxifolia* clade, and the clade of *Lellingeria* plus *Melpomene*. Bootstrap values of the clade supporting the ingroup as sister to the clade of *Ceradenia*, *Enterosora* and *Zygophlebia* were 42%, and supported by two morphological synapomorphies: ventral root insertion (2) and the presence of gland-like cells at the apex of rhizome scales (31). Morphological synapomorphies for the ingroup are blackish sclerenchyma visible along the abaxial pinna costae (55), two vein orders (59), and the presence of receptacular setae (96). The *Terpsichore anfractuosa* clade, the *Terpsichore subscabra* clade, and the *Terpsichore taxifolia* clade are each supported as monophyletic with 100% BS support, and eight (13, 27, 37, 44, 45, 79, 83), eleven (19, 21, 22, 28, 34, 35, 73, 82, 87, 88, 109), and six (7, 16, 24, 52, 63, 190) morphological synapomorphies, respectively. The clade of *Lellingeria* plus *Melpomene* is supported by two (21, 22) morphological synapomorphies and 98% BS support, with five (22, 25, 35, 41, 78) morphological synapomorphies and 100% BS value supporting the monophyly of *Melpomene* as nested within a paraphyletic *Lellingeria*. Morphological synapomorphies recovered in the combined analysis are illustrated on one randomly chosen most parsimonious tree (Fig. 3 A—F). Table 3 summarizes the taxa included in our major clades, including the number of species sampled, the total number of species expected to occur based on morphology and their placement sensu Smith (1993), Smith & Moran (1992), and Smith & al. (1991).

DISCUSSION

Analysis of combined data sets. — Although the overall topology is not affected, the inclusion of morphological data does affect terminal, or near terminal branches. One large change is a polytomy that forms between the clades of *T. subscabra*, *T. taxifolia*, and *Lellingeria* plus *Melpomene* (Fig. 2), a clade that has low BS values in the analysis of plastid data alone (Fig. 1). By comparison, Ranker & al. (2004) found that the inclusion of morphological data resulted in the loss of resolution in the backbone of their phylogeny, with a polytomy forming between their clades I—IV. In addition, the inclusion of morphological data into the analysis provides trees that can be used to establish clade memembership for unplaced taxa more reliably than when characters are mapped onto a tree.

Comparison with previous studies. — The overall topology presented here is similar to that found by Ranker & al. (2004). Relationships among our major ingroup clades also correspond with those sampled by Ranker & al. (2004) except that *Lellingeria* and *Melpomene*, which are affected here by the inclusion of the *L. myosuroides* clade, which was not sampled in the Ranker & al. (2004) analysis. Here, the inclusion of the *L.*

myosuroides clade suggests that *Lellingeria* may be paraphyletic. Geiger & al. (2007) found the same result in their study, which focused on the placement of *L. saffordii*, a Hawaiian endemic of the *L. myosuroides* clade.

This analysis differs from previous studies by finding strong support for the clade of *Ceradenia* plus *Enterosora* and *Zygophlebia* as sister to our ingroup (Figs. 1, 2). Bootstrap values were 92% for this clade in the plastid-only analysis. This sister group relationship was also supported by the MP strict consensus tree of Ranker & al. (2004) but without strong BS or posterior probability values. They found equal support from ML and PP analyses for the clade of Old World tropical Asian genera as sister to our ingroup clade. This latter clade of Old World genera was also found as sister to the clade corresponding to our ingroup in the broad study of fern phylogeny of Schuettpelz & Pryer (2007) but again with weak PP support. In our study, the inclusion of morphological data provides two morphological synapomorphies: ventral root insertion (2) and the presence of gland-like cells at the apices of rhizome scales (31). We also found that *Zygophlebia* belongs to this clade. Although the placement of *Zygophlebia* among these congeners was anticipated by Bishop (1989) when he described it, its relationship recovered here--nested within *Enterosora* rather than within or as sister to *Ceradenia*-- is new, and was not anticipated by previous workers (Bishop, 1989; Rakotondrainibe & Deroin, 2006).

Outgroup relationships — Although not specifically designed to address relationships within the sister group, our study supports some long-held hypotheses about this group of neotropical non-hydathodous grammitids that should be noted (Fig. 3 C). The clade formed by *Ceradenia*, *Enterosora* and *Zygophlebia* is supported by the presence of branch buds along the rhizome (7), rhizome scales with turgid cells (16), fronds that lack hydathodes (62), with simple (77) hairs composed of more than 3 cells (78), and medial sori (86). *Ceradenia* itself is supported by lustrous rhizome scales (24) and paraphyses (94) that bear globose glandular branch cells (95), the latter being the primary distinguishing character used by Bishop (1989) to establish his new genus. He also used the presence of gaps in the ventral side of the stele, which he termed "accessory stelar perforations," as evidence for the separation of *Zygophlebia* from other grammitids, and from *Ceradenia* in particular. We find that these gaps, which create a perforated dictyostele, are widespread in the grammitids and do not distinguish clades; however, a perforated dictyostele may in fact be a synapomorphy for the Polypodiaceae, Davalliaceae, and Oleandraceae.

We find *Ceradenia* resolved as two clades that correspond to the two subgenera deined by Bishop (1988). *Ceradenia* subgenus *Ceradenia* Bishop, represented here by three species (four terminals), is supported by radially symmetrical rhizomes (4), which lack scales (14), and by laminar hairs bearing globose glandular branch cells (79) that secrete a whitish wax (80). Each of these characters were cited by Bishop in his original description of the subgenus. Bishop (1988) included one additional character, short petioles, which was not scored in our matrix because we excluded quantitative characters. *Ceradenia* subgenus *Filicipectin* Bishop, represented here by eight species (10 terminals), is supported by the presence of phyllopodia (8), petioles with the outermost layer of cells darkly sclerotized (39), a truncate blade base (42), thickened laminae (47), blackish sclerenchyma present on the pinna costae and first-order veins (52), and trichomidia present along the laminar margins (83). Dorsiventral rhizomes and laminae with hairs that lack globose glandular branch cells, characters that were cited by Bishop (1988) for distinguishing subgenus *Filicipectin*, are not synapomorphic for the subgenus in our analysis. Nonetheless, they are still useful diagnostic characters for the genus. Two additional characters used by Bishop (1988), petiole length and spore size, were not scored in our matrix because we did not score quantitative characters.

The Terpsichore anfractuosa clade. — The *Terpsichore anfractuosa* clade (Fig. 3 D) is an assemblage of species that had either been placed in group 2 of Smith's (1993) informal classification of *Terpsichore*, or considered incertae sedis at that time. Only five species that belong to this clade were known to Smith at the time *Terpsichore* was published in 1993.

Four additional species belonging to this clade have been published since then (León & Smith, 2003; Sundue & Kessler, 2008), but its recognition as a taxonomic group has not previously been suggested. This clade is currently the subject of monographic revision by the first author who estimates that it contains 17 species. Morphological synapomorphies for this clade are numerous, including dark-reddish (22) clathrate rhizome scales (21) with a cordate base (19), and margins with reddish-colored setae (28), hemi-dimorphic fertile fronds (34) where the fertile portion of the lamina is more setose than sterile portions of the lamina (35), the loss of setae on the adaxial lamina surface (73), and slightly elliptic sori (88) that are confined to the distal portion of the blade. The presence of *Acrospermum* ascomes and mycelia (109) also acts as a synapomorphy for this clade. This epibiotic bitunicate ascomycete fungus can be found on nearly every specimen on all of the species in this clade. Under high magnification, *Acrospermum* mycelia can be seen encircling and entering stomata where they presumably derives nutrition from the fern host without incurring any apparent harm.

The ten exemplars included of *Terpsichore anfractuosa*, which represent some of the geographic and morphological variation in that species, are resolved as monophyletic with strong BS values (100%) in both of our analyses. They are sister to all other species of this clade. These *Terpsichore anfractuosa* accessions are united by having proliferous roots (3) by which new plants are produced asexually, ovate

(20) and iridescent (23) rhizome scales, and petioles that are distally marginate (41). The wide distribution of this species, from Mexico to Bolivia, the Guianas, and West Indies, contrasts with the remainder of the clade, which is composed of narrowly-restricted species. Among the accessions included here, plants from disparate geographic areas are found to be closely related, and no obvious geographic pattern is revealed.

The remaining species of the *Terpsichore anfractuosa* clade are found primarily along the eastern slope of the Andes from Venezuela and Colombia to Bolivia, or among the central volcanic highlands of Ecuador, with one species (*T. angustipes* (Copel.) A. R. Sm.) endemic to the western slope of the Andes in the Chocó region of Colombia. Morphological synapomorphies uniting these species include rhizome scales with indurate cell walls (17), terete petioles (41), basally 1-pinnate laminae (44), with the dark sclerenchyma of the rachis visible adaxially (54), and cretaceous hydathodes (63). By their lack of monophyly, we also see support for the taxonomic distinction of both *T. nana* Sundue & Kessler and *T. dilatata* Sundue & Kessler, as distinct from *T. david-smithii*, to which they had previously been referred (Sundue & Kessler, 2008). This is also true of *T. colombiensis* ined., which has been lumped under *T. pichinchae*.

The Terpsichore subscabra clade. — *Terpsichore subscabra* and its sister species *T. delicatula* are two morphologically similar species unique among grammitids in having hairs with translucent clavate glands that secrete a sticky exudate. Morphological evidence (2, 31, 54, 55, 59) clearly places them within the ingroup, but a close affinity among ingroup taxa cannot be seen. Data from plastid markers alone support these two species as sister to the clade of *Lellingeria* plus *Melpomene* but with low bootstrap values (64%). Ranker & al. (2004) found this same topology with 88% BS support and 100% posterior probability. Total evidence supports this pair of species as either sister to the clade of *Lellingeria* plus *Melpomene* or to the *Terpsichore taxifolia* clade. In the latter case, rhizome scales with turgid cells (16) is a synapomorphy for that sister grouping (Fig. 3 E).

Lellingeria. — *Lellingeria* is a genus of about 70 species (P. Labiak, pers. com.) that are primarily distributed in the neotropics. Smith & al. (1991) established an informal classification of four species groups, the *L. mitchellae* group, the *L. suprasculpta* group, the *L. myosuroides* group, and the *L. apiculata* group, the last of which includes the type. Ranker & al. (2004) demonstrated the polyphyly of *Lellingeria* showing that species included in the *L. mitchellae* group of Smith & al. (1991) are unrelated to *Lellingeria* pro parte; these are not discussed further here because they reside outside of the study group. *Lellingeria* pro parte was recovered as sister to *Melpomene* in Ranker & al. (2004), but a smaller study with increased sampling of *Lellingeria*, Geiger & al. (2007), found a paraphyletic *Lellingeria* with *Melpomene* nested within.

Our analysis includes members from the remaining three groups defined by Smith & al. (1991), the *L. myosuroides* group, the *L. apiculata* group, and the *L. suprasculpta* group. Our expanded analysis supports either a paraphyletic *Lellingeria* pro parte with *Melpomene* nested within it (total evidence) (Fig. 2) or a polytomy formed by *Melpomene*, the *L. myosuroides* group, *L. hirsuta*, and the remainder of *Lellingeria* pro parte (plastid data alone) (Fig. 1). In both analyses, we find strong support for a monophyletic *L. myosuroides* group (100% BS) defined by the morphological synapomorphies of radially symmetrical rhizomes (4) the presence of branch buds (7), and ovate (20) scales with reddish setae (28) that are restricted to the scale apex (26), the loss of setae upon leaves (66), hairs bearing acicular cells (79), elongate sori (88), and hemidimorphic fronds expressed as fertile portions of fertile fronds being less dissected than sterile portions (35) (Fig. 3 E). Of these, characters 26 and 35 were cited by Smith & al. (1991) for this group. The *L. myosuroides* group contains about 13 species and is unique among groups of *Lellingeria* by extending beyond the neotropics, with species distributed in Africa, Madagascar, and the Pacific Islands as well (Smith & al., 1991).

The remaining taxa, *Lellingeria* pro parte, are supported as monophyletic in our total evidence analyses by having non-lustrous rhizome scales (24) with whitish (28) marginal setae, the loss of setae one the leaves (66), and medial sori (86). This clade includes four species included in the *L. apiculata* group, as well as *L. suprasculpta* — the single representative of the *L. suprascultpa* group included by us, and five species that were not placed to group by Smith & al. (1991).

In their original description, Smith & al. (1991) cited radially symmetrical rhizomes, clathrate scales, and forked hairs with an acicular branch cell as diagnostic for *Lellingeria*. They also mentioned that sunken sori and hyaline setae along the margins of rhizome scales as characters of frequent occurrence in *Lellingeria*. We find that radially symmetrical rhizomes (4) are found only in the *Lellingeria myosuroides* group and the unrelated *Lellingeria mitchellae* group, and that *Lellingeria* pro parte has bilaterally symmetrical rhizomes. We also restrict the presence of whitish rhizome scale setae (28) to *Lellingeria* pro parte; when present in the *L. myosuroides* group, setae of scale margins are reddish. Most species of *Lellingeria* have characteristic pale hairs with at least one cell that is acicular (76, 77, 78, 79), but these are lost in *L. suspensa* and *L. suprasculpta* so that the character does not optimize as a synapomorphy for the clade in this study. This type of hair can also be found in the tropical Asian genus *Prosaptia*, but those differ by being reddish in color.

Melpomene. — *Melpomene* was distinguished from *Grammitis* by Smith & Moran in 1992 who recognized 20 species. They distinguished the genus by its rhizome scales, which are clathrate, basally cordate, and entire except at the apex where they are provided with 1-10 minute papillae. The authors also noted a peculiar sweet aroma emitted by dried specimens. This odor is caused by coumarins, which are unique to *Melpomene*. The circumscription of *Melpomene* has not been questioned except for the exclusion of one species, now combined as *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A. R. Sm. (León & Smith, 2003). The monophyly of *Melpomene* was confirmed by Ranker & al. (2004), who included three species (four terminals). *Melpomene* has recently been the subject of monographic revision by M. Lehnert (unpublished) who recognizes 29 species and 10 varieties.

Our analysis, based on eight species including the type (*M. moniliformis* (Lag. ex Sw.) A. R. Sm. & R. C. Moran, does not dispute the monophyly of the genus but does call into question how it is defined and diagnosed. In our analysis (Fig. 3 E), synapomorphies for *Melpomene* include reddish-brown rhizome scales (22), with entire margins (25), petioles that are distally marginate (41), hairs that are composed of more than three cells (78), and the coumarin odor (110). Only the last character state is unique to *Melpomene;* the others occurr in other genera as well. The presence of a papillate cell upon rhizome scale apices (31), which was thought to be unique to *Melpomene* by Smith & Moran (1992), was found to be widespread among grammitid ferns in this study and act as a synapomorphy uniting the ingroup with its sister clade. The presence of papillate cells (32) at the apex of rhizome scales is not unique to

Melpomene either, although its occurrence is rare elsewhere; multiple gland-like cells also appear in *Ceradenia* sp. ined. 1, and in *Enterosora trifurcata*. As these cells are difficult to observe, and easily broken off of specimens, they might be found to be more widespread in the grammitid ferns. Two other characters used by Smith and Moran (1992) to distinguish *Melpomene* -- clathrate scales (21) with an auriculate base (19) -- are found here to unite *Melpomene* with the *Lellingeria myosuroides* clade. These two characters also occur together in the *Terpsichore anfractuosa* clade; which is why *Terpsichore anfractuosa* was included in *Melpomene* by Smith & Moran (1992). Additional diagnostic characters for *Melpomene* include the presence of hydathodes (62) that are not cretaceous (63) and iridescent rhizome scales (23).

Melpomene is a primarily neotropical genus with a single species, *M. flabelliformis*, present in Africa, Madagascar, and the Mascarenes. *Melpomene flabelliformis* is nested among neotropical congeners in both our total-evidence and molecular analysis suggesting that its trans-Atlantic (including Madagascar) distribution results from long-distance dispersal from the neotropics to the Old World. *Melpomene flabelliformis* has a reduced spore number of 16 (102), suggesting that the species may be apogamous, which might promote its success as a long-distance disperser.

The Terpsichore taxifolia clade. — The *Terpsichore taxifolia* clade is supported by 100% BS values in both analyses and by the morphological synapomorphies of glossy (24) rhizome scales with turgid cells (16), dark sclerenchyma present along the pinna costae and first order veins (52), cretaceous hydathodes (63), and the presence of *Acrospermum* ascomes (109) (Fig. 3 F). The fundamental bifurcation of this clade resolves *Terpsichore subtilis* and *T. cretata*, group four of Smith's (1993) informal classification of *Terpsichore*, as sister to a clade of species that were placed in Smith's group two or which have been described or delineated since then. These terminals constitute what is known informally as the "*Terpsichore taxifolia* group," and are united by basally 1-pinnate laminae (44), pinna costae (56) and veins (57) with dark sclerenchyma that is visible on the abaxial side of the lamina, and medial sori (86). Whereas grammitids as a whole are known for having rare and localized species (Smith & Kessler, 2008), the *T. taxifolia* group contains relatively widespread and frequently collected species. This might be due to their large size compared to most other grammitid ferns. This clade is currently the subject of monographic revision by the first author, who recognizes ca. 30 species distributed in humid montane forests from southern Mexico to Bolivia, the Guianas, southeastern Brazil, and the West Indies. The species included in this study are resolved as two well-resolved clades: the clade including *Terpsichore taxifolia* and the clade which includes the well-known species *T. semihirsuta* and *T. alsopteris*. The clade including *T. taxifolia*, which includes about seven species, is supported by having rhizome scales with setae restricted to the scale apex (26), although the number of setae present may vary. The *T. semihirsuta* clade, including about 20 species, is supported by phyllopodia (8), lack of receptacular setae (96) supramedial sori (86), and rachis setae of two distinctly different lengths (70). The position of two species, *T. zeledoniana* and *T. pacifica* ined., are not well supported. These terminals form a polytomy along with the other clades in strict consensus trees of our analyses.

One example of a species being non-monophyletic occurs in our analysis here, with examplars of *Terpsichore* sp. aff. *semihirsuta* 1 from Bolivia forming a clade separate from those of Peru, Ecuador, and Colombia. Vouchers of these terminals have identical character combinations and do not differ appreciably in quantitative characters which are not scored in our analysis. The polyphyly of this taxon may represent cryptic speciation not detected with morphology or could have resulted if the taxon is of hybrid origin, in which case the two clades represent plastid characters inherited from each of the two parental taxa.

Nomenclatural consequences. — At present, we can solve some but not all of the nomenclatural problems raised by our results. Among ingroup genera, only *Melpomene* is clearly monophyletic. *Terpsichore* is resolved as paraphyletic in all analyses, and *Lellingeria* is resolved as monophyletic in some MP trees based on plastid data but is paraphyletic in others; it is paraphyletic in our total evidence analysis. The maintenance of monophyletic genera necessitates numerous nomenclatural changes for any given solution. We favor the retention of the established genera *Melpomene* and *Lellingeria* because they are well known and easily diagnosed, and we therefore reject the possible solution of combining all of the ingroup under *Lellingeria*, the oldest generic type. Similarly, we reject the solution of recognizing the *Terpsichore anfractuosa* group as one genus and the remainder of the ingroup as *Lellingeria*. Although diagnosable in either case, these genera would be too polymorphic and too large to be of value. We favor the recognition of both the *Terpsichore anfractuosa* clade and the *T. taxifolia* clade at the generic level. Both clades are clearly monophyletic, easily diagnosed, and morphologically distinct from other clades. Further sampling of *Lellingeria* is required before a nomenclatural solution can be proposed for those species. While additional data may argue for a monophyletic *Lellingeria*, the *L. myosuroides* group may be better described as a distinct lineage from *Lellingeria* pro parte. Because its phylogenetic position is uncertain, we also refrain from proposing a nomenclatural solution for the *Terpsichore subscabra* clade.

Table 1. Summary of infrageneric groups recognized in *Lellingeria* (Smith & al., 1991) and *Terpsichore* (Smith, 1993), the number of species estimated for these groups, the number of species included in this study, their ingroup status, and their placement to clade in Ranker & al. (2004).

Genus	Infrageneric group	# of spp. included in group	# of spp. sampled here	Ingroup status	Clade as found by Ranker & al., 2004
Lellingeria	*apiculata* group	7	4	ingroup	Va
Lellingeria	*mitchellae* group	4	2	outgroup	VII
Lellingeria	*myosuroides* group	13	4	ingroup	Va
Lellingeria	*suprasculpta* group	3	1	ingroup	--
Lellingeria	unplaced to group	ca. 45	7	ingroup	--
Terpsichore	Group 1	12	2	outgroup	X
Terpsichore	Group 2	13	6	ingroup	Va, Vb
Terpsichore	Group 3	16	4	outgroup	VII
Terpsichore	Group 4	2	2	ingroup	Va
Terpsichore	Group 5	3	2	outgroup	IVa
Terpsichore	unplaced to group	1	17	ingroup	--

Table 2. Summary of results showing for each ingroup clade the number of species included here, the total number of species estimated based on morphology, and previous classification. Infrageneric group names for *Lellingeria* and *Terpsichore* are from Smith & al. (1991) and Smith (1993) respectively.

Clade	# spp. included	Total # spp. estimated	Previous classification
I	13	17	*Terpsichore* group 2 or unplaced
II	2	2	*Terpsichore* group 3
III	10	55	*Lellingeria apiculata* group and *suprasculpta* group
IV	5	13	*Lellingeria myosuroides* group
V	8	29	*Melpomene*
VIa	2	2	*Terpsichore* group 4
VIb	23	30	*Terpsichore* group 2 or unplaced

Appendix A. Voucher information and Genbank accession numbers for taxa used in this study. A dash indicates that the marker was not sampled. The $ indicates Genbank vouchers to be aquired.

Calymmodon gracilis (Fee) Copel., Ranker 1771 & Trapp (COLO, UC), Papua New Guinea, *atpB:* $, *rbcL:* $, *trnLF:* $; *Calymmodon luerssenianus* (Domin) Copel., Ranker 1771 & Trapp (COLO, UC), Papua New Guinea, *atpB:* AY459452, *rbcL:* AY460618, *trnLF:* --; *Campyloneurum angustifolium* (Sw.) Fee, Chisaki & Carter 1004 (UC), Costa Rica, *atpB:* AY459515, *rbcL:* AF470344, *trnLF:* $; *Ceradenia aulaeifolia* L. E. Bishop ex A. R. Sm., Rojas, A. 3232 (CR, INB, MO, UC), Costa Rica, *atpB:* AY459453, *rbcL:* AY460619, *trnLF:* $; *Ceradenia aulaeifolia* L. E. Bishop ex A. R. Sm., Sundue et al. 1705 (INB, NY, UC), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia fucoides* (H. Christ) L. E. Bishop, Sundue et al. 1766 (INB, NY, UC), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia intonsa* L. E. Bishop, Sundue & Vasco 1321 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia jungermannioides* (Klotzsch) L.E. Bishop, A. R. Smith 2576 (UC), Costa Rica, *atpB:* AY459454, *rbcL:* AY460620, *trnLF:* --; *Ceradenia kalbreyeri* (Baker) L. E. Bishop, Sundue & Vasco 1213 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia kalbreyeri* (Baker) L. E. Bishop, Sundue et al. 1759 (INB, NY, UC), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia pilipes* (Hook.) L. E. Bishop, Rojas, A. 3233 (INB, NY), Costa Rica, *atpB:* AY459456, *rbcL:* AY460622, *trnLF:* $; *Ceradenia pilipes* (Hook.) L. E. Bishop, Sundue 1120 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia sp*. Moran 7520, Moran 7520 (QCA), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia sp*. aff. *kalbreyeri* (Baker) L. E. Bishop, Vasco & Sundue 701 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia sp.* ined. 1, Sundue & Vasco 1238 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia sp*. ined. 1, Sundue & Vasco 1242 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Ceradenia spixiana* (Mart. ex Mett.) L.E. Bishop, Salino 3008 (UC), Brazil, *atpB:* AY459457, *rbcL:* AY460623, *trnLF:* --; *Chrysogrammitis musgraveana* (Baker) Parris, Kessler 12570 (UC), Sabah, *atpB:* AY459458, *rbcL:* AY460624, *trnLF:* $; *Cochlidium punctatum* (Raddi) L. E. Bishop, Salino 3127 (BHCB, UC), Brazil, *atpB:* AY459520, *rbcL:* AY460625, *trnLF:* $; *Cochlidium punctatum* (Raddi) L. E. Bishop, Silva 3914 (UC), Brazil, *atpB:* $, *rbcL:* $, *trnLF:* $; *Cochlidium rostratum* (Hook.) Maxon ex C. Chr., I. Valdespino & J. Aranda 180 (UC), Panama, *atpB:* AY459459, *rbcL:* AY460626, *trnLF:* --; *Cochlidium seminudum* (Willd.) Maxon, S. R. Hill 29102A no voucher, Dominican Republic, *atpB:* AY459460, *rbcL:* AY460627, *trnLF:* --; *Ctenopteris heterophylla* (Labill.) Tindale, A. R. Smith 2614 (UC), New Zealand, *atpB:* AY459461, *rbcL:* AY460629, *trnLF:* --; *Ctenopteris heterophylla* (Labill.) Tindale, Parris 12419 (AK), New Zealand, *atpB:* AY459462, *rbcL:* AY460630, *trnLF:* --; *Ctenopteris* *lasiostipes* (Mett.) Brownlie, Hodel 1448 (UC), New Caledonia, *atpB:* AY459463, *rbcL:* AY460630, *trnLF:* --; *Ctenopteris nutans* (Blume) J. Sm., Ranker 1765 & Trapp (COLO, UC), Papua New Guinea, *atpB:* AY459464, *rbcL:* AY460631, *trnLF:* --; *Ctenopteris repandula* (Mett.) C. Chr. & Tardieu, Ranker 1767 & Trapp (COLO, UC), Papua New Guinea, *atpB:* AY459466, *rbcL:* AY460633, *trnLF:* --; *Ctenopteris rhodocarpa* Copel., Ranker 1764 & Trapp (COLO, UC), Papua New Guinea, *atpB:* AY459467, *rbcL:* AY460634, *trnLF:* --; *Enterosora barbatula* (Baker) Parris, D. Strausberg 28-5-93 (REU), La Réunion, *atpB:* --, *rbcL:* --, *trnLF:* $; *Enterosora enterosoroides* (H. Christ) A. Rojas, Sundue 1172 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* --, *trnLF:* $; *Enterosora percrassa* (Baker) L. E. Bishop, Moraga & Rojas 508 (INB), Costa Rica, *atpB:* AY459468, *rbcL:* AY460635, *trnLF:* $; *Enterosora percrassa* (Baker) L. E. Bishop, Sundue et al. 1665 (INB, NY, UC), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Enterosora trichosora* (Hook.) L. E. Bishop, Moran 7659 (NY, QCA), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Enterosora trifurcata* (L.) L. E. Bishop, Moran 7515 (NY, QCA), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Enterosora trifurcata* (L.) L. E. Bishop, Ranker 1608 (COLO), Puerto Rico, *atpB:* AY459521, *rbcL:* AY460636, *trnLF:* $; *Enterosora trifurcata* (L.) L. E. Bishop, Sundue 1774 et al. (INB, NY, UC), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Grammitis billardieri* Willd., Parris 12421 (AK), New Zealand, *atpB:* AY459469, *rbcL:* AY460637, *trnLF:* --; *Grammitis ciliata* Colenso, A. R. Smith 2615 (UC), New

Zealand, *atpB:* AY459470, *rbcL:* AY460638, *trnLF:* --; *Grammitis deplanchei* Copel., Hodel 1450 (UC), New Caledonia, *atpB:* AY460630, *rbcL:* AY459463, *trnLF:* $; *Grammitis forbesiana* W. H. Wagner, Ranker 1321 (COLO), Hawaii, U.S.A., *atpB:* AY460640, *rbcL:* AY459472, *trnLF:* --; *Grammitis knutsfordiana* (Baker) Copel., J. Game 95-81 (UC), Fiji, *atpB:* AY459474, *rbcL:* AY362342, *trnLF:* $; *Grammitis melanoloma* (Cordem.) Tardieu, Ranker & Adsersen 1504 (COLO), La Réunion, *atpB:* AY459475, *rbcL:* AY460643, *trnLF:* $; *Grammitis parva* (Brause) Copel., Ranker 1763a (COLO, UC), Papua New Guinea, *atpB:* AY459476, *rbcL:* AY460644, *trnLF:* --; *Grammitis poeppigiana* (Mett.) Pic. Serm., C. Taylor 6072 (UC), Chile, *atpB:* AY459479, *rbcL:* AY460646, *trnLF:* --; *Grammitis poeppigiana* (Mett.) Pic. Serm., Weber 13772 (COLO), Australia, *atpB:* AY459478, *rbcL:* AY460647, *trnLF:* --; *Grammitis pseudociliata* Parris, Parris 12420 (AK), New Zealand, *atpB:* AY459477, *rbcL:* AY460645, *trnLF:* --; *Lellingeria apiculata* (Kunze ex Klotzsch) A. R. Sm. & R. C. Moran, Salino 3009, Brazil, *atpB:* AY459480, *rbcL:* AY362343, *trnLF:* $; *Lellingeria apiculata* (Kunze ex Klotzsch) A. R. Sm. & R. C. Moran, A. Rojas & al. 3298 (UC), Costa Rica, *atpB:* AY459481, *rbcL:* AY460648, *trnLF:* --; *Lellingeria barbensis* (Lellinger) A. R. Sm. & R. C. Moran, Ranker 1857 (COLO), Costa Rica, *atpB:* --, *rbcL:* --, *trnLF:* $; *Lellingeria hellwigii* (Mickel & Beitel) A. R. Sm. & R. C. Moran, J.T. Mickel 4324 & R.L. Hellwig (NY, UC), Mexico, *atpB:* --, *rbcL:* --, *trnLF:* $; *Lellingeria hirsuta* (Baker ex Hemsl.) A. R.

Sm. & R. C. Moran, A. Rojas & E. Fletes 3145 (UC), Costa Rica, *atpB:* AY459482, *rbcL:* AY460649, *trnLF:* --; *Lellingeria hirsuta* A. R. Sm. & R. C. Moran, A. Rojas & E. Fletes 3145 (UC), Costa Rica, *atpB:* AY459482, *rbcL:* AY460649, *trnLF:* $; *Lellingeria humilis* (Mett.) A. R. Sm. & R. C. Moran, Sundue & Vasco 1289 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria limula* (H. Christ) A. R. Sm. & R. C. Moran, Moraga & Rojas 501 (UC), Costa Rica, *atpB:* AY459523, *rbcL:* AY460650, *trnLF:* --; *Lellingeria limula* (H. Christ) A. R. Sm. & R. C. Moran, Sundue et al. 1736 (INB, NY, UC, UPCB), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria limula* (H. Christ) A. R. Sm. & R. C. Moran, Sundue et al. 1761 (INB, NY, UC, UPCB), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria major* (Copel.) A. R. Sm. & R. C. Moran, Sundue 1147 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria major* (Copel.) A. R. Sm. & R. C. Moran, Sundue 1171 (NY, QCA, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria myosuroides* (Sw.) A. R. Sm. & R. C. Moran, Rakotondrainibe 6882 (P), La Réunion, *atpB:* --, *rbcL:* --, *trnLF:* $; *Lellingeria myosuroides* (Sw.) A. R. Sm. & R. C. Moran, A. Liogier 17085 (NY), Dominican Republic, *atpB:* --, *rbcL:* --, *trnLF:* $; *Lellingeria oreophila* (Maxon) A. R. Sm. & R. C. Moran, Sundue 1134 (NY, QCA, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria prionoides* (Mickel & Beitel) A. R. Sm. & R. C. Moran, J.T. Mickel 4270 & R.L. Hellwig (NY, UC), Mexico, *atpB:* --, *rbcL:* --, *trnLF:* $; *Lellingeria pseudomitchellae* (Lellinger) A. R. Sm. &

R. C. Moran, A. Rojas 3005 (MO), Costa Rica, *atpB:* AY459484, *rbcL:* AY460652, *trnLF:* --; *Lellingeria saffordii* (Maxon) A. R. Sm. & R. C. Moran, Ranker 1892 (PTPG), Hawaii, *atpB:* --, *rbcL:* $, *trnLF:* $; *Lellingeria schenckei* (Hieron.) A. R. Sm. & R. C. Moran, Salino 4547 (BHCB, UC), Brazil, *atpB:* AY460651, *rbcL:* AY459483, *trnLF:* $; *Lellingeria sp*. aff. *hirsuta* A. R. Sm. & R. C. Moran, Sundue 1159 (NY, QCA, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria sp*. ined., Sundue 1126 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria subsessilis* (Baker) A. R. Sm. & R. C. Moran, A. Rojas 3022 & M. Mata (UC), Costa Rica, *atpB:* AY460653, *rbcL:* AY459485, *trnLF:* $; *Lellingeria subsessilis* (Baker) A. R. Sm. & R. C. Moran, Sundue 1170 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria subsessilis* (Baker) A. R. Sm. & R. C. Moran, A. Rojas 3022 & M. Mata (UC), Costa Rica, *atpB:* AY459485, *rbcL:* AY460653, *trnLF:* $; *Lellingeria suprasculpta* (H. Christ) A. R. Sm. & R. C. Moran, Sundue et al. 1767 (INB, NY, UC, UPCB), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria suspensa* (L.). A. R. Sm. & R. C. Moran, Vasco & Sundue 625 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Lellingeria suspensa* (L.). A. R. Sm. & R. C. Moran, Vasco & Sundue 704 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Melpomene anazalea* Sundue & Lehnert ined., Sundue & Vasco 1290 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Melpomene firma* (J. Sm.) A. R. Sm. & R. C. Moran, Sundue 1072 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Melpomene flabelliformis* (Poir.), P. Sanchez-B. 183 (UC), Colombia, *atpB:* AY459488, *rbcL:* AY460656, *trnLF:* --; *Melpomene moniliformis* (Lag. ex Sw.) A. R. Sm. & R. C. Moran, M. Moraga & A. Rojas 446 (INB), Costa Rica, *atpB:* AY459486, *rbcL:* AY460654, *trnLF:* $; Melpomene moniliformis (Lag. ex Sw.) A. R. Sm. & R. C. Moran, M. Moraga & A. Rojas 446 (INB), Costa Rica, *atpB:* AY460654, *rbcL:* AY459486, *trnLF:* $; *Melpomene occidentalis* Lehnert ined., Sundue 1157 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Melpomene occidentalis* Lehnert ined., Sundue 1168 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; Melpomene personata Lehnert ined., Sundue 1281 & Vasco (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Melpomene pseudonutans* (H. Christ & Rosenst.) A. R. Sm. & R. C. Moran, K. A. Wilson 2806 (UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* --; *Melpomene vernicosa* (Maxon ex Copel.) A. R. Sm. & R. C. Moran, Sundue 1112 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Microgramma percussa* (Cav.) de la Sota, A. Smith 1357 (UC), Venezuela, *atpB:* AY459516, *rbcL:* AY362574, *trnLF:* $; *Microgramma squamulosa* (Kaulf.) de la Sota, NYBG 954/95A (UC), cultivated source, *atpB:* AY459517, *rbcL:* AY362579, *trnLF:* DQ642229; *Micropolypodium hyalinum* (Maxon) A.R. Sm., A. Rojas & al. 3210 (CR, INB, MO, UC), Costa Rica, *atpB:* AY459490, *rbcL:* AY362344, *trnLF:* $; *Micropolypodium taenifolium* (Jenman) A.R. Sm., A. Rojas 3007 (UC), Costa Rica, *atpB:* AY459491, *rbcL:* AY460658, *trnLF:* $;

Micropolypodium zurquinum (Copel.) A.R. Sm., A. Rojas 3021 & M. Mata (UC), Costa Rica, *atpB:* AY459492, *rbcL:* AY460659, *trnLF:* --; *Oreogrammitis hookeri* (Brack.) Parris, A.C. Smith 903 (UC), Fiji, *atpB:* AY459473, *rbcL:* AY460642, *trnLF:* --; *Pecluma alfredii* (Rosenst.) M.G. Price, Kimnach 95 (UC), Mexico, *atpB:* AY459519, *rbcL:* AY096206, *trnLF:* --; *Polypodium glycyrrhiza* D.C. Eaton, Haufler & Mesler s.n. (KANU), USA, *atpB:* AY459518, *rbcL:* U21146, *trnLF:* $; *Prosaptia alata* (Blume) H. Christ, T. Flynn 6004 (UC, AD, BISH, PTBG, US), Kosrae, *atpB:* AY459493, *rbcL:* AY460660, *trnLF:* --; *Prosaptia contigua* (G. Forst.) C. Presl, Chiou 97-09-12-05 (COLO, UC, TAIF), Taiwan, *atpB:* AY459494, *rbcL:* AY362345, *trnLF:* --; *Prosaptia obliquata* (Blume) Mett., Chiou 97-09-12-04 (COLO, UC, TAIF), Taiwan, *atpB:* AY459495, *rbcL:* AY460661, *trnLF:* --; *Prosaptia pubipes* Copel., J. Game 95-65 (UC), Fiji, *atpB:* AY459496, *rbcL:* AY460663, *trnLF:* --; *Scleroglossum sulcatum* (Kuhn) Alderw., Bowden-Kerby 24182b (UC, GUAM), Pohnpei, *atpB:* AY459498, *rbcL:* AY460665, *trnLF:* --; *Scleroglossum sulcatum* (Kuhn) Alderw., T. Flynn 6287 (PTBG, US, UC), Pohnpei, *atpB:* AY459497, *rbcL:* AY460664, *trnLF:* --; *Terpsichore achilleifolia* (Kaulf.) A.R. Sm., J. Cordeiro & O. Ribas 1398 (UC), Brazil, *atpB:* AY459499, *rbcL:* AY460666, *trnLF:* --; *Terpsichore amphidasyon* (Mett. ex Kunze) A. R. Sm., Moran 7646 (NY, QCA), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore amphidasyon* (Mett. ex Kunze) A. R. Sm., Sundue 1129 (NY, QCA, QCNE, UC), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:*

$; *Terpsichore amphidasyon* (Mett. ex Kunze) A. R. Sm., Sundue 1135 (NY, QCA, QCNE, UC), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., Kessler 13517 (NY), Mexico, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., Moran s.n. (NY), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., Moran 7567 (NY), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* --; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., Lehnert 499 (GOET, LPB, UC), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., Lehnert 315 (GOETpp), Peru, *atpB:* $, *rbcL:* $, *trnLF:* --; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., Lehnert 1035 (GOET, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., Kessler 13507 (UC), Mexico, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., I. Jimenez 1399 (LPB), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., Lehnert 212 (GOET, UC), Peru, *atpB:* $, *rbcL:* $, *trnLF:* --; *Terpsichore angustipes* (Copel.) A. R. Sm., Sundue 1237 (HUA, NY, UC), Colombia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore angustipes* (Copel.) A. R. Sm., W. Rodriguez 5124 (HUA, NY), Colombia, *atpB:* --, *rbcL:* --, *trnLF:* $; *Terpsichore athyrioides* (Hook.) A. R. Sm., Lehnert 261 (GOET, UC), Peru, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore attenuatissima* (Copel.) A. R. Sm., Sundue 1098 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore attenuatissima* (Copel.) A. R. Sm., Sundue 1038 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore attenuatissima* (Copel.) A. R. Sm., Lehnert & Kessler 1162 (GOET, NY, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore attenuatissima* (Copel.) A. R. Sm., K. A. Wilson 2609a (UC), Ecuador, *atpB:* AY459500, *rbcL:* AY460667, *trnLF:* --; *Terpsichore clathrata* Sundue, Kromer 1237 (LPB, UC), Bolivia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore clavigera* ined., J. Schneider 2400 (UC), Venezuela, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore colombiense* ined., C. Dassler 94-7-13-1 (OS), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore colombiense* ined., Sundue & Vasco 1316 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore communis* Moguel ined., Kessler 13511 (LPB, UC), Mexico, *atpB:* --, *rbcL:* --, *trnLF:* $; *Terpsichore cretata* (Maxon) A. R. Sm., M. Alford 2719 (NY), Dominican Republic, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore cuencana* (Hieron.) Comb. ined., Lehnert 1164 (GOET), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore cultrata* (Bory ex Willd.) A. R. Sm., C. Dassler 94-7-19-1 (ILLS), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* --; *Terpsichore david*-smithii (Stolze) A. R. Sm., I. Jimenez 1246 (UC), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore david-smithii* (Stolze) A. R. Sm., Sundue 785 (LPB, NY, UC, USZ), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore david-smithii* (Stolze) A. R. Sm., I. Jimenez 1452 (LPB, UC), Bolivia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore david-smithii* (Stolze) A. R. Sm., I. Jimenez 1215 (UC), Bolivia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore david-smithii* (Stolze) A. R. Sm., I. Jimenez 894 (UC), Bolivia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore delicatula* (M. Martens & Galeotii) A. R. Sm., Kessler 13527 (LPB, UC), Mexico, *atpB:* --, *rbcL:* --, *trnLF:* $; *Terpsichore dilatata* Sundue, I. Jimenez 1156 (UC), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore dilatata* Sundue, I. Jimenez 954 (UC), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore hanekeana* (Proctor) A.R. Sm, Ranker 1610 (COLO), Puerto Rico, *atpB:* AY459503, *rbcL:* AY460670, *trnLF:* --; *Terpsichore lanigera* (Desv.) A.R. Sm., A. Rojas et al. 3207, Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore lanigera* (Desv.) A.R. Sm., B. León 3647 (USM, UC), Peru, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore lehmanniana* (Hieron.) A.R. Sm., K. Wilson 2589 (UC), Ecuador, *atpB:* AY459506, *rbcL:* AY460673, *trnLF:* --; *Terpsichore leucosticton* (J Sm.) A. R. Sm., Moran 7590 (QCA), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore leucosticton* (J Sm.) A. R. Sm., Lehnert 1128 (UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore loja* ined., Sundue 1164 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore loja* ined., Sundue 1125 (NY, QCA, QCNE, UC), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore loja* ined., Lehnert 1233pp (UC), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore longicaulis* Sundue, I. Jimenez 373 (LPB, UC), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore longipilosa* ined., Sundue & Martin 1033 (NY, QCA, QCNE, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore longipilosa* ined., Sundue & Martin 1037 (NY, QCA, QCNE, UC), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore longisetosa* (Hook.) A.R. Sm., A. Rojas & al. 3209 (CR, INB, MO, UC), Costa Rica, *atpB:* AY460674, *rbcL:* AY459507, *trnLF:* --; *Terpsichore mollissima* (Fee) A. R. Sm., Kessler 13443 (LPB, UC), Bolivia, *atpB:* --, *rbcL:* --, *trnLF:* $; *Terpsichore nana* Sundue, Sundue 866 (NY, USZ, LPB, UC), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore pacifica* ined., A. Rojas & Mata 3072 (CR, INB, UC), Costa Rica, *atpB:* --, *rbcL:* --, *trnLF:* $; *Terpsichore pichinchae* (Sodiro) A. R. Sm., K. Wilson 2816a (UC), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore pichinchense* (Hieron.) A. R. Sm., Lehnert 1577 (UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore pichinchense* (Hieron.) A. R. Sm., J. E. Ramos 7329 (MO, UC), Ecuador, *atpB:* --, *rbcL:* --, *trnLF:* $; *Terpsichore pichinchense* (Hieron.) A. R. Sm., J. Rodriguez 646 (QCA), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore praeceps* Sundue, I. Jimenenz 2173 (LPB, UC), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore semihirsuta* (Klotzsch) A. R. Sm., Sundue & Vasco 1246 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore senilis* (Fee) A. R. Sm., A. Rojas & al. 3196 (INB), Costa Rica, *atpB:* AY459510, *rbcL:* AY096208, *trnLF:* $; *Terpsichore sp*. Sundue 1160, Sundue 1160 (NY, QCA), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. Sundue 1167, Sundue 1167 (NY, QCA), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff *alsopteris* ined. 1, I. Jimenez 1451

(LPB), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff *alsopteris* ined. 1, I. Jimenez 1487 (LPB), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff *alsopteris* ined. 1, I. Jimenez 1491 (LPB), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff *alsopteris* ined. 1, I. Jimenez 1504 (LPB), Bolivia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff *semihirsuta* ined. 3, Kessler 13508 (NY), Mexico, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *alsopteris* ined. 2, Moran s.n. (NY), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *semihirsuta* ined. 1, Sundue & Vasco 1313 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *semihirsuta* ined. 1, I. Jimenez 1238 (LPB), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *semihirsuta* ined. 1, R. Nunez C. 524 (MO), Bolivia, *atpB:* $, *rbcL:* $, *trnLF:* $; Terpsichore sp. aff. semihirsuta ined. 1, Lehnert 1144 (NY, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *semihirsuta* ined. 1, Lehnert 313 (GOET, NY, UC), Peru, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *semihirsuta* ined. 1, Sundue & Vasco 1234 (HUA, NY, UC), Colombia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *semihirsuta* ined. 2, Moran 8077 (NY), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *subtilis* ined., Sundue & Schuettpelz 1077 (NY), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *taxifolia* (L.) A. R. Sm., Sundue & Werner 1161 (NY, QCA, UC), Ecuador, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore sp*. aff. *taxifolia* ined., Sundue & Vasco 1215 (HUA, NY, UC), Colombia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore subscabra* (Fée)

A.R. Sm., A. Rojas & al. 3211 (CR, INB, MO, UC), Costa Rica, *atpB:* AY459511, *rbcL:* AY460677, *trnLF:* $; *Terpsichore subscabra* (Klotzsch) B. Leon & A. R. Sm., A. Rojas & al. 3211 (CR, INB, MO, UC), Costa Rica, *atpB:* AY459511, *rbcL:* AY460677, *trnLF:* $; *Terpsichore subscabra* (Klotzsch) B. Leon & A. R. Sm., Moran 8078 (NY), Costa Rica, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore subtilis* (Kunze ex Klotzsch) A. R. Sm., Sundue 1142 (NY, QCA, QCNE), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* $; *Terpsichore subtilis* (Kunze ex Klotzsch) A.R. Sm., M. Moraga & A. Rojas 505 (INB), Costa Rica, *atpB:* AY459512, *rbcL:* AY460678, *trnLF:* --; *Terpsichore taxifolia* (L.) A. R. Sm., Labiak 4018 (NY, UPCB), Brazil, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore vascoi* ined., Sundue & Vasco 1235 (HUA, NY, UC), Colombia, *atpB:* $, *rbcL:* $, *trnLF:* $; *Terpsichore zeledoniana* (Lellinger) A. R. Sm., Sundue & Nitta 1806 (INB, NY, UC), Costa Rica, *atpB:* --, *rbcL:* $, *trnLF:* --; *Xiphopteris conjunctisora* (Baker) Copel., Ranker 1758 & Trapp (COLO, UC), Papua New Guinea, *atpB:* AY459514, *rbcL:* AY460680, *trnLF:* --; *Zygophlebia mathewsii* (Kunze ex Mett.) L. E. Bishop, Sundue & Vasco 1254 (HUA, NY, UC), Colombia, *atpB:* --, *rbcL:* $, *trnLF:* $; *Zygophlebia mathewsii* (Kunze ex Mett.) L. E. Bishop, Sundue 1119 (NY, UC), Ecuador, *atpB:* --, *rbcL:* $, *trnLF:* --; *Zygophlebia sectifrons* (Kunze ex Mett.) L. E. Bishop, Sundue 1757 (INB, NY), Costa Rica, *atpB:* --, *rbcL:* $, *trnLF:* --;

Appendix B. Morphological matrix, characters 0—55; key: A = 0,1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5
Taxon	**0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5**
Calymmodon gracilis	0 0 0 0 0 ? 0 0 0 1 ? 0 0 - 1 0 0 1 0 A 1 0 0 0 1 1 1 0 2 0 0 1 0 0 0 - 0 0 1 1 0 0 0 0 2 1 1 2 ? 0 ? 0 0 1 0 0
Calymmodon luerssenianus	0 ? 0 0 0 ? 0 ? 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 2 0 ? ? ? ? ? ? ? ? ? 0 0 - 0 0 ? ? ? ? 0 1 2 1 0 0 ? 0 ? 0 ? ? ? ?
Campyloneurum angustifolium	0 2 1 0 1 1 1 0 1 1 1 0 0 - 1 0 0 1 0 1 0 0 1 0 0 0 - - - 0 0 0 - 0 0 - 1 1 0 1 2 1 0 ? 0 - - 0 0 0 ? 0 4 0 0 0
Ceradenia aulaeifolia	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 1 0 - 0 1 0 1 0 ? 0 0 1 1 0 2 0 0 3 1 1 0 ? 0 ? 0 2 1 1 1
Ceradenia fucoides	0 2 0 0 0 ? 0 1 0 1 0 0 1 0 0 - - - - - - - - - - - - - - - - - - 0 0 - 0 0 1 1 0 0 0 0 1 1 0 0 ? 0 ? 0 0 0 0 0
Ceradenia intonsa	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 1 - 0 1 0 0 0 ? 0 0 1 0 1 2 1 0 2 1 0 2 ? 0 ? 0 1 1 0 0
Ceradenia jungermannioides	0 0 1 0 0 ? 0 1 0 1 0 0 0 - 0 - - - - - - - - - - - - - - - - 0 - 0 0 - 0 0 1 ? 0 ? ? ? 0 - - 0 ? 0 ? 0 0 ? ? ?
Ceradenia kalberyeri Sundue 1759	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 0 1 2 1 0 2 1 0 2 ? 0 ? 0 1 1 1 0
Ceradenia kalbreyeri sundue 1213	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 0 0 2 1 1 2 1 0 2 ? 0 ? 0 1 1 1 2
Ceradenia pilipes	0 2 0 0 0 ? 0 1 0 1 0 0 0 - 0 0 1 1 0 0 1 0 0 0 2 1 0 A 0 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 3 1 1 0
Ceradenia sp. aff. *kalbreyeri* Vasco 701	0 2 1 0 1 ? 0 ? ? 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 ? ? 0 0 - 0 0 1 0 0 2 1 0 2 1 0 2 ? 0 ? 0 1 1 1 0
Ceradenia sp. ined. 1 Sundue 1238	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 A 1 - 0 1 1 0 0 - 0 0 1 0 1 2 1 0 3 1 0 2 ? 0 ? 0 1 1 1 0
Ceradenia sp. Moran 7520	0 2 1 0 1 ? 0 ? ? 1 ? 0 0 - 1 0 1 1 0 0 1 0 0 0 2 ? ? ? ? ? 0 1 ? 0 0 - 0 0 1 0 ? 2 1 0 2 1 0 2 ? 0 ? 0 ? 0 0 0
Ceradenia sp. ined. 1 Sundue 1242	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 A 1 - 0 1 1 0 0 - 0 0 1 0 1 2 1 0 3 1 0 2 ? 0 ? 0 1 1 1 0
Ceradenia spixiana	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 A 1 - 0 1 0 0 0 - 0 0 1 0 0 2 1 0 2 1 0 2 ? 0 ? 0 2 0 ? 0
Chrysogrammitis musgraveana	0 ? 0 0 1 ? ? ? 0 1 ? 0 0 - 1 0 0 - - 0 0 0 2 0 1 1 0 1 ? ? ? ? ? ? 0 0 - 0 0 ? ? ? ? 0 0 2 ? ? ? ? ? 0 ? 0 ? ? ? ?
Cochlidium punctatum	0 ? 0 0 0 ? 0 ? 0 1 0 0 0 - 1 ? 0 1 0 A 1 0 0 0 0 0 - - - 1 0 ? ? 0 1 1 0 0 1 1 0 ? 0 ? 0 - - 2 ? 0 ? 0 4 0 0 -
Cochlidium rostratum	0 ? 0 0 0 ? 0 ? 0 1 0 0 0 - 1 1 0 1 0 A 1 0 0 0 0 0 - - - 1 0 0 - 0 1 1 0 0 1 1 0 ? 0 ? 0 - - 2 ? 0 ? 0 4 0 0 -
Cochlidium seminudum	0 0 0 0 0 ? 0 ? 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 0 0 0 0 - - - 0 0 0 - 0 0 - 0 0 1 1 0 ? 0 ? 0 - - 2 ? 0 ? 0 4 1 0 -
Ctenopteris heterophylla	B ? 0 0 1 ? ? ? 0 1 ? 0 0 - 1 0 0 - - 0 1 0 2 0 1 0 - - - 0 - - - 0 0 - 0 0 ? ? ? ? 0 0 1 ? ? ? ? ? 0 ? 0 ? ? ? ?
Ctenopteris lasiostipes	0 ? 0 0 1 ? ? ? 0 1 ? 0 0 - 1 0 0 - - 0 1 1 1 0 1 0 - - - 0 - - - 0 0 - 0 0 ? ? ? ? 0 0 3 ? ? ? ? ? 0 ? 0 ? ? ? ?
Ctenopteris nutans	0 ? 0 0 1 ? ? ? 1 1 ? 0 0 - 1 0 0 - - 0 1 3 1 0 1 1 0 0 - - - - - 0 0 - 1 0 ? ? ? ? 0 0 2 ? ? ? ? ? 0 ? 0 ? ? ? ?
Ctenopteris repandula	C ? 0 0 0 ? ? ? 0 1 ? 0 0 - 1 0 0 - - 0 1 0 3 0 1 0 - - - 0 - - - 0 0 - 0 0 ? ? ? ? 0 0 2 ? ? ? ? ? 0 ? 0 ? ? ? ?
Ctenopteris rhodocarpa	0 ? 0 0 1 ? ? ? 1 1 ? 0 0 - 1 0 0 - - 0 1 1 1 0 1 1 0 0 - - - - - 0 0 - 1 0 ? ? ? ? 0 0 2 ? ? ? ? ? 0 ? 0 ? ? ? ?
Enterosora barbatula	0 2 1 0 1 ? 0 ? 1 0 ? 0 0 - 1 0 ? 1 0 0 1 0 3 0 ? 1 0 1 3 - 0 ? ? 0 0 - ? 0 ? ? ? 2 0 ? 0 - - 2 ? 1 ? 0 ? 0 0 0
Enterosora enterosoroides	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 0 1 0 0 1 0 3 0 1 0 - - - 1 0 0 - 0 0 - 0 0 1 0 0 2 0 ? 0 - - 2 0 1 ? 0 5 0 0 0
Enterosora percrassa	0 2 1 0 1 1 0 ? 1 1 0 0 0 - 1 0 1 1 0 0 1 0 3 0 1 1 0 1 3 - 1 1 0 0 0 - 0 0 1 1 1 2 0 ? 0 - - 2 1 1 ? 0 0 0 0 0
Enterosora trichosora	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 3 0 1 0 - - - 1 0 ? - 0 0 - 0 0 1 1 0 2 0 ? 0 - - 2 1 1 ? 0 1 0 0 0
Enterosora trifurcata	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 3 0 1 1 0 1 0 0 1 1 1 0 0 - 0 0 1 0 1 2 0 0 1 1 A 2 1 1 ? 0 1 0 0 0
Grammitis billardieri	A ? 1 0 1 0 0 0 0 1 1 0 0 - 1 0 0 1 0 0 1 0 3 0 0 0 - - - 0 0 1 0 0 0 - 0 0 1 1 0 1 0 ? 0 - - 0 ? 0 ? 0 2 1 0 0
Grammitis ciliata	D ? 0 0 0 ? 0 ? 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 3 0 1 0 - - - 0 0 - - 0 0 - 0 0 ? ? ? ? 0 - 0 - - 0 ? 0 ? 0 ? ? ? 0
Grammitis deplanchei	0 0 1 0 1 1 0 0 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 1 0 - - - 1 0 0 - 0 0 - 0 0 1 1 0 0 0 ? 0 - - 2 ? 0 ? 0 1 0 0 0
Grammitis forbesiana	0 ? 0 0 1 ? 0 ? 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 3 0 1 0 - - - 0 0 - - 0 0 - 0 0 ? ? ? ? 0 - 0 - - 0 ? 0 ? 0 ? ? ? ?
Grammitis knutsfordiana	0 0 0 0 1 ? 1 0 0 1 ? 0 0 - 1 1 0 1 0 0 1 0 0 1 1 0 - - - 0 0 0 - 0 0 - 0 0 1 1 0 2 0 ? 0 - - 0 ? 0 ? 0 1 1 1 0
Grammitis melanoloma	0 ? 0 0 0 ? 0 ? 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 3 0 1 0 - - - 0 0 ? ? 0 0 - 0 0 ? ? ? ? 0 ? 0 - - 0 ? 0 ? 1 ? ? ? ?
Grammitis parva	0 ? 0 0 0 ? 0 ? 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 3 0 1 0 - - - 0 0 - - 0 0 - 0 0 ? ? ? ? 0 - 0 - - 0 ? 0 ? 0 ? ? ? ?
Grammitis poeppigiana	2 0 0 0 1 ? 0 1 0 0 0 0 0 - 1 0 0 1 0 0 1 0 0 0 1 0 - - - 0 0 0 - 0 0 - 0 0 1 1 0 0 ? ? 0 - - 2 0 0 ? 0 4 0 0 -
Grammitis pseudociliata	0 ? 0 0 1 ? 0 ? 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 3 0 1 0 - - - 0 0 - - 0 0 - 0 0 ? ? ? ? 0 - 0 - - 0 ? 0 ? 0 ? ? ? ?
Lelligeria barbensis	0 2 ? 0 ? ? 0 ? ? 1 - ? - - 1 - 0 - - - 1 1 1 0 - 1 0 0 1 - - - - 0 0 - 0 - - - - - 0 0 2 1 0 - ? ? ? 0 - 1 1 1
Lelligeria hellwigii	0 0 1 0 0 ? 0 1 0 1 ? 0 0 - 1 1 0 0 0 0 0 1 1 1 1 1 1 0 2 0 0 1 0 0 1 1 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 4 1 1 -
Lelligeria myosuroides	0 0 1 0 0 ? 0 1 0 1 0 0 0 - 1 0 0 0 0 1 0 1 1 1 1 1 1 0 2 1 0 1 0 0 1 1 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1

Appendix B. Morphological matrix, characters 0—55; key: A = 0,1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

Taxon	0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55
Lelligeria prionodes	0 0 1 0 0 ? 0 1 0 1 ? 0 0 - 1 1 0 1 0 0 0 1 1 1 1 1 1 0 2 0 0 1 0 0 1 1 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1
Lellingeria apiculata	0 1 1 0 1 ? 0 0 0 1 0 0 0 - 1 0 0 1 0 0 1 1 1 0 1 1 0 0 1 - 1 1 0 0 0 - 0 0 1 1 0 2 1 0 3 1 0 0 ? 0 ? 0 0 1 1 0
Lellingeria hirsuta	0 1 1 0 1 1 0 0 0 1 0 0 0 - 1 0 0 1 0 0 1 1 1 0 0 1 0 0 1 - 0 1 0 0 0 - 0 0 1 1 0 2 1 1 3 1 0 0 ? 0 ? 0 0 1 1 1
Lellingeria humilis	1 1 1 0 1 ? 0 0 0 1 1 0 0 - 1 0 0 1 0 0 0 1 1 0 0 1 0 0 1 - 0 ? ? 0 0 - 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 3 1 1 0
Lellingeria limula	0 0 1 0 0 ? 0 1 0 1 0 0 0 - 1 0 0 0 0 1 0 1 1 1 1 0 - - - 0 0 1 ? 0 0 1 0 0 1 1 0 1 0 0 2 1 0 0 ? 0 ? 0 ? 1 1 0
Lellingeria major	0 1 1 0 1 ? 0 1 0 1 1 0 0 - 1 0 1 1 0 0 1 1 1 0 0 1 0 0 1 - 0 1 0 0 0 - 0 ? 1 1 1 2 0 0 3 1 0 0 ? 0 ? 0 G 1 1 0
Lellingeria myosuroides	0 0 1 0 0 ? 0 1 0 1 0 0 0 - 1 0 0 0 0 1 0 1 1 1 1 1 1 0 2 1 0 1 0 0 1 1 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1
Lellingeria oreophila	0 1 1 0 1 ? 0 0 0 1 1 0 0 - 1 0 1 1 0 0 1 1 2 0 0 1 0 0 1 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 1 0 0 ? 0 ? 0 3 1 1 1
Lellingeria pseudomitchellae	0 0 0 0 0 ? 0 ? 0 1 - ? 0 - 0 - - - - - - - - - - - - - - - - - - - 0 0 1 0 0 1 1 0 1 0 0 1 0 1 0 ? 0 ? 0 0 1 0 0
Lellingeria saffordii	0 0 0 0 0 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 1 1 1 1 1 1 1 0 2 0 0 1 0 0 1 1 0 0 1 1 0 1 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1
Lellingeria schenckei	0 1 0 0 0 ? 0 ? 0 1 0 ? ? - 1 0 0 0 0 0 1 1 1 0 1 1 0 0 ? 0 0 ? ? 0 0 - 0 0 1 1 0 0 0 0 2 0 0 1 ? 0 ? 0 0 1 0 0
Lellingeria sp aff *hirsuta* Sundue 1159	0 2 1 0 1 ? 0 ? 0 1 ? 0 0 - 1 0 1 1 0 0 1 1 1 0 0 1 0 0 1 - 0 1 ? 0 0 - 0 0 1 1 0 2 0 1 2 1 0 0 ? 0 ? 0 0 1 1 1
Lellingeria sp. aff *humilis* ined. Sundue 1126	0 1 1 0 1 ? 0 1 0 1 0 0 0 - 1 0 1 1 0 0 1 1 1 0 0 1 0 0 1 - 0 1 0 0 0 - 0 0 1 1 0 0 0 0 1 1 1 0 1 1 ? 0 0 A 0 0
Lellingeria subsessilis	0 2 1 0 1 ? 0 0 0 1 0 0 0 - 1 0 1 1 0 0 1 1 1 0 0 1 0 0 1 - 0 1 0 0 0 - 0 0 1 1 0 1 0 0 1 1 0 0 0 1 1 0 0 1 0 0
Lellingeria suprasculpta Sundue 1767	0 2 0 0 1 ? 0 0 0 1 0 0 0 - 1 0 1 0 0 0 1 1 2 0 0 0 - - - 0 0 ? ? 0 0 - 0 0 1 1 0 1 0 0 1 1 0 1 ? 0 ? 0 1 1 0 1
Lellingeria suspensa	0 2 0 0 1 ? 0 ? 0 1 0 0 0 - 1 0 0 1 0 0 1 1 1 1 2 0 - - - 0 0 1 0 0 0 - 0 0 1 1 0 1 0 0 2 1 0 0 ? 0 ? 0 1 1 1 0
Melpomene anazalea ined.	1 3 1 0 1 ? 1 1 0 0 ? 0 0 - 1 0 0 1 0 1 1 1 2 1 1 0 - - - 0 0 1 1 0 0 - 0 0 1 1 0 1 0 0 2 1 1 2 ? 0 ? 0 0 1 1 0
Melpomene firma	0 1 1 0 1 ? 0 ? 0 1 1 0 0 - 1 0 0 1 1 1 1 1 2 1 2 0 - - - 0 0 1 0 0 0 - 0 0 1 1 0 1 1 0 3 0 0 0 ? 0 ? 0 0 1 1 1
Melpomene flabelliformis	E 0 1 0 1 ? 1 ? 0 0 0 0 0 - 1 0 0 1 0 A 1 1 2 1 2 0 - - - 0 0 1 1 0 1 0 0 0 1 1 0 0 0 0 2 1 1 2 ? 0 ? 0 0 1 1 0
Melpomene moniliformis	F 0 1 0 1 ? 1 1 0 0 1 0 0 - 1 0 0 1 0 1 1 1 1 1 2 0 - - - 0 0 1 1 0 0 - 0 0 1 0 0 0 0 0 2 1 1 2 ? 0 ? 0 0 1 1 0
Melpomene occidentalis ined.	0 0 1 0 1 1 0 1 0 1 1 0 0 - 1 0 0 1 0 1 1 1 2 1 1 0 - - - 0 0 1 0 0 1 0 0 0 1 1 1 0 0 0 3 1 0 0 ? 0 ? 0 0 1 1 1
Melpomene personata ined.	0 1 1 0 1 ? 0 0 0 1 ? 0 0 - 1 0 0 1 0 0 1 1 2 1 2 0 - - - 0 0 1 0 0 1 0 0 0 1 1 0 1 1 0 2 1 1 0 - 0 ? 0 0 1 1 0
Melpomene pseudonutans	E 1 1 0 1 ? 0 ? 0 1 1 0 0 - 1 0 0 1 0 1 1 1 2 1 2 0 - - - 0 0 1 1 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 1 0 0 0 0 1 1 0
Melpomene vernicosa	0 1 1 0 1 ? 0 0 0 1 1 0 0 - 1 0 0 1 0 1 1 1 2 1 2 0 - - - 0 0 1 1 0 0 - 0 0 1 1 0 2 1 0 2 1 1 2 ? 0 ? 0 0 1 1 0
Micrgramma percussa	0 0 1 0 1 1 1 0 1 0 1 0 0 - 1 0 0 1 0 1 1 1 1 0 0 0 - - - 1 0 0 - 0 0 - 1 1 0 1 2 2 0 ? 0 - - 0 ? 0 ? 0 5 0 0 0
Micrgramma squamulosa	0 0 1 0 1 1 1 0 1 0 1 0 0 - 1 0 0 1 0 1 1 1 1 0 0 1 0 0 1 1 0 0 - 0 0 - 1 1 0 1 2 2 0 ? 0 - - 0 ? 0 ? 0 5 0 0 0
Micropolypodium hyalinum	0 2 0 0 0 ? 1 0 0 1 0 1 1 1 1 0 1 1 0 1 1 0 0 0 2 1 0 A 2 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 4 0 0 -
Micropolypodium taenifolium	0 2 0 0 0 ? 0 0 0 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 4 1 0 -
Micropolypodium zurquinum	0 2 0 0 0 ? 0 0 0 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 0 - - - 0 0 1 0 0 0 - 0 0 1 1 0 2 0 0 2 1 0 0 ? 0 ? 0 4 0 0 -
Oreogrammitis hookeri	0 1 0 0 1 ? 0 1 0 1 0 0 0 - 1 1 0 1 0 0 1 0 0 1 1 0 - - - 0 0 0 - 0 0 - 0 0 1 1 0 2 0 ? 0 - - 0 0 1 1 0 1 0 0 0
Pecluma alfredii	0 1 1 0 1 1 0 0 1 1 0 0 0 - 1 0 0 1 0 0 0 0 2 0 0 0 - - - 0 0 0 - 0 0 - 1 0 1 0 1 2 1 0 2 1 0 0 ? 0 ? 0 0 1 1 1
Polypodium glycyrrhiza	1 1 1 0 1 1 1 ? 1 0 0 0 0 - 1 0 0 1 0 0 1 0 0 0 0 0 - - - 1 0 0 - 0 0 - 1 1 0 1 2 2 1 1 2 1 0 0 ? 0 ? 0 0 0 0 1
Prosaptia alata	0 2 1 0 1 1 0 ? 1 1 0 0 0 - 1 0 0 0 0 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 0 - 1 0 1 1 0 1 0 0 1 1 0 0 ? 0 ? 0 1 0 0 0
Prosaptia contigua	0 ? 1 0 1 1 0 ? 1 1 0 0 0 - 1 0 0 0 0 0 1 1 1 0 1 1 0 0 2 - 0 1 0 0 0 - 0 0 1 1 0 1 0 0 2 1 0 0 ? 0 ? 0 0 1 1 1
Prosaptia obliquata	0 1 0 0 1 1 0 ? 1 1 0 0 0 - 1 0 0 0 0 0 1 1 3 0 1 1 0 0 2 - 0 0 - 0 0 - 1 0 1 1 0 1 0 0 3 1 0 0 ? 0 ? 0 1 0 0 0
Prosaptia pubipes	E ? 1 0 1 ? 0 0 1 1 ? 0 0 - 1 0 0 0 0 0 1 1 1 1 1 1 0 0 2 - 0 0 - 0 0 - 0 0 1 1 0 1 0 0 2 1 0 0 ? 0 ? 0 0 1 1 1
Scleroglossum sulcatum	1 0 0 0 0 ? 0 ? 0 1 ? 0 0 - 1 1 0 1 0 0 1 0 0 0 0 0 - - - 0 0 0 - 0 0 - 0 0 1 1 ? 2 0 ? 0 - - 2 ? 0 ? 0 4 0 0 -
Scleroglossum sulcatum	1 0 0 0 0 ? 0 ? 0 1 ? 0 0 - 1 1 0 1 0 0 1 0 0 0 0 0 - - - 0 0 0 - 0 0 - 0 0 1 1 ? 2 0 ? 0 - - 2 ? 0 ? 0 4 0 0 -
Terpisichore pacifica ined.	0 2 1 0 1 1 0 0 0 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 1 0 0 0 0 1 1 0 0 - 0 0 1 1 0 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1
Terpsichore achilleifolia	A ? 0 0 0 ? 0 0 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 0 0 0 0 - - 0 0 0 0 - 0 0 - 0 0 1 1 0 1 0 0 2 0 0 0 ? 0 ? 0 1 0 0 0
Terpsichore sp. aff *taxifolia* ined.	0 1 1 0 1 ? 0 1 0 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 1 0 0 0 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1

Appendix B. Morphological matrix, characters 0—55; key: A = 0,1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

Taxon	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5
Terpsichore sp. aff. *alsopteris* ined. 1	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 1 2 0 0 3 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore attenutissima	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 1 2 0 0 3 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore sp. aff. *alsopteris* ined. 2	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 1 0 0 0 0 1 0 0 0 - 0 0 1 1 1 2 0 0 3 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore amphidasyon	0 1 1 0 1 1 0 0 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 1 2 1 1 0 1 0 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 0 1 0 ? 0 ? 0 1 1 1 1
Terpsichore anfractuosa Jimenez 1399	0 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 0 1 1 1 1 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1
Terpsichore anfractuosa Kessler 13517	0 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 1 0 1 0 1 1 1 1 0 - 0 - - 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1
Terpsichore anfractuosa Lehnert 1035	A 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 0 1 1 1 1 1 1 0 2 0 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 1 0
Terpsichore anfractuosa Lehnert 315	0 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 0 1 1 1 1 0 - - - 0 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 1 0
Terpsichore anfractuosa Lehnert 499	0 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 0 1 1 1 1 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1
Terpsichore anfractuosa Kessler 13507	0 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 0 1 1 1 1 0 - 0 - - 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1
Terpsichore anfractuosa Moran 7567	0 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 0 1 1 1 1 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 1 0
Terpsichore anfractuosa Moran s.n.	0 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 0 1 1 1 1 ? ? ? ? ? 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 1 0
Terpsichore anfractuosa Lehnert 212	2 0 1 1 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 0 1 1 1 1 1 0 0 1 - 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 0 1
Terpsichore angustipes sund1237	0 2 1 0 1 ? 0 ? 0 1 ? 0 0 - 1 0 0 0 0 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 0 1 0 0 2 1 1 0 ? 0 ? 0 0 1 1 1
Terpsichore athyrioides	0 2 1 0 1 0 0 0 0 1 0 0 0 - 1 0 0 0 1 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 0 - 0 0 1 1 1 1 0 0 4 1 0 0 ? 0 ? 0 ? 1 1 1
Terpsichore clathrata	0 2 1 0 1 ? 0 1 0 1 ? 0 0 - 1 0 0 0 0 1 1 1 1 1 1 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 ? 2 ? 0 3 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore clavigera	0 1 1 0 1 1 0 1 0 1 0 0 0 - 1 0 0 0 1 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 0 - 0 0 1 1 1 1 0 0 2 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore colombiense ined.	0 1 1 0 1 1 0 1 0 1 0 0 0 - 1 0 0 0 1 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 1 1 0 0 3 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore communis ined.	0 2 0 0 0 0 0 0 0 1 0 1 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 1 ? ? 1 0 - 0 0 1 1 1 2 0 0 3 1 1 1 0 0 ? 0 0 1 1 1
Terpsichore cretata	0 2 1 0 1 ? 0 1 0 1 ? 0 0 - 1 0 1 1 1 0 1 0 1 0 0 1 1 0 0 0 0 1 0 0 0 - 0 0 1 1 0 0 0 0 2 1 1 1 1 0 0 0 3 1 1 A
Terpsichore cuencana	0 0 1 0 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 0 1 0 0 2 1 0 0 ? 0 ? 0 ? 1 1 1
Terpsichore cultrata	0 2 0 0 0 ? 0 0 0 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 1 - 0 0 - 1 0 - 0 0 1 1 0 2 0 0 3 1 1 1 ? 0 ? 0 0 1 1 1
Terpsichore david-smithii	0 0 1 0 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 1 1 1 0 0 1 0 0 F - 0 1 0 0 1 0 0 0 1 1 0 1 0 0 3 0 0 0 ? 0 ? 0 0 1 1 1
Terpsichore delicatula	0 2 1 0 1 0 0 0 0 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 0 1 0 1 0 - 1 1 0 1 0 - 0 0 1 1 0 2 0 1 3 0 0 1 ? 0 ? 0 0 1 1 1
Terpsichore dilatata	0 1 1 0 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore hanekeana	0 2 1 0 1 ? 0 0 1 1 0 1 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 A 0 - 1 0 - 0 0 - 0 0 1 1 0 2 0 0 2 1 1 0 ? 0 ? 0 0 1 1 0
Terpsichore lanigera	0 2 1 0 1 0 0 0 0 1 0 1 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 1 0 0 0 0 - 0 0 1 1 1 2 0 0 2 1 1 1 0 0 ? 0 0 1 1 1
Terpsichore lehmanniana	0 2 1 0 0 ? 0 0 0 1 0 0 0 - 1 0 0 1 0 0 0 0 3 0 0 1 0 0 3 - 1 0 0 0 0 - 0 0 1 1 0 2 1 0 3 1 0 1 ? 0 ? 0 1 1 1 0
Terpsichore leucosticta	0 2 1 0 1 1 0 1 1 1 ? 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 1 2 0 0 3 1 1 0 ? 0 ? 0 1 1 1 1
Terpsichore loja ined.	0 1 1 0 1 ? 0 0 0 1 0 0 0 - 1 0 0 0 0 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 0 0 0 0 2 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore longicaulis	2 1 1 0 1 ? 1 1 0 0 ? 0 0 - 1 0 1 1 0 1 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 0 1 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1
Terpsichore longipilosa	0 1 1 0 1 1 0 0 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 1 0 1 0 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 0 0 0 ? 0 ? 0 1 1 1 1
Terpsichore longisetosa	A ? 0 0 1 1 0 1 0 1 ? 0 0 - 1 0 0 1 0 0 1 0 0 0 1 1 0 1 0 ? 0 0 - 0 0 - 0 0 1 1 0 1 0 0 4 0 0 0 0 0 ? 0 1 1 1 1
Terpsichore mollissima	0 2 0 0 0 ? 0 ? 0 1 ? 1 0 - 0 - - - - - - - - - - - - - - - - - 1 0 - 0 0 1 1 0 2 0 0 3 1 1 1 ? 0 ? 0 0 1 1 0
Terpsichore nana	0 0 1 0 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 1 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 1 0 0 0 1 0 0 1 0 0 3 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore pichinchae	0 1 1 0 1 1 0 0 0 1 0 0 0 - 1 0 0 0 0 1 1 1 1 0 0 1 0 0 2 - 0 1 0 0 0 - 0 0 1 1 0 1 0 0 3 1 0 0 ? 0 ? 0 0 1 1 1
Terpsichore pichinchense	0 2 1 0 1 ? 0 0 0 1 ? 0 0 - 1 0 0 0 0 1 1 1 1 0 1 1 0 0 2 - 0 1 0 0 1 0 0 0 1 1 0 1 0 0 3 1 1 1 0 0 0 0 0 1 A 0
Terpsichore praeceps	1 ? 1 0 1 ? 0 1 0 0 ? 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 1 0 0 0 0 1 0 1 0 - 0 0 1 1 0 2 0 0 3 1 1 1 ? 0 ? 0 0 1 1 1
Terpsichore sp. aff. *semihirsuta* ined. 2	0 2 1 0 1 ? 0 1 0 1 ? 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1
Terpsichore sp. aff. *semihirsuta* ined. 3	0 2 1 0 1 ? 0 1 0 1 ? 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1
Terpsichore semihirsuta	0 2 1 0 1 ? 0 1 1 1 0 0 0 - 1 0 1 1 0 0 0 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1

Appendix B. Morphological matrix, characters 0—55; key: A = 0,1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

Taxon	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5
Terpsichore sp. aff. *semihirsuta* ined. 1	0 2 1 0 1 1 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 0 0 0 ? 0 ? 0 1 1 1 1
Terpsichore senilis	0 2 0 0 0 ? 0 0 0 1 0 1 0 - 1 0 1 1 0 0 0 0 0 0 0 1 0 0 1 - 1 0 - 1 0 - 0 0 1 1 0 2 0 0 3 1 1 1 ? 0 ? 0 0 1 1 0
Terpsichore sp. Sundue 1167	0 2 1 0 1 ? 0 ? 0 1 ? 0 0 - 1 0 1 1 1 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 1 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1
Terpsichore sp. aff. *subtilis* ined.	0 2 1 0 1 ? 0 1 0 1 ? 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 ? 0 - 0 0 1 1 0 2 0 0 2 1 1 1 ? 0 ? 0 1 1 1 1
Terpsichore sp. Sundue 1160	0 2 1 0 1 ? 0 ? 0 1 ? 0 0 - 1 0 1 1 0 1 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1
Terpsichore subscabra	0 2 1 0 1 1 0 0 0 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 1 1 0 1 0 - 0 1 0 1 0 - 0 0 1 1 0 2 0 0 3 0 0 1 ? 0 ? 0 0 1 1 1
Terpsichore subtilis	0 2 1 0 1 ? 0 ? 0 1 0 0 0 - 1 0 1 1 1 0 1 0 1 0 2 1 0 0 1 - 0 ? ? 0 0 - 0 0 1 1 0 2 0 0 2 1 1 1 ? 0 ? 0 1 1 1 0
Terpsichore taxifolia	0 1 1 0 1 1 0 ? 0 1 ? 0 0 - 1 0 1 1 0 0 0 0 0 0 2 1 1 0 1 0 0 1 0 0 0 - 0 0 1 1 1 2 0 0 3 0 1 0 ? 0 ? 0 1 ? 1 1
Terpsichore aff. *taxifolia*	0 1 1 0 1 1 0 ? 0 1 ? 0 0 - 1 0 1 1 0 0 0 0 0 0 2 1 1 0 1 0 0 1 0 0 0 - 0 0 1 1 1 2 0 0 3 0 1 0 ? 0 ? 0 1 1 1 1
Terpsichore vascoi ined.	0 2 1 0 1 1 0 1 0 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 1 0 0 0 - 0 1 0 0 0 - 0 0 1 1 0 2 0 0 3 0 0 0 ? 0 ? 0 1 1 1 1
Terpsichore zeledoniana	0 1 1 0 1 1 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 0 - - - 0 0 0 - 0 0 - 0 0 1 1 1 2 0 0 3 1 0 0 ? 0 ? 0 1 1 1 1
Xiphopteris conjunctisora	? 2 0 0 1 1 0 0 0 1 1 0 0 - 1 0 0 1 0 1 1 1 0 1 1 0 - - - 0 0 0 - 0 0 - 0 0 1 1 1 2 0 0 2 1 1 0 ? 0 ? 0 0 0 0 0
Zygophlebia mathewsii	0 2 1 0 1 1 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 0 - - - 0 0 1 0 0 0 - 0 0 1 1 1 2 1 0 1 1 0 2 0 0 0 0 1 0 0 0
Zygophlebia sectifrons	0 2 1 0 1 1 0 1 1 1 0 0 0 - 1 0 1 1 0 0 1 0 0 0 2 0 - - - 0 0 1 0 0 0 - 0 0 1 1 1 2 1 1 1 1 0 2 ? 0 ? 0 0 0 0 0

Appendix B. Morphological matrix, characters 56—110; key: A = 0,1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

	1 1 1 1 1 1 1 1 1 1 1 (characters 100–110)
	5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9 0 0 0 0 0 0 0 0 0 0 1
Taxon	**6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0**
Calymmodon gracilis	0 - - 0 ? 0 1 0 0 - 1 0 1 1 0 1 0 1 1 1 1 1 1 1 - - 0 0 0 0 1 1 0 ? - 0 1 0 ? ? 0 1 0 - - 1 0 1 0 1 1 1 ? 0 0
Calymmodon luerssenianus	? ? ? 0 - 0 ? ? 0 - 1 0 1 1 0 1 0 1 1 - - - - - - - ? ? 0 0 0 1 1 0 - 0 1 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Campyloneurum angustifolium	0 0 0 2 1 1 1 0 1 1 0 - - - - - - - - - 0 - - - - - ? 0 1 0 1 0 0 0 - 0 0 0 0 - 0 0 0 - - 0 0 0 0 0 0 0 0 0 0
Ceradenia aulaeifolia	1 0 0 1 1 0 0 - 0 - 1 0 1 1 0 1 0 0 0 0 1 2 2 3 - - - 1 0 0 1 0 0 0 - 0 0 0 1 1 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia fucoides	0 0 0 0 - 0 0 - 0 - 1 0 1 0 0 0 - 0 0 0 1 2 2 2 0 1 ? 0 0 0 2 0 1 0 - 0 0 0 1 1 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia intonsa	0 0 0 1 1 0 0 - 0 - 1 0 1 1 0 1 0 1 1 1 1 A 2 3 - - ? 1 0 0 2 0 0 0 - 0 0 0 1 2 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia jungermannioides	? ? ? 1 1 0 0 - 0 - 1 0 1 1 0 1 0 1 1 ? 1 0 1 2 0 1 ? ? 0 0 1 0 0 0 - 0 0 0 ? - ? 1 0 - - 1 0 1 0 1 1 1 0 0 0
Ceradenia kalberyeri Sundue 1759	0 0 0 1 1 0 0 - 0 - 1 0 1 1 0 0 - 0 1 0 1 D 2 3 - - ? 1 0 0 1 0 0 0 - 0 0 0 1 0 0 1 0 - - 1 0 1 1 1 1 1 ? 0 0
Ceradenia kalbreyeri sundue 1213	0 0 0 1 1 0 0 - 0 - 1 0 0 1 0 1 0 0 0 0 1 E 2 1 - - ? 1 0 0 1 0 1 0 - 0 0 0 1 1 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia pilipes	0 0 0 1 1 0 0 - 0 - 1 0 1 0 0 0 - 0 0 0 1 2 2 H 0 1 ? 1 0 0 1 1 0 0 - 0 0 0 1 1 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia sp. aff. *kalbreyeri* Vasco 701	? 0 0 1 1 0 0 - 0 - 1 0 1 ? 0 0 - ? 0 ? 1 0 A 2 0 1 ? 0 0 0 2 0 1 1 0 0 0 0 1 1 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia sp. ined. 1 Sundue 1238	0 0 0 1 1 0 0 - 0 - 1 0 1 1 0 1 0 0 0 0 1 2 2 I 1 1 ? 1 0 0 1 0 1 0 - 0 0 0 1 1 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia sp. Moran 7520	0 0 0 - 1 0 0 - 0 - 1 0 1 - 0 1 0 - 1 - - - - - - - ? ? 0 0 2 0 1 0 - 0 0 0 1 1 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia sp. ined. 1 Sundue 1242	0 0 0 1 1 0 0 - 0 - 1 0 1 1 0 1 0 0 0 0 1 2 2 I 1 - ? 1 0 0 1 0 1 0 - 0 0 0 1 1 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ceradenia spixiana	? 0 - 1 1 0 0 - 0 - 1 0 1 ? 0 1 0 ? 1 ? 1 2 2 ? ? ? ? 0 0 0 1 0 0 0 - 0 0 0 1 J 0 1 0 - - 1 0 1 1 1 1 1 0 0 0
Chrysogrammitis musgraveana	? ? ? 2 1 0 0 0 0 - 1 0 - - - - - - - - 1 - - - - - ? ? 0 0 - 1 0 0 - 0 0 0 - - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Cochlidium punctatum	- - - 3 - 0 1 0 0 - 0 - - - - - - - - - 1 0 1 3 - - 2 0 0 1 0 1 2 1 0 0 0 0 0 - ? 1 0 - - 1 1 1 1 1 1 1 ? 0 0
Cochlidium rostratum	- - - 3 - 0 0 - 0 - 0 - - - - - - - - - 0 - - - - - ? 0 0 1 0 1 2 1 1 0 0 0 ? ? ? 1 0 - - 1 0 1 0 1 1 1 3 0 0
Cochlidium seminudum	- - - 3 - 0 0 - 0 - 0 - - - - - - - - - 1 0 F 3 - - 2 0 0 1 0 1 2 0 - 0 0 0 0 - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ctenopteris heterophylla	? ? ? 1 1 0 1 0 0 - 1 0 ? ? ? ? ? ? ? ? 1 - - - - - ? ? 0 0 - 1 0 0 - 0 0 0 - - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ctenopteris lasiostipes	? ? ? 1 1 0 1 0 0 - 1 0 ? ? ? ? ? ? ? ? 1 - - - - - ? ? 0 0 - 1 0 0 - 0 0 0 - - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ctenopteris nutans	? ? ? 1 1 0 0 0 0 - 1 0 ? ? ? ? ? ? ? ? 1 - - - - - ? ? 0 0 - 1 0 0 - 0 0 0 - - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ctenopteris repandula	? ? ? 1 1 0 1 0 0 - 1 0 ? ? ? ? ? ? ? ? 1 - - - - - ? ? 0 0 - 1 0 0 - 0 0 0 - - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Ctenopteris rhodocarpa	? ? ? 1 1 0 0 0 0 - 1 0 ? ? ? ? ? ? ? ? 1 - - - - - ? ? 0 0 - 1 0 0 - 0 0 0 - - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Enterosora barbatula	0 ? ? 2 1 A 0 - 0 - 1 0 1 1 0 1 0 1 1 1 1 ? 2 2 1 - 0 0 0 0 1 0 1 1 0 0 0 0 1 2 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Enterosora enterosoroides	0 0 0 1 1 0 0 - 0 - 1 0 1 0 0 1 0 0 0 0 1 1 2 2 1 0 0 0 0 0 1 0 1 1 1 0 0 0 0 - 0 1 0 - - 1 0 1 1 1 1 1 0 0 0
Enterosora percrassa	0 0 0 1 1 1 0 - 0 - 1 0 1 1 0 1 0 1 1 ? 0 ? ? ? ? ? ? 0 0 0 1 0 1 1 1 0 0 0 0 - 0 1 0 - - 1 0 1 1 1 1 1 0 0 0
Enterosora trichosora	0 0 0 1 1 0 0 - 0 - 1 0 1 1 0 1 0 1 1 ? 1 0 2 2 1 - ? 0 0 0 1 0 2 1 0 0 0 0 0 - 1 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Enterosora trifurcata	0 0 0 1 1 A 0 - 0 - 1 0 1 1 0 0 - 0 0 0 1 2 2 3 - - ? ? 0 0 1 0 2 1 0 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 0 0 0
Grammitis billardieri	0 0 0 1 1 0 0 - 0 - 1 0 1 0 0 0 - 0 0 0 1 H 2 0 - - 1 0 0 0 0 1 1 1 0 1 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 0 0 0
Grammitis ciliata	0 ? ? 0 - 0 0 - 0 - 0 - - - - - - - - - 1 ? ? ? ? ? ? ? 0 0 2 0 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 0 1 1 1 ? 0 0
Grammitis deplanchei	0 0 0 1 0 0 0 - 0 - 0 - - - - - - - - - 0 - - - - - ? ? 0 0 2 1 1 0 - 0 0 0 0 - 0 1 1 1 1 1 0 1 0 1 1 1 ? 0 0
Grammitis forbesiana	? ? ? 0 - 0 0 - 0 - 1 - - - - - - - - - 0 - - - - - ? ? 0 0 0 0 0 0 - 0 0 0 0 - 0 1 1 1 1 1 0 1 ? 1 1 1 ? 0 0
Grammitis knutsfordiana	0 0 0 1 1 0 0 - 0 - 1 0 1 1 0 1 0 1 1 0 0 - - - - - ? 0 0 0 0 1 1 0 - 0 0 0 0 - 1 1 1 0 1 1 0 1 0 1 1 1 ? 0 0
Grammitis melanoloma	? ? ? 1 0 0 0 - 0 - 0 - - - - - - - - - 0 - - - - - ? ? 0 0 0 1 0 0 - 0 0 0 0 - ? 1 0 - - 1 0 1 ? 1 1 1 0 0 0
Grammitis parva	? ? ? 1 0 0 0 - 0 - 1 - - - - - - - - - 1 - - - - - ? ? 0 0 0 1 0 0 - 0 0 0 0 - - 1 1 0 1 1 0 1 ? 1 1 1 ? 0 0
Grammitis poeppigiana	- - - 1 0 0 0 - 0 - 0 - - - - - - - - - 1 2 2 3 - - 1 0 0 0 0 1 1 0 - 0 0 0 0 - 0 1 0 0 - 1 0 1 1 1 1 1 0 0 0
Grammitis pseudociliata	? ? ? 0 - 0 0 - 0 - 1 0 ? ? ? ? ? ? ? ? 1 - - - - - ? ? 0 0 0 1 A 0 - 0 0 0 0 - - 1 0 - - 1 0 1 1 1 1 1 0 0 0
Lelligeria barbensis	1 ? ? 0 - 0 1 0 0 - 0 - - - - - - - - - 1 1 1 0 - - ? ? 0 0 - - - - - - 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lelligeria hellwigii	- - - 3 - ? 1 0 0 - 0 - - - - - - - - - 1 1 1 0 - - 0 0 0 0 0 1 1 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lelligeria myosuroides	0 - - 3 - ? 1 0 0 - 0 - - - - - - - - - 1 1 1 0 - - 1 0 0 0 0 1 1 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0

Appendix B. Morphological matrix, characters 56—110; key: A = 0,1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

Taxon	**1 1 1 1 1 1 1 1 1 1 1** **5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9 0 0 0 0 0 0 0 0 0 0 1** **6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0**
Lelligeria prionodes	0 - - 3 - ? 1 0 0 - 0 - - - - - - - - - 1 1 1 0 - - 0 0 0 0 0 1 1 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria apiculata	0 0 0 0 - 0 1 0 0 - 0 - - - - - - - - - 1 1 F 0 - - ? 1 0 0 1 1 0 0 - 0 0 0 0 - - 1 0 - - 1 0 1 1 1 1 1 ? 0 0
Lellingeria hirsuta	1 ? ? 0 - 0 1 0 0 - 0 - - - - - - - - - 1 0 3 0 - - 0 0 0 0 1 ? 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria humilis	0 0 0 0 - 0 1 0 0 - 0 - - - - - - - - - 1 2 F 0 - - ? 0 0 0 1 0 0 0 - 0 1 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria limula	0 0 0 0 - 0 1 0 0 - 0 - - - - - - - - - 1 1 1 0 - - ? 0 0 1 0 1 2 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 3 0 0
Lellingeria major	0 0 0 0 - 0 1 1 0 - 0 - - - - - - - - - 1 1 1 0 - - ? 0 0 0 1 1 0 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria myosuroides	0 - - 3 - ? 1 0 0 - 0 - - - - - - - - - 1 1 1 0 - - 1 0 0 0 0 1 1 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria oreophila	0 0 0 0 - 0 1 0 0 - 0 - - - - - - - - - 1 2 F 0 - - ? 0 0 0 1 1 0 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria pseudomitchellae	0 0 0 0 - 0 1 0 0 - 1 0 1 1 0 1 1 1 1 1 1 1 0 1 - - 0 0 0 0 0 1 0 0 - 0 0 0 0 0 - 1 0 - - 1 0 1 1 1 1 1 ? 0 0
Lellingeria saffordii	0 - - 3 - ? 1 0 0 - 0 - - - - - - - - - 1 1 1 0 - - 1 0 0 0 0 1 1 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria schenckei	0 0 0 0 - 0 1 0 0 - 1 0 1 1 ? 1 1 0 1 0 1 1 0 0 - - 0 0 0 0 0 1 0 0 - 0 0 0 0 0 0 1 0 - - 1 0 1 1 1 1 1 ? 0 0
Lellingeria sp aff *hirsuta* Sundue 1159	0 0 0 0 - 0 1 1 0 - 0 - - - - - - - - - 1 1 1 0 - - ? 1 0 0 1 1 0 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria sp. aff *humilis* ined. Sundue 1126	0 0 0 0 - 0 1 1 0 - 0 - - - - - - - - - 1 1 1 0 - - ? 0 0 0 1 0 0 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria subsessilis	0 0 0 0 - 0 1 1 0 - 0 - - - - - - - - - 1 1 1 0 - - ? 1 0 0 1 0 0 1 - 1 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria suprasculpta Sundue 1767	0 0 0 0 - 0 1 0 0 - 0 - - - - - - - - - 0 - - - - - ? 0 0 0 0 0 0 1 - 1 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Lellingeria suspensa	0 0 0 0 - 0 1 0 0 - 0 - - - - - - - - - 1 1 A 3 - - ? 0 0 0 1 0 0 1 - 1 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Melpomene anazalea ined.	0 0 0 0 - 0 1 0 0 - 1 0 1 1 0 1 0 1 1 1 1 1 2 3 - - ? 0 0 0 1 0 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 ? 1 1 1 ? 0 1
Melpomene firma	1 0 0 0 - 0 1 0 0 - 1 0 1 1 0 0 - 0 1 1 1 1 D J - - ? 1 0 0 0 1 0 0 - 0 0 0 0 - 1 1 0 - - 1 1 1 ? 1 1 1 ? 0 1
Melpomene flabelliformis	0 0 0 0 - 0 1 0 0 - 1 0 0 0 0 0 - 0 0 0 1 1 2 3 - - ? 1 0 0 1 1 0 0 - 0 0 0 0 - 1 1 0 - - 1 2 1 0 1 1 1 0 0 1
Melpomene moniliformis	0 0 0 0 - 0 1 0 0 - 1 0 1 1 0 0 - 0 0 0 1 D 2 3 - - 0 0 0 0 1 1 ? 0 - 0 0 0 0 - 0 1 0 - - 1 1 1 ? 1 1 1 0 0 1
Melpomene occidentalis ined.	1 - - 0 - 0 1 0 0 - 1 0 0 0 ? 0 - 0 1 0 1 1 2 3 - - 0 1 0 0 0 1 1 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 1
Melpomene personata ined.	0 0 0 0 - 0 1 0 0 - 1 0 1 0 0 1 0 1 1 0 1 1 2 3 - - - 0 0 0 0 0 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 ? 1 1 1 ? 0 1
Melpomene pseudonutans	0 0 0 0 - 0 1 0 0 - 1 0 0 0 0 0 - 0 1 0 1 F 2 3 - - 0 1 0 0 1 1 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 1 1 1 1 0 0 1
Melpomene vernicosa	0 0 0 0 - 0 1 0 0 - 1 0 1 1 0 1 1 0 1 0 1 1 F J - - 0 0 0 0 1 1 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 ? 1 1 1 ? 0 1
Microgramma percussa	0 0 0 2 1 1 1 0 1 1 0 - - - - - - - - - 0 - - - - - ? 0 1 0 1 0 0 0 - 1 0 0 1 - 0 0 0 - - 0 0 0 0 0 0 0 0 0 0
Microgramma squamulosa	0 0 0 2 1 1 1 0 1 1 0 - - - - - - - - - 0 - - - - - ? 0 1 0 1 0 0 0 - 0 0 0 1 - 0 0 0 - - 0 0 0 0 0 0 0 0 0 0
Micropolypodium hyalinum	- - - 0 - 0 1 0 0 - 1 0 1 1 0 1 0 1 1 0 1 1 2 3 - - 1 0 0 0 0 1 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 1 1 1 1 0 0 0
Micropolypodium taenifolium	- - - 0 - 0 1 0 0 - 1 0 1 1 0 1 0 0 1 0 1 1 2 1 - - 1 0 0 0 0 1 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 2 1 1 1 0 0 0
Micropolypodium zurquinum	- - - 0 - 0 1 0 0 - 1 0 1 1 0 1 0 1 1 1 1 F 2 3 - - 1 0 0 0 0 1 0 0 - 0 0 0 0 - - 1 0 - - 1 0 1 ? 1 1 1 0 0 0
Oreogrammitis hookeri	0 0 0 1 1 0 0 - 0 - 1 0 1 1 0 1 0 1 1 0 1 0 0 3 - - ? 0 0 0 0 0 0 0 - 0 0 0 0 - - 1 1 0 1 1 0 1 0 1 1 1 ? 0 0
Pecluma alfredii	0 - - 1 1 0 1 0 0 - 0 - - - - - - - - - 1 0 F 3 - - 0 0 0 0 2 0 0 0 - 0 0 0 0 - - 0 0 - - 0 0 0 0 0 0 0 0 0 0
Polypodium glycyrrhiza	0 0 0 1 1 A 1 0 1 0 0 - - - - - - - - - 1 0 0 3 - - 0 0 1 0 0 0 0 0 - 0 0 0 0 - - 0 0 - - 0 0 0 0 0 0 0 0 0 0
Prosaptia alata	0 0 0 1 0 0 0 - 0 - 1 0 1 1 0 1 0 0 1 0 1 1 1 0 - - 1 0 ? 0 2 1 0 1 1 1 0 1 0 - 0 1 0 - - 1 0 1 0 1 1 1 0 0 0
Prosaptia contigua	0 - - 0 - 0 0 - 0 - 1 0 1 1 0 1 0 0 1 0 1 1 1 0 - - 1 1 ? 0 2 1 0 1 1 1 0 1 0 - 0 1 0 - - 1 0 1 0 1 1 1 0 0 0
Prosaptia obliquata	0 0 0 1 1 0 0 - 0 - 1 0 1 1 0 1 0 0 1 0 1 1 1 0 - - 1 0 0 0 1 1 0 1 1 1 0 1 0 - 0 1 0 - - 1 0 1 0 1 1 1 0 0 0
Prosaptia pubipes	1 - - 0 - 0 0 - 0 - 1 0 1 1 0 1 0 0 1 1 1 1 1 0 - - 1 0 ? 0 2 1 0 1 1 1 0 1 0 - 0 1 0 - - 1 0 1 0 1 1 1 0 0 0
Scleroglossum sulcatum	- - - 3 - ? 0 - 0 - 0 - - - - - - - - - 1 A 2 3 - - 1 0 0 1 2 1 2 1 0 0 0 1 0 - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Scleroglossum sulcatum	- - - 3 - ? 0 - 0 - 0 - - - - - - - - - 1 A 2 3 - - 1 0 0 1 2 1 2 1 0 0 0 1 0 - ? 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Terpisichore pacifica ined.	1 1 0 0 - 0 1 1 0 - 1 0 1 1 0 0 - 0 1 0 1 1 1 1 - - 1 0 0 0 1 0 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 ? 1 1 1 ? 1 0
Terpsichore achilleifolia	0 0 0 0 1 0 1 0 0 - 1 0 1 1 0 0 - 1 1 1 1 F 2 3 - - 1 0 0 0 0 0 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 1 1 1 1 0 0 0
Terpsichore sp. aff *taxifolia* ined.	1 1 0 0 - 0 1 0 0 - 1 0 1 1 0 0 - 0 1 0 1 1 1 3 - - ? 0 0 0 1 0 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 ? 1 1 1 ? 1 0

Appendix B. Morphological matrix, characters 56—110; key: A = 0,1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

Taxon	0000000000000000000000000000000000000000000011111111111 5555666666666677777777778888888888999999999900000000001 6789012345678901234567890123456789012345678901234567890
Terpsichore sp. aff. *alsopteris* ined. 1	1--0-0110-10111100101113--10002000-0000-010--101?111?10
Terpsichore attenutissima	1--0-0110-10111100101113--10002000-0000-010--101?111?10
Terpsichore sp. aff. *alsopteris* ined. 2	1--0-0110-101110-0101113--10002000-0000-010--101?111?10
Terpsichore amphidasyon	1100-0110-10110101111113--?0001000-0000-110--101?111?10
Terpsichore anfractuosa Jimenez 1399	0--0-0110-10110A10101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Kessler 13517	0--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Lehnert 1035	0--0-0110-101100-0101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Lehnert 315	0--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Lehnert 499	0--0-0110-10110A10101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Kessler 13507	0--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Moran 7567	0--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Moran s.n.	0--0-0100-10110100101113--10000110-0000-110--101?111?10
Terpsichore anfractuosa Lehnert 212	0--0-0110-10110100101113--10000110-0000-110--101?111?10
Terpsichore angustipes sund1237	0--0-0110-101100-A111113--11000010-0000-010--101?111?10
Terpsichore athyrioides	1000-0110-101100-0001113--10001010-0000-010--101?111?10
Terpsichore clathrata	1--0-0100-101100-0101113--11000010-0000-110--101?111?10
Terpsichore clavigera	1--0-0100-101100-0001113--11000110-0000-010--101?111?10
Terpsichore colombiense ined.	1--0-0100-101100-0111113--11000110-0000-110--101-111?10
Terpsichore communis ined.	1--0-0100-1A110101111321--10000000-0000-01100101?111?00
Terpsichore cretata	0000-0110-10100101111120--A1000000-0000-110--101?111?10
Terpsichore cuencana	1000-0110-10110100101113--10000110-0000-110--101?111?10
Terpsichore cultrata	1--0-0100-1D110101111321--10000000-0000-0110010A1111000
Terpsichore david-smithii	0000-0110-101100-0101113--11000110-0000-110--101?111?10
Terpsichore delicatula	0--0-0100-1011010111 1A3211010000000-0000-110--101?111?00
Terpsichore dilatata	1000-0110-101100-0111113--11000110-0000-110--1011111?10
Terpsichore hanekeana	0--110100-10110101101123--10000000-0000-01100101?111000
Terpsichore lanigera	1--0-0100-1A110101111323--10000000-0000-011001010111000
Terpsichore lehmanniana	000110100-1011010111 10A3--00000000-0000-01A00101?111000
Terpsichore leucosticta	1100-0110-10111100101003--10002000-0000-010--101?111?10
Terpsichore loja ined.	1000-0110-10110000111113--11000110-0000-110--1011111?10
Terpsichore longicaulis	1100-0110-101100-0001113--10002000-0000-010--101?111?10
Terpsichore longipilosa	0100-0110-10110101111113--?0001100-0000-010--101?111?10
Terpsichore longisetosa	0--0-0100-101100-1111323--10000000-0000-110--1?1?111?00
Terpsichore mollissima	0--0-0100-1E11010111 10?2110000 2000-0000-01100101?111?00
Terpsichore nana	1000-0110-10110110101AF3--10000110-0000-010--101?111?10
Terpsichore pichinchae	1--0-0110-10110101111113--10000010-0000-110--101?111?10
Terpsichore pichinchense	0000-0110-10110101111123--10000110-0000-110--1011111?10
Terpsichore praeceps	0--0-0110-10110101111113--10002000-0000-010--101?111?00
Terpsichore sp. aff. *semihirsuta* ined. 2	1100-0110-101110-0001003--10002000-0000-010--101?111?10
Terpsichore sp. aff. *semihirsuta* ined. 3	1100-0110-10111100001113--10002000-0000-010--101?111?10
Terpsichore semihirsuta	1100-0110-101110-0001003--10002000-0000-010--101?111?10

Appendix B. Morphological matrix, characters 56—110; key: A = 0,1; B = 0, 1, 2, 3; C = 0, 1, 3; D = 0, 1, 2; E = 0, 2; F = 1, 2; G = 0, 3; H = 2, 3; I = 1, 2, 3; J = 1, 3.

Taxon	**1 1 1 1 1 1 1 1 1 1 1** **5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9 0 0 0 0 0 0 0 0 0 0 1** **6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0**
Terpsichore sp. aff. *semihirsuta* ined. 1	1 1 0 0 - 0 1 1 0 - 1 0 1 1 1 1 1 0 0 0 0 1 1 1 3 - - 1 0 0 0 2 0 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 1 0
Terpsichore senilis	0 - - 0 - 0 1 0 0 - 1 0 1 1 0 1 0 1 1 0 1 3 2 1 - - 0 0 0 0 0 0 0 0 - 0 0 0 0 - 0 1 1 0 0 1 0 0 ? 1 1 1 ? 0 0
Terpsichore sp. Sundue 1167	1 1 0 0 - 0 1 1 0 - 1 0 1 1 0 1 0 0 1 0 1 1 1 3 - - 1 0 0 0 ? ? ? 0 - 0 0 0 0 - ? 1 0 - - 1 0 1 ? 1 1 1 ? 1 0
Terpsichore sp. aff. *subtilis* ined.	1 1 0 0 - 0 1 1 0 - 1 0 1 1 1 1 0 1 1 1 1 1 1 3 - - 1 0 0 0 ? ? 0 0 - 0 0 0 0 - ? 1 ? - - 1 0 1 ? 1 1 1 ? 1 0
Terpsichore sp. Sundue 1160	1 1 0 0 - 0 1 1 0 - 1 0 1 1 0 0 - 1 0 1 1 0 0 3 - - 1 0 0 0 2 0 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 1 0
Terpsichore subscabra	1 - - 0 - 0 1 0 0 - 0 - - - - - - - - - 1 A F 2 1 1 0 1 0 0 0 0 0 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Terpsichore subtilis	0 0 0 0 1 0 1 1 0 - 1 0 1 0 0 1 0 A 1 1 1 1 1 1 - - A 0 0 0 0 0 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 1 1 1 1 ? 1 0
Terpsichore taxifolia	1 1 0 0 - 0 1 1 0 - 1 0 1 1 0 1 0 0 0 0 1 1 1 3 - - 1 0 0 0 1 0 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 1 0
Terpsichore aff. *taxifolia*	1 1 0 0 - 0 1 1 0 - 1 0 1 1 0 1 0 0 0 0 1 1 1 3 - - 1 0 0 0 1 0 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 1 0
Terpsichore vascoi ined.	1 1 0 0 - 0 1 1 0 - 1 0 1 1 1 1 0 0 1 0 1 0 0 3 - - 1 0 0 0 0 0 0 0 - 0 0 0 0 - 0 1 0 - - 1 0 1 ? 1 1 1 ? 1 0
Terpsichore zeledoniana	1 1 0 0 - 0 1 1 0 - 1 0 1 1 1 0 - 0 1 0 1 0 0 3 - - 1 0 0 0 1 0 0 0 - 0 0 0 0 - 1 1 0 - - 1 0 1 ? 1 1 1 ? 1 0
Xiphopteris conjunctisora	0 - - 0 - 0 1 0 0 - A 0 0 0 0 0 - 0 A 0 0 - - - - - ? ? 0 0 0 1 0 0 - 0 0 0 0 - ? 1 0 - - 1 0 1 0 1 1 1 ? 0 0
Zygophlebia mathewsii	0 0 0 1 1 1 0 - 0 - 1 0 1 1 0 1 0 1 1 1 1 2 2 2 1 - ? 0 1 0 1 0 1 0 - 0 0 0 1 2 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0
Zygophlebia sectifrons	0 0 0 1 1 1 0 - 0 - 1 0 1 0 0 0 - 0 0 0 1 0 2 2 1 - ? 0 1 0 1 0 1 0 - 0 0 0 1 2 0 1 0 - - 1 0 1 ? 1 1 1 ? 0 0

Fig. 1. Strict consensus of the 180,000 most parsimonious trees generated from *atpB*, *rbcL*, and *trnLF* plastid sequence data (Length = 3026, CI = 0.37, RI = 0.79). Numbers above nodes indicate boostrap values.

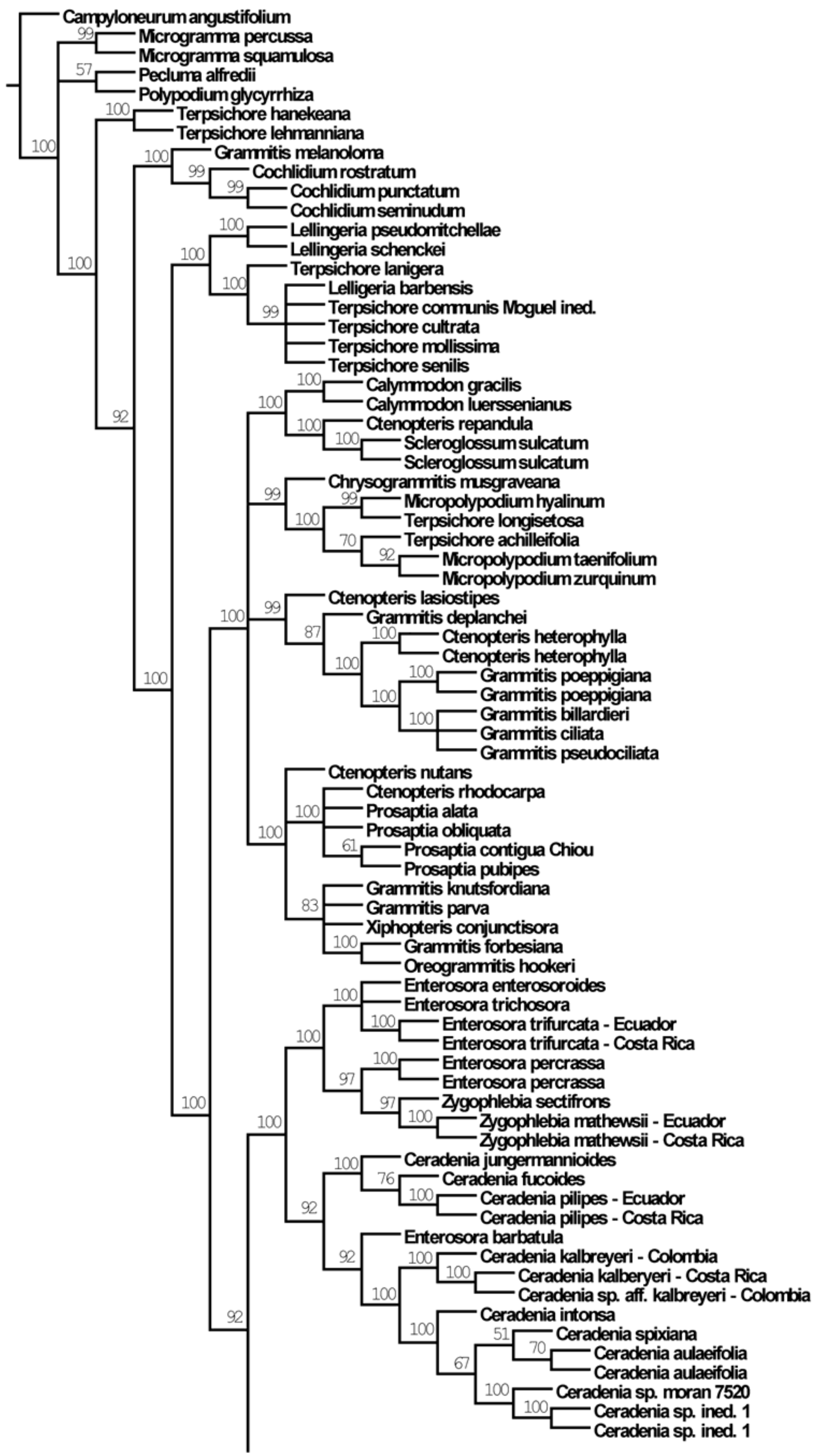
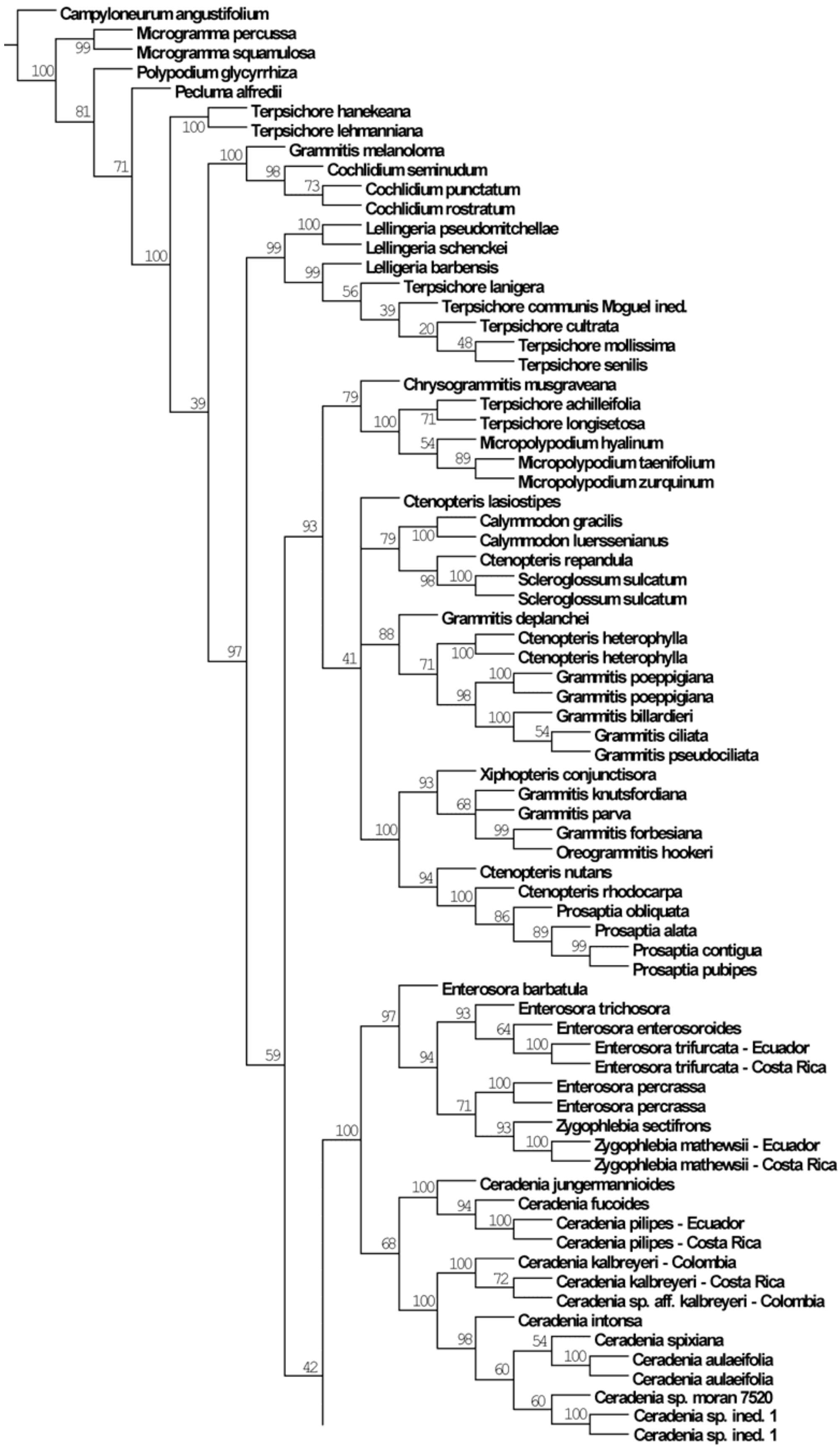

Campyloneurum angustifolium
Microgramma percussa
Microgramma squamulosa
Pecluma alfredii
Polypodium glycyrrhiza
Terpsichore hanekeana
Terpsichore lehmanniana
Grammitis melanoloma
Cochlidium rostratum
Cochlidium punctatum
Cochlidium seminudum
Lellingeria pseudomitchellae
Lellingeria schenckei
Terpsichore lanigera
Lelligeria barbensis
Terpsichore communis Moguel ined.
Terpsichore cultrata
Terpsichore mollissima
Terpsichore senilis
Calymmodon gracilis
Calymmodon luerssenianus
Ctenopteris repandula
Scleroglossum sulcatum
Scleroglossum sulcatum
Chrysogrammitis musgraveana
Micropolypodium hyalinum
Terpsichore longisetosa
Terpsichore achilleifolia
Micropolypodium taenifolium
Micropolypodium zurquinum
Ctenopteris lasiostipes
Grammitis deplanchei
Ctenopteris heterophylla
Ctenopteris heterophylla
Grammitis poeppigiana
Grammitis poeppigiana
Grammitis billardieri
Grammitis ciliata
Grammitis pseudociliata
Ctenopteris nutans
Ctenopteris rhodocarpa
Prosaptia alata
Prosaptia obliquata
Prosaptia contigua Chiou
Prosaptia pubipes
Grammitis knutsfordiana
Grammitis parva
Xiphopteris conjunctisora
Grammitis forbesiana
Oreogrammitis hookeri
Enterosora enterosoroides
Enterosora trichosora
Enterosora trifurcata - Ecuador
Enterosora trifurcata - Costa Rica
Enterosora percrassa
Enterosora percrassa
Zygophlebia sectifrons
Zygophlebia mathewsii - Ecuador
Zygophlebia mathewsii - Costa Rica
Ceradenia jungermannioides
Ceradenia fucoides
Ceradenia pilipes - Ecuador
Ceradenia pilipes - Costa Rica
Enterosora barbatula
Ceradenia kalbreyeri - Colombia
Ceradenia kalberyeri - Costa Rica
Ceradenia sp. aff. kalbreyeri - Colombia
Ceradenia intonsa
Ceradenia spixiana
Ceradenia aulaeifolia
Ceradenia aulaeifolia
Ceradenia sp. moran 7520
Ceradenia sp. ined. 1
Ceradenia sp. ined. 1

Fig. 1 cont. Strict consensus of the 180,000 most parsimonious trees generated from *atpB*, *rbcL*, and *trnLF* plastid sequence data (Length = 3026, CI = 0.37, RI = 0.79). Numbers above nodes indicate boostrap values.


Terpsichore anfractuosa - Mexico
Terpsichore anfractuosa - Bolivia
Terpsichore anfractuosa - Bolivia
Terpsichore anfractuosa - Peru
Terpsichore anfractuosa - Mexico
Terpsichore anfractuosa - Peru
Terpsichore anfractuosa - Ecuador
Terpsichore anfractuosa - Ecuador
Terpsichore anfractuosa - Costa Rica
Terpsichore nana
Terpsichore pichinchense
Terpsichore pichinchense
Terpsichore pichinchense
Terpsichore athyrioides
Terpsichore cuencana
Terpsichore pichinchae
Terpsichore colombiense ined.
Terpsichore colombiense ined.
Terpsichore clathrata
Terpsichore clavigera inded.
Terpsichore dilatata
Terpsichore dilatata
Terpsichore angustipes
Terpsichore angustipes
Terpsichore loja ined.
Terpsichore loja ined.
Terpsichore loja ined.
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore subscabra
Terpsichore subscabra
Terpsichore delicatula
Lellingeria hirsuta
Lelligeria prionodes
Lellingeria limula
Lellingeria limula
Lellingeria limula
Lelligeria myosuroides
Lellingeria myosuroides
Lelligeria hellwigii
Lellingeria saffordii
Melpomene firma
Melpomene occidentalis
Melpomene occidentalis
Melpomene anazalea ined.
Melpomene personata ined.
Melpomene sp. Sundue 1112
Melpomene moniliformis
Melpomene pseudonutans
Melpomene flabelliformis
Lellingeria suprasculpta
Lellingeria suspensa
Lellingeria suspensa
Lellingeria sp aff. humilis ined.
Lellingeria subsessilis - Ecuador
Lellingeria sp aff hirsuta Sundue 1159
Lellingeria subsessilis - Costa Rica
Lellingeria humilis
Lellingeria oreophila
Lellingeria apiculata - Costa Rica
Lellingeria major
Lellingeria apiculata - Brazil
Lellingeria major
Terpsichore cretata
Terpsichore subtilis
Terpsichore subtilis
Terpsichore zeledoniana
Terpisichore pacifiaca ined.
Terpsichore sp. aff. taxifolia ined.
Terpsichore longipilosa inded.
Terpsichore longipilosa ined.
Terpsichore aff. taxifolia Sundue 1161 - Ecuador
Terpsichore taxifolia - Brazil
Terpsichore amphidasyon
Terpsichore amphidasyon
Terpsichore amphidasyon
Terpsichore sp. aff. alsopteris ined. 1 - Bolivia
Terpsichore sp. aff. alsopteris ined. 1 - Bolivia
Terpsichore sp. aff. alsopteris ined. 1 - Bolivia
Terpsichore sp. aff. alsopteris ined. 1 - Bolivia
Terpsichore sp. aff. semihirsuta ined. 1 - Bolivia
Terpsichore sp. aff. semihirsuta ined. 1 - Bolivia
Terpsichore sp. aff. alsopteris ined. 2 - Costa Rica
Terpsichore alsopteris
Terpsichore attenuatissima
Terpsichore attenuatissima
Terpsichore longicaulis
Terpsichore praeceps
Terpsichore sp. aff semihirsuta ined. 2 - Costa Rica
Terpsichore sp. aff. semihirsuta ined. 3 - Mexico
T semihirsuta setose Lehnert 1144
Terpsichore sp. aff. semihirsuta ined. 1 - Peru
Terpsichore sp. aff. semihirsuta ined. 1 - Colombia
Terpsichore sp. aff. semihirsuta ined. 1 - Colombia
Terpsichore sp. Sundue 1167
Terpsichore sp. aff. subtilis ined.
Terpsichore sp. Sundue 1160
Terpsichore vascoi ined.
Terpsichore attenuatissima
Terpsichore semihirsuta s.s.
Terpsichore leucosticta
Terpsichore leucosticta

Fig. 2. Strict consensus of the 180,000 most parsimonious trees generated from the combined set of morphological characters and plastid sequence data (Length = 3956, CI = 0.37, RI = 0.77). Numbers above nodes indicate bootstrap values.



Campyloneurum angustifolium
Microgramma percussa
Microgramma squamulosa
Polypodium glycyrrhiza
Pecluma alfredii
Terpsichore hanekeana
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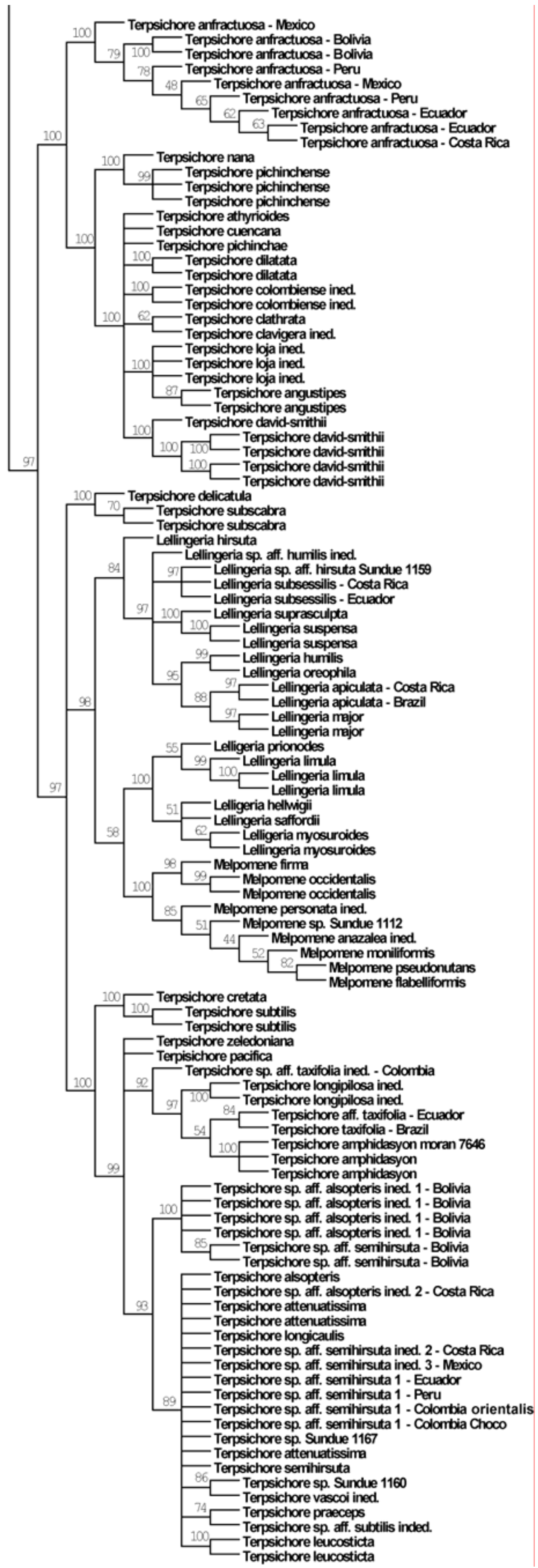
Grammitis melanoloma
Cochlidium seminudum
Cochlidium punctatum
Cochlidium rostratum
Lellingeria pseudomitchellae
Lellingeria schenckei
Lelligeria barbensis
Terpsichore lanigera
Terpsichore communis Moguel ined.
Terpsichore cultrata
Terpsichore mollissima
Terpsichore senilis
Chrysogrammitis musgraveana
Terpsichore achilleifolia
Terpsichore longisetosa
Micropolypodium hyalinum
Micropolypodium taenifolium
Micropolypodium zurquinum
Ctenopteris lasiostipes
Calymmodon gracilis
Calymmodon luerssenianus
Ctenopteris repandula
Scleroglossum sulcatum
Scleroglossum sulcatum
Grammitis deplanchei
Ctenopteris heterophylla
Ctenopteris heterophylla
Grammitis poeppigiana
Grammitis poeppigiana
Grammitis billardieri
Grammitis ciliata
Grammitis pseudociliata
Xiphopteris conjunctisora
Grammitis knutsfordiana
Grammitis parva
Grammitis forbesiana
Oreogrammitis hookeri
Ctenopteris nutans
Ctenopteris rhodocarpa
Prosaptia obliquata
Prosaptia alata
Prosaptia contigua
Prosaptia pubipes
Enterosora barbatula
Enterosora trichosora
Enterosora enterosoroides
Enterosora trifurcata - Ecuador
Enterosora trifurcata - Costa Rica
Enterosora percrassa
Enterosora percrassa
Zygophlebia sectifrons
Zygophlebia mathewsii - Ecuador
Zygophlebia mathewsii - Costa Rica
Ceradenia jungermannioides
Ceradenia fucoides
Ceradenia pilipes - Ecuador
Ceradenia pilipes - Costa Rica
Ceradenia kalbreyeri - Colombia
Ceradenia kalbreyeri - Costa Rica
Ceradenia sp. aff. kalbreyeri - Colombia
Ceradenia intonsa
Ceradenia spixiana
Ceradenia aulaeifolia
Ceradenia aulaeifolia
Ceradenia sp. moran 7520
Ceradenia sp. ined. 1
Ceradenia sp. ined. 1

Fig. 2 cont. Strict consensus of the 180,000 most parsimonious trees generated from the combined set of morphological characters and plastid sequence data (Length = 3956, CI = 0.37, RI = 0.77). Numbers above nodes indicate bootstrap values.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Terpsichore anfractuosa - Bolivia
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Terpsichore anfractuosa - Mexico
Terpsichore anfractuosa - Peru
Terpsichore anfractuosa - Ecuador
Terpsichore anfractuosa - Ecuador
Terpsichore anfractuosa - Costa Rica
Terpsichore nana
Terpsichore pichinchense
Terpsichore pichinchense
Terpsichore pichinchense
Terpsichore athyrioides
Terpsichore cuencana
Terpsichore pichinchae
Terpsichore dilatata
Terpsichore dilatata
Terpsichore colombiense ined.
Terpsichore colombiense ined.
Terpsichore clathrata
Terpsichore clavigera ined.
Terpsichore loja ined.
Terpsichore loja ined.
Terpsichore loja ined.
Terpsichore angustipes
Terpsichore angustipes
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore delicatula
Terpsichore subscabra
Terpsichore subscabra
Lellingeria hirsuta
Lellingeria sp. aff. humilis ined.
Lellingeria sp. aff. hirsuta Sundue 1159
Lellingeria subsessilis - Costa Rica
Lellingeria subsessilis - Ecuador
Lellingeria suprasculpta
Lellingeria suspensa
Lellingeria suspensa
Lellingeria humilis
Lellingeria oreophila
Lellingeria apiculata - Costa Rica
Lellingeria apiculata - Brazil
Lellingeria major
Lellingeria major
Lelligeria prionodes
Lellingeria limula
Lellingeria limula
Lellingeria limula
Lelligeria hellwigii
Lellingeria saffordii
Lelligeria myosuroides
Lellingeria myosuroides
Melpomene firma
Melpomene occidentalis
Melpomene occidentalis
Melpomene personata ined.
Melpomene sp. Sundue 1112
Melpomene anazalea ined.
Melpomene moniliformis
Melpomene pseudonutans
Melpomene flabelliformis
Terpsichore cretata
Terpsichore subtilis
Terpsichore subtilis
Terpsichore zeledoniana
Terpisichore pacifica
Terpsichore sp. aff. taxifolia ined. - Colombia
Terpsichore longipilosa ined.
Terpsichore longipilosa ined.
Terpsichore aff. taxifolia - Ecuador
Terpsichore taxifolia - Brazil
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Terpsichore amphidasyon
Terpsichore amphidasyon
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Terpsichore sp. aff. alsopteris ined. 1 - Bolivia
Terpsichore sp. aff. alsopteris ined. 1 - Bolivia
Terpsichore sp. aff. semihirsuta - Bolivia
Terpsichore sp. aff. semihirsuta - Bolivia
Terpsichore alsopteris
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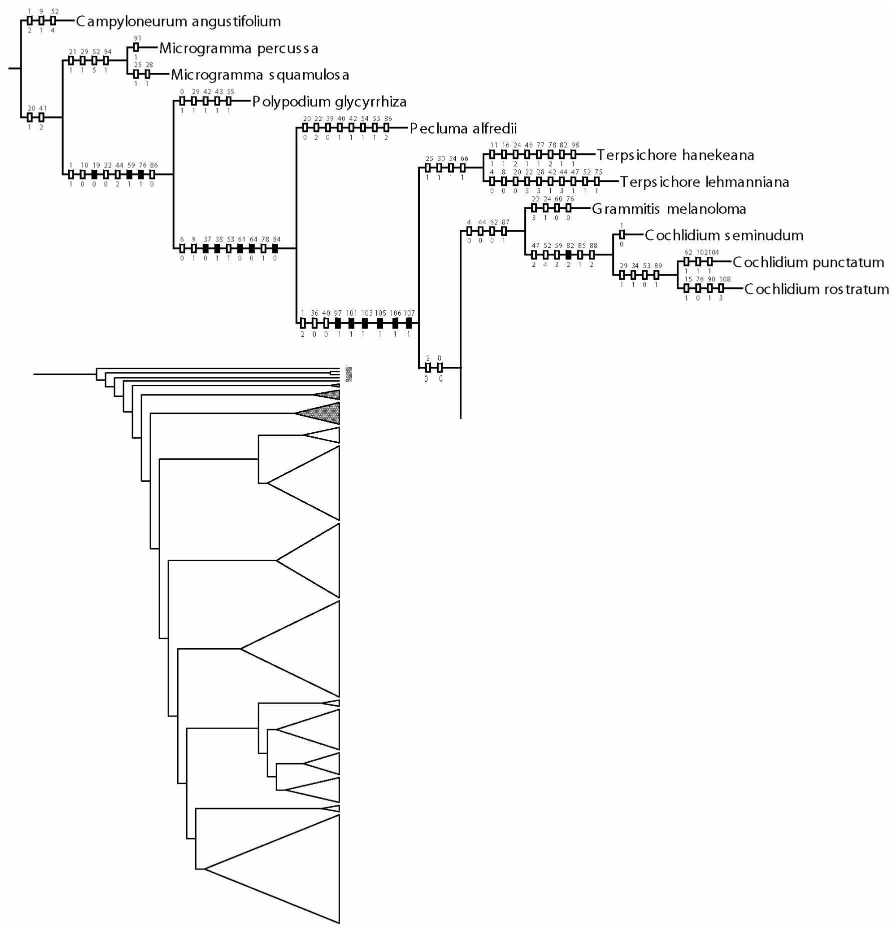
Terpsichore attenuatissima
Terpsichore attenuatissima
Terpsichore longicaulis
Terpsichore sp. aff. semihirsuta ined. 2 - Costa Rica
Terpsichore sp. aff. semihirsuta ined. 3 - Mexico
Terpsichore sp. aff. semihirsuta 1 - Ecuador
Terpsichore sp. aff. semihirsuta 1 - Peru
Terpsichore sp. aff. semihirsuta 1 - Colombia orientalis
Terpsichore sp. aff. semihirsuta 1 - Colombia Choco
Terpsichore sp. Sundue 1167
Terpsichore attenuatissima
Terpsichore semihirsuta
Terpsichore sp. Sundue 1160
Terpsichore vascoi ined.
Terpsichore praeceps
Terpsichore sp. aff. subtilis inded.
Terpsichore leucosticta
Terpsichore leucosticta

Fig. 3, A. Character evolution in grammitid ferns as inferred by illustrating the morphological characters on an exemplar tree from the combined analysis, and detail of area highlighted in grey. Numbers above and below squares are characters and character states from Appendix A and B. Black squares indicate characters without homoplasy. White circles indicate characters with homoplasy.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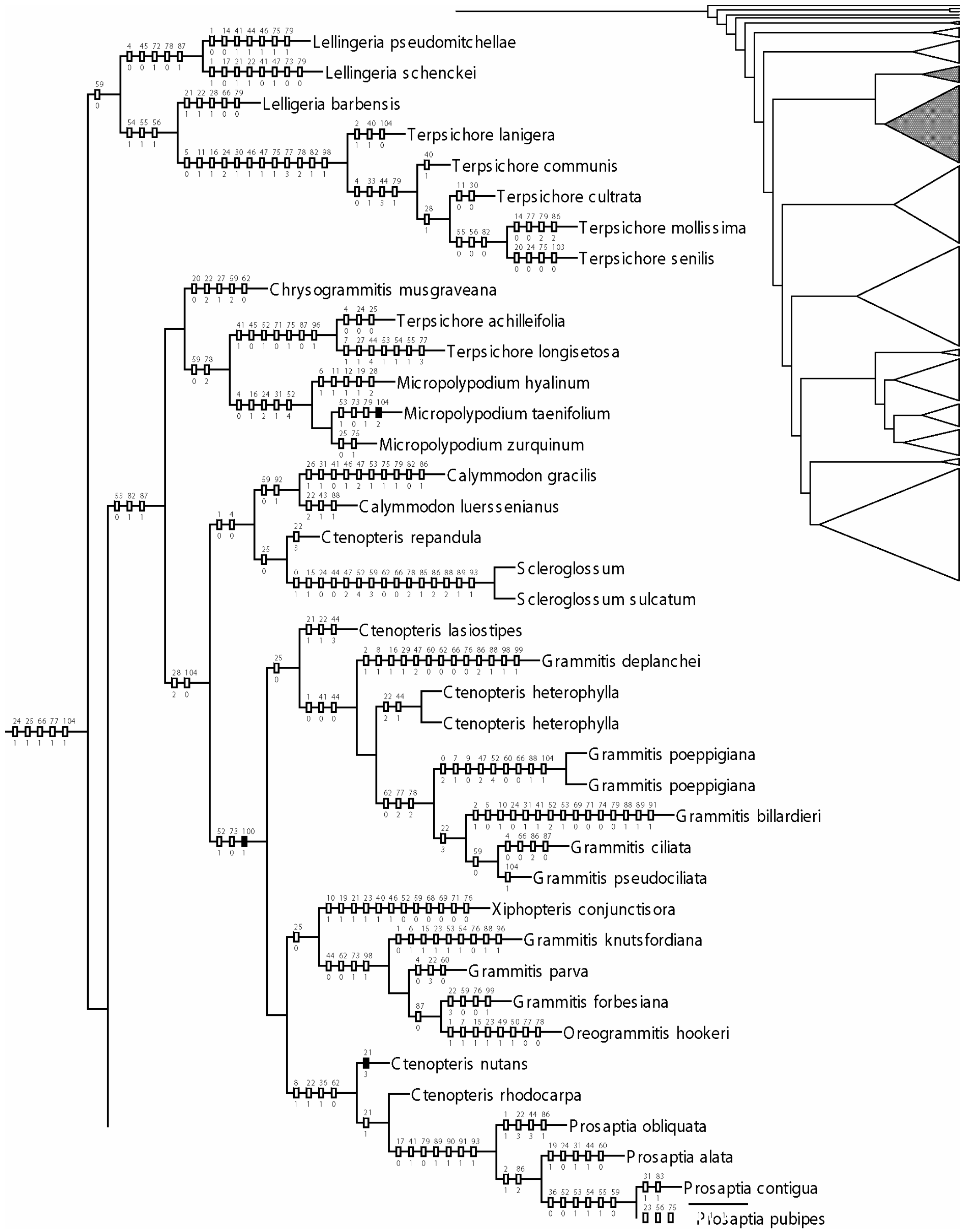
Microgramma percussa
Microgramma squamulosa
Polypodium glycyrrhiza
Pecluma alfredii
Terpsichore hanekeana
Terpsichore lehmanniana
Grammitis melanoloma
Cochlidium seminudum
Cochlidium punctatum
Cochlidium rostratum

Fig. 3, B. Character evolution in grammitid ferns as inferred by illustrating the morphological characters on an exemplar tree from the combined analysis, and detail of area highlighted in grey. Numbers above and below squares are characters and character states from Appendix A and B. Black squares indicate characters without homoplasy. White circles indicate characters with homoplasy.


Lellingeria pseudomitchellae
Lellingeria schenckei
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Terpsichore communis
Terpsichore cultrata
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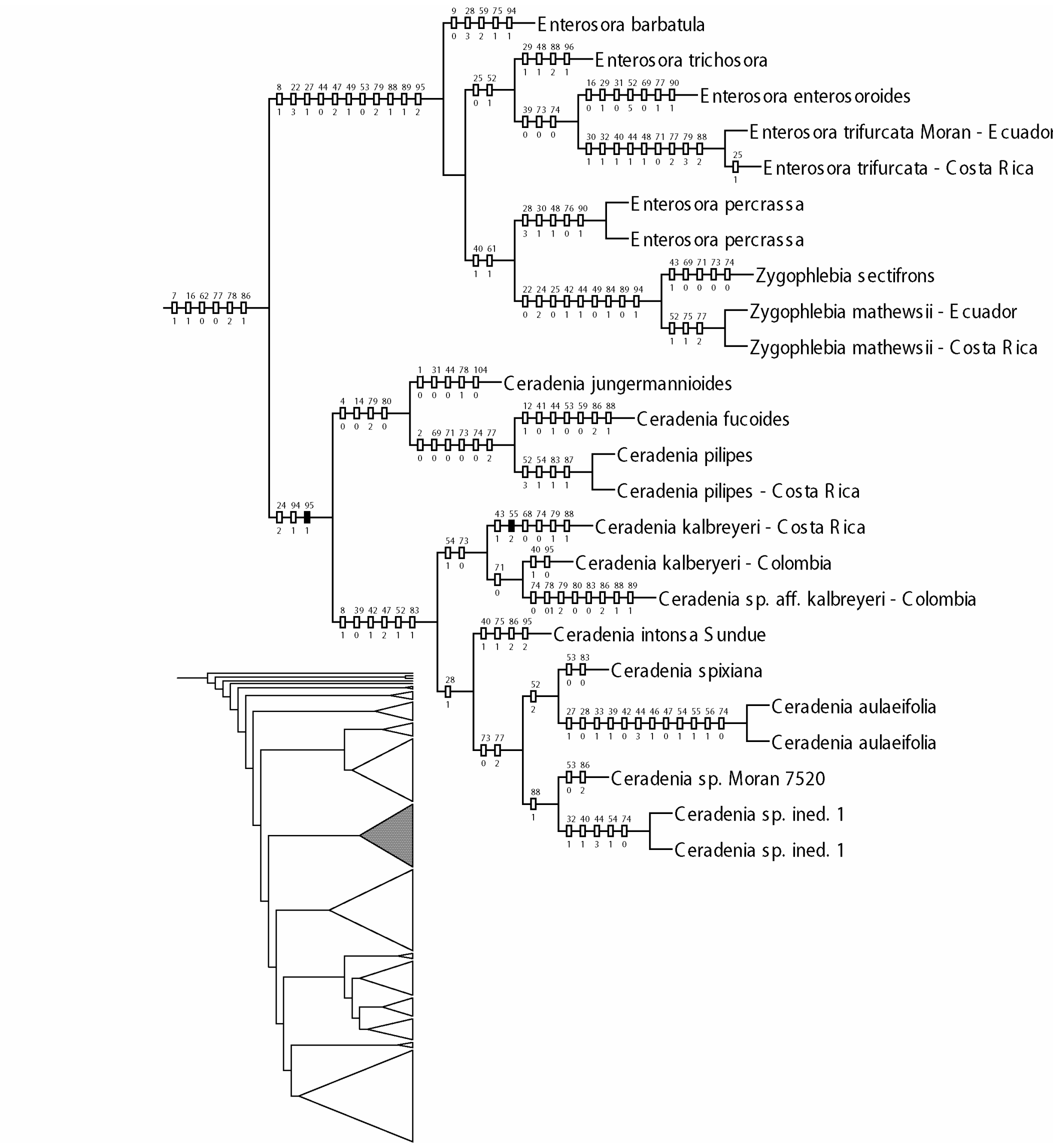
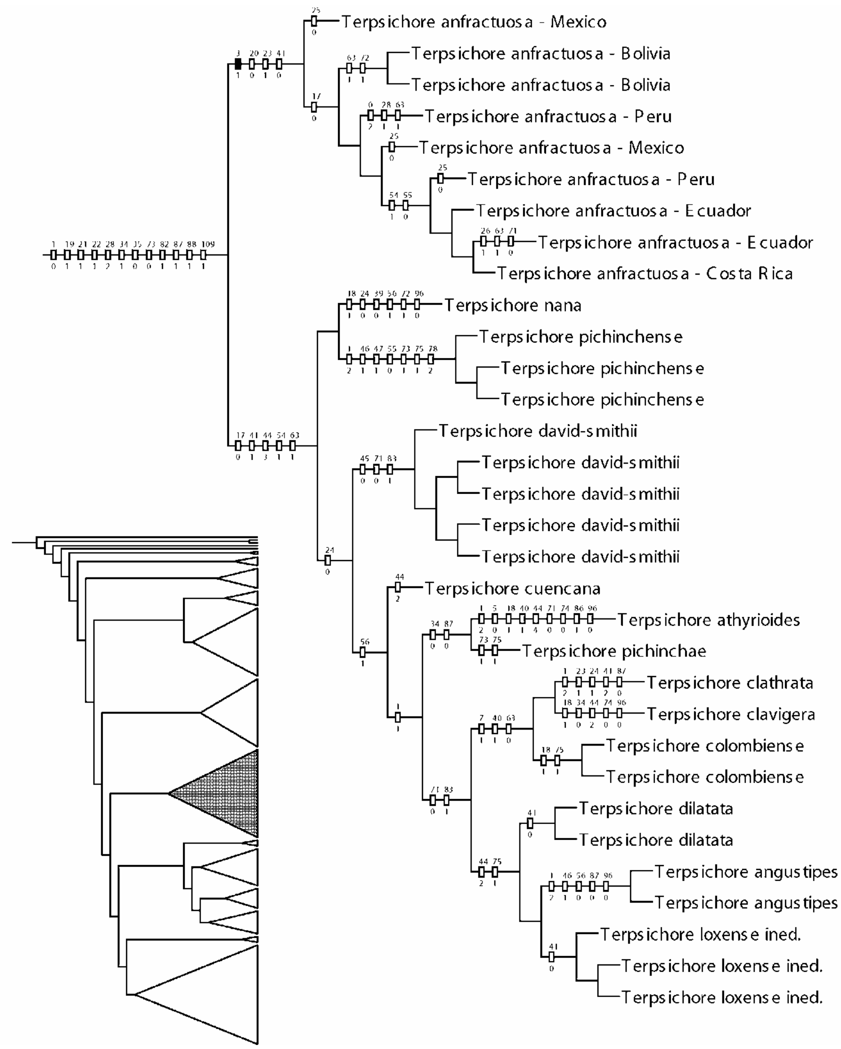
Terpsichore senilis
Chrysogrammitis musgraveana
Terpsichore achilleifolia
Terpsichore longisetosa
Micropolypodium hyalinum
Micropolypodium taenifolium
Micropolypodium zurquinum
Calymmodon gracilis
Calymmodon luerssenianus
Ctenopteris repandula
Scleroglossum
Scleroglossum sulcatum
Ctenopteris lasiostipes
Grammitis deplanchei
Ctenopteris heterophylla
Ctenopteris heterophylla
Grammitis poeppigiana
Grammitis poeppigiana
Grammitis billardieri
Grammitis ciliata
Grammitis pseudociliata
Xiphopteris conjunctisora
Grammitis knutsfordiana
Grammitis parva
Grammitis forbesiana
Oreogrammitis hookeri
Ctenopteris nutans
Ctenopteris rhodocarpa
Prosaptia obliquata
Prosaptia alata
Prosaptia contigua
Prosaptia pubipes

Fig. 3, C. Character evolution in grammitid ferns as inferred by illustrating the morphological characters on an exemplar tree from the combined analysis, and detail of area highlighted in grey. Numbers above and below squares are characters and character states from Appendix A and B. Black squares indicate characters without reversal. White circles indicate characters with homoplasy.



Enterosora barbatula
Enterosora trichosora
Enterosora enterosoroides
Enterosora trifurcata Moran - Ecuador
Enterosora trifurcata - Costa Rica
Enterosora percrassa
Enterosora percrassa
Zygophlebia sectifrons
Zygophlebia mathewsii - Ecuador
Zygophlebia mathewsii - Costa Rica
Ceradenia jungermannioides
Ceradenia fucoides
Ceradenia pilipes
Ceradenia pilipes - Costa Rica
Ceradenia kalbreyeri - Costa Rica
Ceradenia kalberyeri - Colombia
Ceradenia sp. aff. kalbreyeri - Colombia
Ceradenia intonsa Sundue
Ceradenia spixiana
Ceradenia aulaeifolia
Ceradenia aulaeifolia
Ceradenia sp. Moran 7520
Ceradenia sp. ined. 1
Ceradenia sp. ined. 1

Fig. 3, D. Character evolution in grammitid ferns as inferred by illustrating the morphological characters on an exemplar tree from the combined analysis, and detail of area highlighted in grey. Numbers above and below squares are characters and character states from Appendix A and B. Black squares indicate characters without reversal. White circles indicate characters with homoplasy.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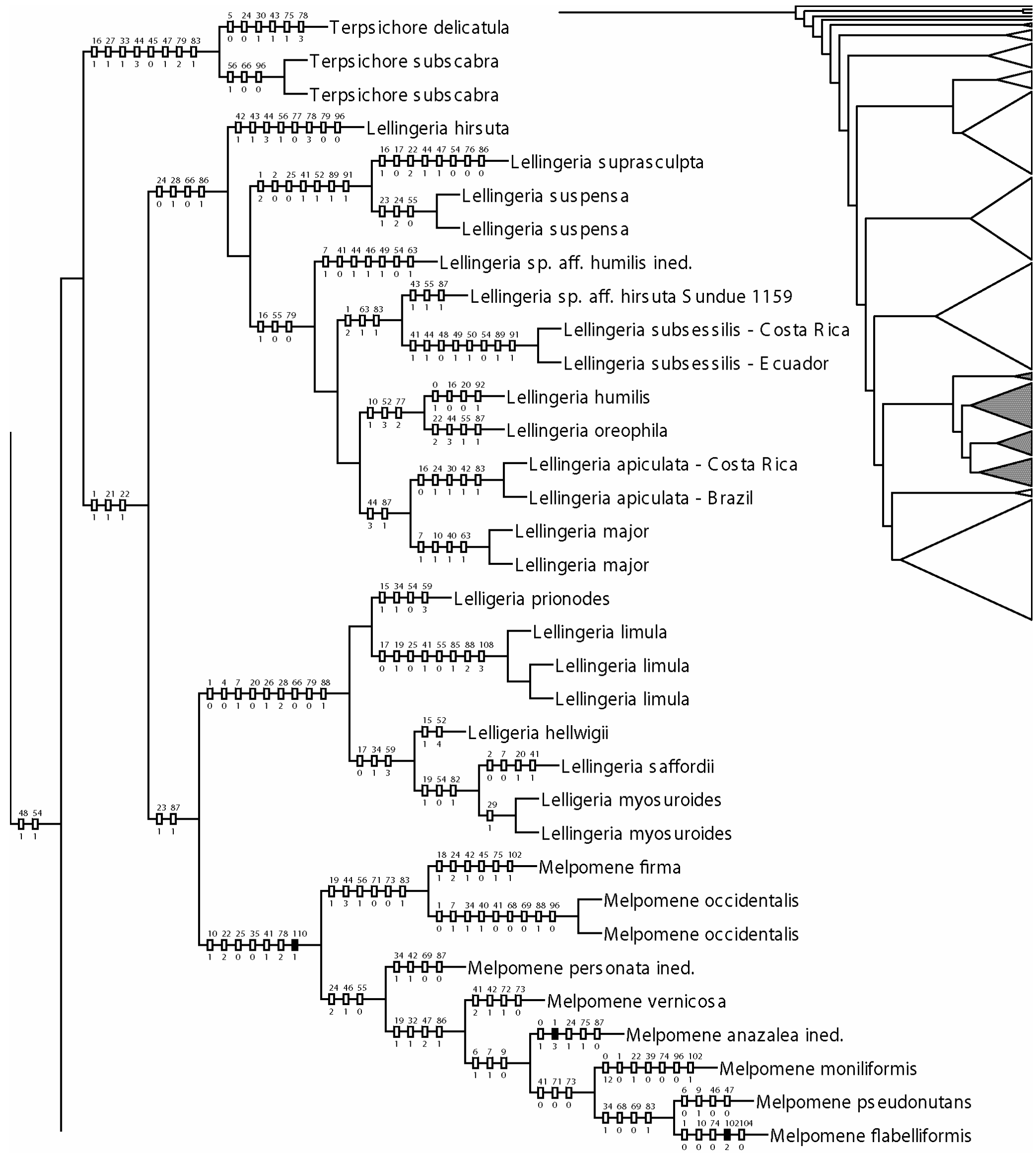
Terpsichore anfractuosa - Bolivia
Terpsichore anfractuosa - Peru
Terpsichore anfractuosa - Mexico
Terpsichore anfractuosa - Peru
Terpsichore anfractuosa - Ecuador
Terpsichore anfractuosa - Ecuador
Terpsichore anfractuosa - Costa Rica
Terpsichore nana
Terpsichore pichinchense
Terpsichore pichinchense
Terpsichore pichinchense
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore david-smithii
Terpsichore cuencana
Terpsichore athyrioides
Terpsichore pichinchae
Terpsichore clathrata
Terpsichore clavigera
Terpsichore colombiense
Terpsichore colombiense
Terpsichore dilatata
Terpsichore dilatata
Terpsichore angustipes
Terpsichore angustipes
Terpsichore loxense ined.
Terpsichore loxense ined.
Terpsichore loxense ined.

Fig. 3, E. Character evolution in grammitid ferns as inferred by illustrating the morphological characters on an exemplar tree from the combined analysis, and detail of area highlighted in grey. Numbers above and below squares are characters and character states from Appendix A and B. Black squares indicate characters without reversal. White circles indicate characters with homoplasy.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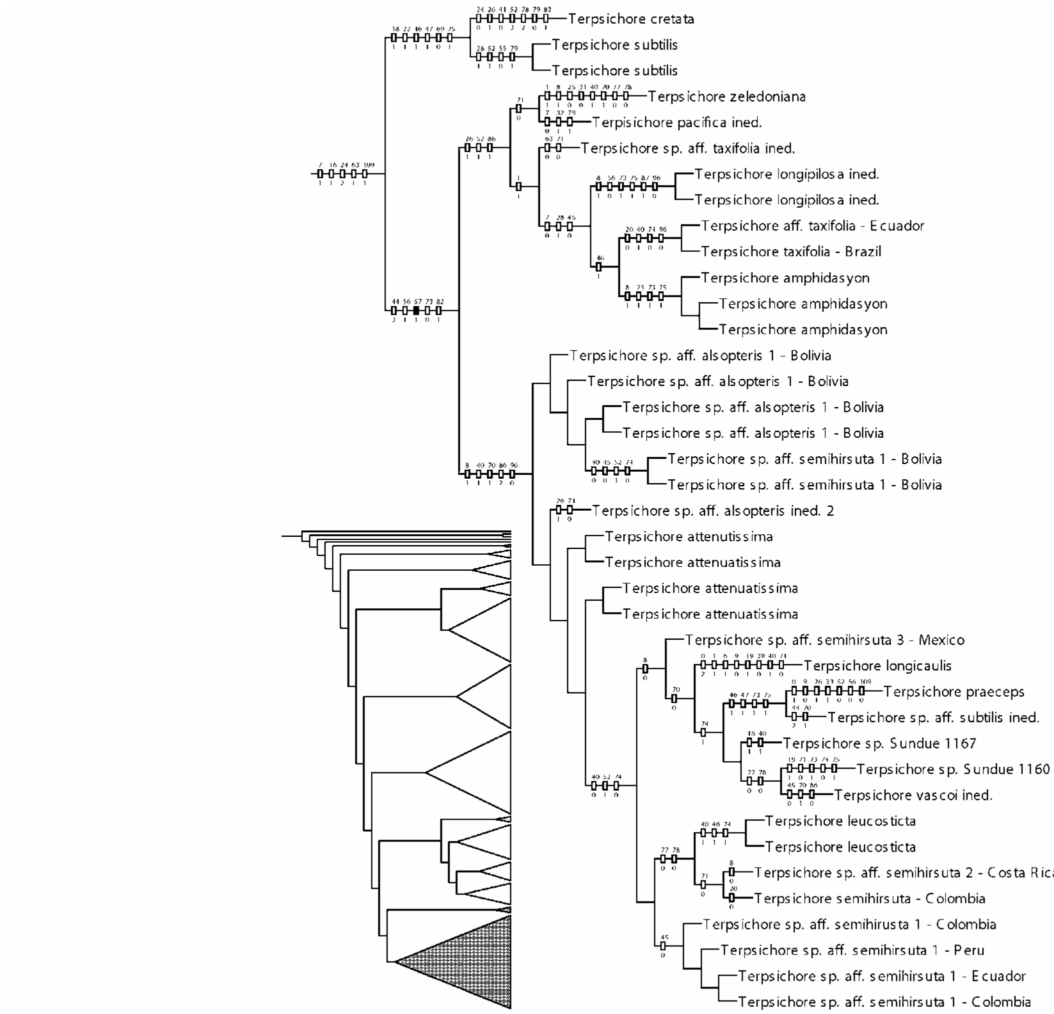
Lellingeria suprasculpta
Lellingeria suspensa
Lellingeria suspensa
Lellingeria sp. aff. humilis ined.
Lellingeria sp. aff. hirsuta Sundue 1159
Lellingeria subsessilis - Costa Rica
Lellingeria subsessilis - Ecuador
Lellingeria humilis
Lellingeria oreophila
Lellingeria apiculata - Costa Rica
Lellingeria apiculata - Brazil
Lellingeria major
Lellingeria major
Lelligeria prionodes
Lellingeria limula
Lellingeria limula
Lellingeria limula
Lelligeria hellwigii
Lellingeria saffordii
Lelligeria myosuroides
Lellingeria myosuroides
Melpomene firma
Melpomene occidentalis
Melpomene occidentalis
Melpomene personata ined.
Melpomene vernicosa
Melpomene anazalea ined.
Melpomene moniliformis
Melpomene pseudonutans
Melpomene flabelliformis

Fig. 3, F. Character evolution in grammitid ferns as inferred by illustrating the morphological characters on an exemplar tree from the combined analysis, and detail of area highlighted in grey. Numbers above and below squares are characters and character states from Appendix A and B. Black squares indicate characters without reversal. White circles indicate characters with homoplasy.


Terpsichore cretata
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Terpsichore subtilis
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Terpsichore sp. aff. taxifolia ined.
Terpsichore longipilosa ined.
Terpsichore longipilosa ined.
Terpsichore aff. taxifolia - Ecuador
Terpsichore taxifolia - Brazil
Terpsichore amphidasyon
Terpsichore amphidasyon
Terpsichore amphidasyon
Terpsichore sp. aff. alsopteris 1 - Bolivia
Terpsichore sp. aff. alsopteris 1 - Bolivia
Terpsichore sp. aff. alsopteris 1 - Bolivia
Terpsichore sp. aff. alsopteris 1 - Bolivia
Terpsichore sp. aff. semihirsuta 1 - Bolivia
Terpsichore sp. aff. semihirsuta 1 - Bolivia
Terpsichore sp. aff. alsopteris ined. 2
Terpsichore attenutissima
Terpsichore attenuatissima
Terpsichore attenuatissima
Terpsichore attenuatissima
Terpsichore sp. aff. semihirsuta 3 - Mexico
Terpsichore longicaulis
Terpsichore praeceps
Terpsichore sp. aff. subtilis ined.
Terpsichore sp. Sundue 1167
Terpsichore sp. Sundue 1160
Terpsichore vascoi ined.
Terpsichore leucosticta
Terpsichore leucosticta
Terpsichore sp. aff. semihirsuta 2 - Costa Rica
Terpsichore semihirsuta - Colombia
Terpsichore sp. aff. semihirusta 1 - Colombia
Terpsichore sp. aff. semihirsuta 1 - Peru
Terpsichore sp. aff. semihirsuta 1 - Ecuador
Terpsichore sp. aff. semihirsuta 1 - Colombia

CHAPTER 3

Monograph of *Ascogrammitis*, a new genus of grammitid ferns (Polypodiaceae)

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Abstract. This paper describes *Ascogrammitis*, a new genus of grammitid ferns formerly combined under *Terpsichore*. Sixteen species are recognized, including five new ones: **A. clavigera**, **A. colombiensis**, **A. loxensis**, **A. oxapampensis**, and **A. tungurahuae**. New combinations are made for **A. alan-smithii**, **A. anfractuosa**, **A. angustipes**, **A. athyrioides**, **A. clathrata**, **A. cuencana**, **A. david-smithii**, **A. dilatata**, **A. nana**, **A. pichinchae**, **A. pichinchensis**, and a lectotype is chosen for **Polypodium induens**. A key is provided to distinguish the species, and illustrations are provided for 12 species. The genus occurs primarily in neotropical cloud forests, with the greatest diversity in the Andes. *Ascogrammitis* is one of two monophyletic groups of grammitid ferns that is almost constantly

associated with *Acrospermum,* a bitunicate epibiotic black clavate ascomycete.

Key Words: *Acrospermum*, Andes, biogeography, pteridophyte, systematics, taxonomy.

Introduction

Phylogenetic studies combining DNA sequence data and morphological characters support the recognition of two clades whose species were formerly included in the polyphyletic grammitid genus *Terpsichore* (Polypodiaceae) (Sundue dissertation chapter 2). One of these clades is described here as a new genus and its species are treated monographically.

The new genus, *Ascogrammitis,* consists of 16 species distributed in neotropical cloud forests, particularly in the northern and central Andes. It is distinguished from other genera of grammitid ferns by dorsiventral rhizomes with ventral root insertion and clathrate rhizome scales with cordate bases and reddish setose margins. The fronds bear two types of indument: setae and hairs (Fig. 15 C). The setae are similar to those found in most grammitids, being terete, muliticelular, uniseriate, and reddish. The hairs are 1-furcate and 3-celled with one branch that is setiform (Fig. 1 C, 15 D). As in *Melpomene,* the fronds are hemi-dimorphic, with the fertile portions being more densely setose than the sterile portions. The pinna costae are surrounded by dark sclerenchyma visible on the both surfaces of the blade, but this dark coloration is absent from the veins (Fig. 16 H, J). Hydathodes are present and often cretaceous. The sori are inframedial, slightly elliptic (Fig. 17 F), and often confined to the distal portions of the blade. *Ascogrammitis* is one of two clades of grammitid ferns associated with the bitunicate ascomycete *Acrospermum* (the other clade is undescribed; its species are presently placed in *Terpsichore*). The fungus is evident as white mycelia and black clavate ascomes about 1 mm long (Fig. 1 E, 12 A, C, 17 F). Although not restricted to *Ascogrammitis,* the presence of the fungus is another useful diagnostic character for the genus.

Materials and Methods

This monograph is based on 620 collections, representing about 900 herbarium sheets from 22 herbaria (see Acknowledgements). All of the collections cited here have been annotated by me except those from CR and INB because they were studied before taxonomic concepts were determined. Field work was conducted in Ecuador in 2006, Colombia in 2007, and Costa Rica in 2008. Complete sets of collections were deposited locally in QCA and QCNE (Ecuador), HUA (Colombia) and partial setse were deposited in CR, INB, and USJ (Costa Rica). A full set of duplicates is deposited at NY, and a partial set is deposited in UC.

The phylogenetic species concept of Nixon and Wheeler (1990) is followed here. All measurements were made from herbarium specimens. Both habit and the description of the position of the frond relative to the rhizome (i.e., pendent, erect, or arching) are made from personal field observations or recorded from label data. A compound light microscope and SEM were used initially to study morphology, but all characters used in descriptions were scored using a dissecting microscope with maximum 65× magnification. Anatomical characters such as rhizome and petiole vasculature and the distribution of sclerenchyma were determined by performing free-hand sections and staining with phloroglucinol + HCL. Rhizomes of plants up to about four years old can be easily sectioned on herbarium sheets; older plants are usually too brittle to study this way. Dot distribution maps were generated from coordinates provided in label data or, when such information was not provided, by georeferencing collection localities.

Results and Discussion

Morphology.—Roots of *Ascogrammitis* are dark and wiry and provided with reddish or golden-red root hairs. In two species, *A. alan-smithii* and *A. anfractuosa*, new plants develop from roots asexually and produce large colonies. Such proliferous roots are otherwise known within grammitid ferns only from *Cochlidium serrulatum* (Sw.) L.E. Bishop (pers. obs.), and *Lellingeria ruglesii* (Proctor) A. R. Sm. & R. C.

Moran (Proctor, 1953). *Ascogrammitis* has short-creeping, dorsiventral rhizomes, roots inserted ventrally, and distichously arranged fronds that emerge from the dorsal side. Phyllopodia are absent, and the fronds are continuous with (not articulate to) the rhizome. Old petiole bases break irregularly and persist on the rhizome. Branch buds are present in some species, but a branched rhizome has not been observed in any specimen. When present, branch buds can be found on the rhizome behind each petiole as a small protuberance. Stem vasculature is either a dictyostele (Fig. 1 D) or a perforated dictyostele (Schmid, 1982). All steles have leaf gaps, but perforated dictyosteles have additional gaps that are not associated with leaves or roots. In *Ascogrammitis*, the perforations occur ventrally.

Rhizome scales of *Ascogrammitis* are generally clathrate (Fig. 12 B), but this is not always evident for two reasons. First, in some cases such as *A. athyrioides*, the cell lumina are transparent but so narrow that they cannot be seen through without using transmitted light. Under the dissecting microscope these scales appear uniformly blackish. Second, in other cases such as *A. nana*, some lumina are partially to fully occluded and may appear yellowish to castaneous or fully black when viewed with transmitted light. These scales tend to look blackish under the dissecting microscope. In all species, the apex of the scale bears a single papillate cell. This is easilly dislodged and therefore absent on many scales.

Petioles of *Ascogrammitis* contain either one (Fig. 12 D) or two vascular bundles, depending on the species. To determine the number of bundles, the base of the petiole must be sectioned because, if there are two bundles, they soon unite distally to form a single one. The cortex of the petiole is heavily sclerotized and dark brown to castaneous. The epidermis is translucent, not sclerotized, and this can be seen by scraping the surface of the petiole to reveal the dark sclerenchyma beneath (Fig. 12 D). The dark sclerenchyma of the petiole continues into the rachis and pinna costae but stops at the veins. The veins and pinna costae may be visible at the lamina surface, or covered by a layer of parenchyma. When the pinna costae are visible, they appear dark brown to castaneous, whereas veins will have the same or a darker color as the lamina tissue which varies from green to brown in dried specimens. The absence of dark sclerenchyma along the veins is a diagnostic character that serves to separate *Ascogrammitis* from species in the *Terpsichore taxifolia* group with which they have been confused.

Like most grammitids, fronds of *Ascogrammitis* bear two types of indument: setae and hairs. Their distinction is critical for correctly identifying species. Setae, which are present in most grammitids; in fact, they are a synapomorphy that can be used to distinguish grammitids from the rest of the Polypodiaceae (Sundue dissertation chapter 2). The setae are terete, multicellular, uniseriate, and reddish to castaneous. They range from 0.5 to 2.5 mm long and are usually erect or spreading. The apex may be crooked or irregular if the plant was collected while the cells were still differentiating. In contrast, hairs are also present in most grammitid ferns and other Polypodiaceae but are inconspicuous and easily overlooked. Among Neotropical grammitids, hairs have been relied upon heavily as taxonomic characters in *Lellingeria* (Smith et al., 1991) and *Ceradenia* (Bishop, 1988), but have been underutilized in other groups. Most hairs measure only 0.1 mm long. In *Ascogrammitis*, hairs of the petiole and rachis are generally dark in color, 3-celled, and 1-furcate, with one papillate branch and one setiform branch, and measure 0.1 mm long. Density varies and in some cases they can be difficult to locate. They are similar to the hairs of *Lellingeria*, but those are light in color, usually larger, and have an acicular branch instead of a setiform branch. A second type of hair occurs in *Ascogrammitis* that is simple, usually composed of two cells, and hyaline to gray in color. These were called trichomidia by Sundue & Kessler (2008). These hairs are most commonly found along pinna margins, and sometimes the abaxial lamina surface. They occur most often along pinna margins, and in some cases (*A. dilatata*, *A. loxensis*) they are irregularly replaced by setae.

Lamina dissection in *Ascogrammitis* is always greatest at the base of the frond—just as it is in all other ferns. It varies from 1-pinnate to 1-pinnatisect. Careful distinction between 1-pinnatisect and fully 1-pinnate laminae is critical for the correct identification of species. The sinus between segments of a 1-pinnatifid lamina will always retain a band of tissue, though it may be as narrow as 0.1 mm wide.

In most *Ascogrammitis* species, the fertile fronds are more densely setose than the sterile ones and the sterile portions of fertile fronds. On fertile fronds, setae may be associated with the sorus, although they do not necessarily develop from the receptacular tissue. These soral setae are homologous with other setae, and not with the paraphyses of *Ceradenia* or *Zygophlebia*, which represent modified hairs (pers. obs.) Sori are slightly elliptic and inframedial (Fig. 17 F). In most species they are confined to the distal portion of the laminae. Sporangial capsules are glabrous; they do not bear setae as in some species of *Lellingeria* or the *Terpsichore cultrata* group. Spores of *Ascogrammitis* are green at the time of sporangial dehiscence. In the species examined (*A. anfractuosa*, *A. dilatata*, *A. loxensis*, *A. pichinchensis*), spores are two-celled at maturity (Fig. 1 A) and have trilete laesurae (Fig. 1 B). By the third cell division, the spores of *A. anfractuosa* have shed their perispore and are elongate, beginning the filamentous phase of gametophyte growth. Thus, the sporangia of *Ascogrammitis* may contain young gametophytes along with mature spores, as has been described for other grammitid ferns (Stokey & Atkinson, 1958).

Distribution and ecology.—Greater Antilles, Guadeloupe, Central Mexico, to Bolivia; moist forests; subpáramo woodlands, especially in the cool shade of wooded ravines (750–)1800-3200(-3800) m. The genus is absent from the Amazon basin and coastal forests of southeastern Brazil. Unlike the closely related *Lellingeria* A. R. Sm. & R. C. Moran, and *Melpomene* A. R. Sm. & R. C. Moran, none of the species of *Ascogrammitis* inhabit páramos.

Ascogrammitis is most diverse in the Andes (Figs. 2–11); 13 of the 15 species are restricted there. The only extra-Andean species are the widespread *A. anfractuosa* (Fig. 3) and its allied species *A. alan-smithii* which occurs in mesoamerica(Fig. 2).

Within the Andes, one important geographical feature influencing the distribution of *Ascogrammitis* is the distribution of forest on the eastern (or Amazonian) and western (or Chocó) slopes of the northern Andes, and the separation of these forests by dry interandean valleys and páramos. Of the seven species that occur in the northern Andes, five are restricted to one side (i.e., either the eastern or western side). *Ascogrammitis angustipes* (Fig. 6) and *A. pichinchensis* (Fig. 9) are restricted to the western side, whereas *A. clavigera* (Fig. 6), *A. colombiensis* (Fig. 6), and *A. loxensis* (Fig. 9) are restricted to the eastern side. The distribution of *A. tungurahuae* is known with certainty only from the western slope of Mt. Tungurahua, which is part of the eastern cordillera; thus its distribution is not restricted to either the eastern or western slope. Only *A. pichinchae* (Fig. 11) and the widespread species *A. anfractuosa* (Fig. 3) occur on both sides of the Andes. Within *A.*

anfractuosa, however, morphological differences occur between populations on the eastern and western sides of the Andes.

Species of *Ascogrammitis* are primarily epiphytes, but *A. anfractuosa*, *A. cuencana*, and *A. pichinchensis* also grow on rocks. Within *A. anfractuosa*, epipetric plants are common in some regions and uncommon in others.

Relationship with the epibiotic ascomycete Acrospermum.—*Ascogrammitis* is one of two grammitid genera that are associated with the bitunicate ascomycete *Acrospermum* (the other group is the *Terpsichore taxifolia* group, sensu Sundue Dissertation Chapter 2). The fungus is evident by whitish mycelia and 0.5–1.0 mm long black clavate to (rarely) orbicular ascomes on the fronds. *Acrospermum* is epibiotic, presumably deriving energy from its host, but apparently without causing any harm. Necrotic leaf tissue is never associated with *Acrospermum*, nor does the fungus appear to be more prevalent on dead or senescent leaves. SEM photos show hyphae encircling and entering stomata (Fig. 12 A).

Acrospermum maxonii Farlow ex Riddle was described from the leaves of *A. anfractuosa* and *T. delicatula* from the West Indies (Riddle, 1928), and it is this species that appears to be present on *Ascogrammitis* and the *T. taxifolia* group. Morphometric studies suggest that above 3000 m on the eastern slope of the Andes, an undescribed species with more orbicular ascomes is present instead of *A. maxonii* (Doyle et al., 2008).

Acrospermum also occurs on other Polypodiaceae outside of the grammitids, on *Pleopeltis ballivianii* (Rosenst.) A. R. Sm., *P. furfuraceum* (Schltdl. & Cham.) A. R. Sm., and one specimen of *Campyloneurm* currently identified as *C.* sp. aff. *lorentzii* (Hieron.) Ching (Sundue & Doyle, unpubl. data). In these plants, however, the relationship is not as constant: *Acrospermum* is only present on about half the specimens of *P. furfuraceum* and *P. ballivianii* at NY, and not found on any other specimen of *Campyloneurum* at NY.

Systemtic Treatment

Ascogrammitis Sundue, **gen. nov.** Type: *Ascogrammitis athyrioides* (Hook.) Sundue (= *Polypodium athyrioides* Hook.

Squamae rhizomatis clathratae, marginibus setosis, setis russeolis; frondes monomorphae vel hemidimorphae, setigerae atque piligerae, pilis 1-furcatis, 3-cellularibus; venae phaeosclerenchymate carentes; hydathodi praesentes, cretacei; sori inframediales; sporae virides, 2-cellulares.

Plants epiphytic, occasionally saxicolous in *A. anfractuosa*; roots inserted ventrally on the rhizome, proliferous (i.e., producing new plantlets) or non-proliferous; rhizome short-creeping, dorsiventral, bearing fronds along the ventral side, unbranched, bearing lateral extra-axillary branch buds or not, dictyostelic, the dictyostele perforated or not, the cortex provided with bands of parenchyma darkened by phenolic compounds or not, provided throughout with scales, the scales basifixed, ovate to lanceolate, usually clathrate, often appearing concolorous when the lumina are narrow, sometimes truly concolorous, the cell walls indurate, dark red to blackish, the lumina usually transparent, iridescent or not, flattened (not turgid), dull to sub-glossy, clear to partially occluded, the opacity often variable between lumina within one scale, rarely fully occluded and opaque, the base semi-cordate, the apex acute to attenuate, provided with a single papillate cell held at an oblique angle to the apex, the margin usually setose, sometimes entire or provided only with a single apical seta, the setae ca. 0.1–0.2 mm long, usually translucent and reddish, sometimes hyaline in *A. david-smithii*, spreading, the abaxial and adaxial scale surfaces usually glabrous, setose in *A. oxapampensis*; fronds determinate, monomorphic or hemidimorphic, and then the fertile portions of fertile fronds more densely setose than sterile portions of the same frond or than of sterile fronds, distichous, erect, arching, or pendulous, the position apparently determined by the size of the frond, usually provided throughout with the mycelia and ascomes of *Acrospermum maxonii*, provided with setae and hairs, the setae ca. 0.5–2 mm long, multicellular, uniseriate, simple, terete, spreading, reddish to castaneous, sometimes pale toward the apex or when young, usually found on petioles, rachises, and laminae, the hairs usually ca. 0.1 mm long, usually 3-celled and unequally 1-furcate, the shorter branch papillate, the longer branch setiform (Fig. 1 C), up to 1.0 mm long (in *A. angustipes*), sometimes the hairs one- or two-celled and simple, usually found on petioles and rachises, rarely on laminae, if so then generally simple and present along the margin or abaxial surface; petiole non-articulate, with a single vascular bundle, or with two bundles and then the bundles quickly fusing, terete or narrowly marginate, the margin ca. 0.1 mm wide, throughout the length of the petiole, or only along the distal portion, the petiole, rachis, and segment costae dark in color, the cortex sclerenchymatous, castaneous to blackish, the epidermis greenish to hyaline, not sclerified (Fig. 12 D); rachis clearly visible on the abaxial side of the lamina, adaxially sometimes covered by parenchyma of the lamina and not visible; laminae chartaceous to membranaceous, narrowly elliptic, sometimes nearly linear, 1-pinnatisect to 1-pinnate, in general more deeply dissected proximally and less dissected distally, with reduced segments at the apex and base; segments narrowly triangular to oblong, usually entire, pinnatifid in *A. athyrioides*, the base sessile, even-sided or dilated, and then usually decurrent, sometimes surcurrent, the apex rounded to acute, the margins glabrous, setose, or provided with ca. 0.1 mm long simple hairs; segment costae either visible or covered by the parenchyma of the lamina on either side of the blade; veins alternate, simple, green (not darkly colored), usually visible on the abaxial side of the blade, usually not visible on the adaxial side of the blade; hydathodes present, cretaceous or not, the deposit white, sometimes stained red or gray; sori at apices of veins, present throughout the length of the lamina or more commonly confined to the distal portion, usually inframedial, sometimes medial, slightly longer than wide, sometimes provided with receptacular setae; paraphyses absent; sporangia glabrous; spores trilete (Fig. 1 B), green, composed of one or two cells at the time of sporangial dehiscence (Fig. 1 A), the surface tuberculate (Fig 1 B); chromosome number unknown, presumably x=37 as in most Polypodiaceae.

Ascogrammitis is most easily confused with *Lellingeria*, but the latter genus has rhizome scales with hyaline marginal setae, fronds that lack setae, and hairs with an acicular rather than setiform branch. Other diagnostic characters for *Lellingeria* are the tendency for the pinna costa to be obscured by a layer of parenchyma and therefore not visible on the abaxial side of the blade, and the hydathodes to be non-cretaceous. The tendency is the reverse for both characters in *Ascogrammitis*: pinna costae are clearly visible on the abaxial side of the blade, and hydathodes usually have a cretaceous deposit.

The *Terpsichore taxifolia* group (sensu Sundue Dissertation chapter 2) can also be confused with *Ascogrammitis* because that genus has similar indument, similarly shaped laminae and segments, cretaceous hydathodes, and is associated with *Acrospermum*. The *T. taxifolia* group differs from *Ascogrammitis* by orange to castaneous rhizome scales that are concolorous and have turgid cells, monomorphic fronds, medial or supramedial sori, and veins that are surrounded by dark sclerenchyma.

Ascogrammitis anfractuosa was previously combined in *Melpomene*, a genus that also has clathrate rhizome scales with cordate bases, hydathodes, setae, and fronds with 1-furcate hairs. *Melpomene*, however, differs from *Ascogrammitis* by rhizome scales reddish-brown, entire, and frequently with multiple apical papillate cells. *Melpomone* also has hairs composed of more than three cells, non-cretaceous hydathodes, and in dried specimens a sweet-spicy odor probably from coumarins.

Key to the species of *Ascogrammitis*

1. Roots proliferous, the plants forming large colonies; rhizome scales ovate; fronds erect.

2. Hydathodes cretaceous; segment margins setose; adaxial lamina surface setose; rhizome scale margin entire; plants apparently lacking the mycelia and ascomes of *Acrospermum*; epiphytic, 750–1200 m (Mesoamerica). ......*A. alan-smithii*

2. Hydathodes cretaceous or not; segment margins setose or not; adaxial lamina surface glabrous or setose; rhizome scale margins entire or setose;

plants with mycelia and ascomes of *Acrospermum*, epiphytic or epipetric, 1000–3000 m (widespread)..*A. anfractuosa*

1. Roots not proliferous, plants individual or in small colonies; rhizome scales lanceolate; fronds usually arching to pendent, sometimes erect.

3. Laminae 1-pinnatisect, the tissue between segments sometimes very narrow, but always connected.

4. Segment margins setose, simple hairs absent; fronds 0.8–1.6 cm wide (Colombia, Ecuador)..*A. cuencana*

4. Segment margins non-setose, simple hairs present, 0.1 mm long (sometimes specimens of *A. dilatata* and *A. loxensis* with both hairs and scattered setae); fronds (1.6–)2.1–5.0 cm wide.

5. Hydathodes non-cretaceous; setae absent on abaxial lamina surface, or sparse along veins (Venezuela)...*A. clavigera*

5. Hydathodes cretaceous (the whitish deposit sometimes lost); setae present on the the abaxial lamina surface, at least on fertile portions.

6. Receptacular setae absent; sori 4–8 per segment, evenly distributed throughout the lamina; pinna costae not readily visible abaxially (Colombia) ....*A. angustipes*

6. Receptacular setae present; sori up to 12 per segment, confined to the distal portion of the lamina; pinna costae visible abaxially.

7. Lamina base with 4–8 pairs of reduced segments; rhizome scales 1.5–3 × 0.2–0.3 mm; petioles sparsely setose (Central Peru, Bolivia). ....*A. dilatata*

7. Lamina bases with 16–20 pairs of reduced segments; rhizome scales 2.3–4.2 × 0.3–0.6 mm; petioles moderately setose (Ecuador, N. Peru)...................... *A. loxensis*

3. Laminae fully 1-pinnate or more divided, at least proximally.

8. Segments deeply and regularly pinnatifid (Peru, Bolivia). ....*A. athyrioides*

8. Segments entire or nearly so.

9. Hydathodes non-cretaceous; rhizomes bearing branch buds; petiole bases with two vascular bundles.

10. Laminae 5–7.5 cm wide; sterile portions of the abaxial lamina surface densely and evenly provided with erect setae; rhizome scales up to 4.5 mm long; costae adaxially setose; sori distributed evenly throughout the frond; sori 14–22 per segment (Bolivia)... *A. clathrata*

10. Laminae 3–4.5 cm wide; sterile portions of the abaxial lamina surface glabrous or nearly so, or if setose, the setae spreading, not erect; rhizome scales up to 3.5 mm long; costae adaxially lacking setae; sori confined to the distal portion of the frond; sori 8–10 per segment (Colombia)............. *A. colombiensis*

9. Hydathodes cretaceous; rhizomes lacking branch buds; petioles with a single vascular bundle.

11. Laminae membranaceous; fronds pendent; segment apices rounded; dark sclerenchyma of segment costae obscure abaxially (Ecuador). .... *A. pichinchensis*

11. Laminae chartaceous; fronds erect, arching, or pendent; segment apices acute; dark sclerenchyma of segment costae visible abaxially.

12. Segment margins moderately and evenly setose along their length; adaxial lamina surface moderately and evenly setose; sori distributed throughout the length of the lamina (Ecuador). ....*A. pichinchae*

12. Segment margins glabrous or pubescent, the hairs 0.1 mm long, simple, if setose, the setae irregularly present, and usually confined to the segment apex; adaxial lamina surface glabrous, or with scattered setae along pinn costae; sori confined to the distal portion of the lamina.

13. Petioles densely setose, the setae 0.2(–0.3) mm long; segment bases dilated, sursumcurrent; rhizome scales setose on surfaces and margins, the setae red (N. Peru)... *A. oxapampensis*

13. Petioles sparsely to moderately setose, the setae 1–2.5 mm long; segment bases not strongly dilated, sometimes decurrent, never sursumcurrent; surface of rhizome scales glabrous, the marin setose, the setae red or sometimes a mixture of red and hyaline.

14. Fronds 14–20 × 1.2–2.8 cm; veins obscure abaxially; segment margins without hairs; rhizome scales 0.2–0.3 mm wide; petioles moderately setose (Peru, Bolivia). .... *A. nana*

14. Fronds 18–60 × 2–4.5 cm; veins visible abaxially; segment margins pubescent (especially toward the segment apices), the hairs 0.1 mm long; rhizome scales 0.3–0.6 mm; petioles sparsely setose.

15. Rhizome scales with narrow indistinct lumina, blackish in mass; fronds 27–60 cm long (Ecuador)..*A. tungurahuae*

15. Rhizome scales with broad disctinct lumina, dark grey in mass; fronds 18–37 cm long (Bolivia). .... *A. david-smithii*

Ascogrammitis alan-smithii (A. Rojas) Sundue, **comb. nov**. *Melpomene alan-smithii* A. Rojas, Rev. Biol. Trop. 49: 444. 2001. Type: Costa Rica. Alajuela: Upala, Zona Protectora Tenorio, Cordillera de Guanacaste, Bijagua, ridge at Volcán Tenorio, 10º43'00"N, 85º01'00"W, 1000–1500 m, 20 Apr 1995, *D. Penneys et al. 469* (holotype: INB; isotype: MO).

(Fig. 2)

Plants epiphytic, forming large colonies, roots proliferous; rhizome 1.0 mm wide; branch buds absent; rhizome scales 0.5 × 0.2–0.4 mm, ovate, clathrate, the cell walls castaneous to blackish, the apex acute, the margins entire; fronds 2.5–7.5 × 0.4–0.8(–0.9) cm, erect, hemidimorphic, apparently lacking the mycelia and ascomes of *Acrospermum*; petioles 4–6 × 0.2–0.3 mm, narrowly marginate throughout or at least distally, with single vascular bundle, moderately setose, the setae 0.5 mm long, sparsely hairy, the hairs simple or 1-furcate; rachises with castaneous sclerenchyma visible on both sides of the blade, abaxially moderately setose, the setae 0.4 mm long, sparsely hairy, the hairs simple or 1-furcate, adaxially moderately setose, the setae 0.2–0.4 mm long; laminae 1-pinnatisect, 12–25 segment pairs, the base acute, with 1–3 pairs of reduced segments, the apex terminating in a rounded or acute terminal segment; medial segments

2–3.5 × 1.7–2 mm, deltate to oblong, spreading or slightly ascending, the base decurrent with the tissue slightly overlapping the acroscopic edge of the next proximal segment, the apex rounded to acute, the margin entire, moderately and evenly setose, the setae 0.3 mm long; sterile portions of the abaxial lamina surface sparsely to moderately setose, the setae 0.2 mm long, erect, reddish; fertile portion of the abaxial lamina surface moderately to densely setose, the setae up to 0.7 mm long; adaxial lamina surfaces with scattered setae, 0.2 mm long; segment costae with black sclerenchyma visible abaxially, not readily visible adaxially; veins not readily visible; hydathodes present, cretaceous, frequently with bright red spots in the deposit; sori inframedial, confined to the distal portion of the frond, somewhat confluent at maturity, 3–5 per segment; receptacular setae present.

Distribution.—Costa Rica and Panama, Caribbean and Pacific slopes; (600-)750–1200(-1500) m.

Additional specimens examined. COSTA RICA. **ALAJUELA:** Reserva Biológica Monteverde Estación Aleman's, 10°55’32”N, 85°28’2”W, 950 m, 7 May 1991, *Bello & Mendez 2663* (INB); San Carlos, La Fortuna, Finca El Jilguero, área adelante a Arenal Lodge, 10°55’38”N, 85°29’38”W, 21 Nov 1992, *Herrera 5564* (CR); W of San Ramón, ca. 1 km S of Socorro, 1200 m, 25 Jul 1975, *Lellinger & White 1311* (US); Near Poterillos, 4 km E of Piedades sur de San Ramón, 1200 m, 22 Jun 1969, *Lent, 1760* (GH, NY); Santa María National Park, road down Caribbean slope, 1 km E of summit of rd. 4 km W of east side of park, 4 km E of colored house at junction of rode to Hacienda Santa Maria, 600 m, 7 Feb 1978, *Liesner 5082* (MO); Near La Laguna, 6 to 8 km S of Villa Quesada, 1200 m, 19 Feb 1966, *Molina et al. 17522* (NY); near Artezalea and Methodist Rural Center, about 8 km NE of Villa Quesada, 10°43'N, 85°1'W, 550 m, 22 Feb 66, *Molina et al. 17728* (NY); Upala, Cuenca del Zapote, Bijagua, Camino a la Toma de Agua, 650–750 m, 6 Feb 1998, *Rojas 4279* (CR, NY). **GUANACASTE:** Biological Station on the W flank of Volcán Cacão, área de Conservación Guanacaste, 1100 m, 23 Jul 1994, *Alverson & Flores 3101* (CR, MO); Cantón de La Cruz, P. N. Guanacaste, Estación Cacão, 10°55'N, 85°28'W, 1100 m, 24 May 1992, *Espinoza 322* (CR); Tilarán, Cordillera de Tilarán, camino a Tenorio, 10°43'N, 85 0'W, 800–900 m, 1 Sep 1995, *Rojas 2430* (CR, MO); El Silencio, near Tilarán, 750 m, 13 Jan 1926, *Standley & Valerio 44598* (US); El Silencio, near Tilarán, 9°44'2"N, 84°23'32"W, 750 m, 13 Jan 1926, *Standley & Valerio 44610* (US). **HEREDIA:** Along rd. between San Miguel and Cariblanca, 10°18'N, 84°45'W, 700 m, 11 Jul 1983, *Moran, R. C. 3158* (MO). **SAN JOSÉ:** Puriscal, Cerros de Purriscal, San Martín de Purriscal, 800–950 m, 21 Apr 1995, *Morales 3919* (MO).

PANAMÁ. **CHIRIQUÍ:** Cerro Colorado, mining rd. 15.6 mi above bridge over Río San Felix, 1300 m, 21 Sep 1979, *Antonio 2578* (MO); above San Felix along mining rd. 18–27 mi. off of Pan-Am Highway, above Chame or turnoff to Escopeta, 1200–1500 m, 12 Mar 1976, *Croat*

33054 (MO); 17 km NE of San Felix on new rd. to Cerro Colorado copper mines, 16°40’N, 66°28’W, 1000 m, 18–19 Mar 1974, *Nee 10686* (MO). **VERAGUAS:** Caribbean slope above Río Primero Brazo, 5 mi NW of Santa Fe, 1200 m, 18–19 Mar 1973, *Croat 23166* (MO); 0.2 mi beyond fork in road at Escuela Agrícola Alto Piedra on road to Río Calovebora, 750 m, 3 Apr 1976, *Croat & Folsom 33898* (MO); N of Santa Fe, ca. 2 km N of Escuela Agrícola Alto de Piedera, 18 Oct 1974, *Mori & Kallunki 2653* (MO).

Like *Ascogrammitis anfractuosa*, *A. alan-smithii* reproduces by proliferous roots and forms large colonies. These two species could be considered conspecific if a very broad concept of *A. anfractuosa* were adopted. *Ascogrammitis alan-smithii* differs from Mesoamerican plants of *A. anfractuosa* by adaxially setose laminae, presence of cretaceous hydathodes, occurrence at a lower elevation, and apparent lack of association with *Acrospermum*. Two of these characters—adaxially setose laminae and cretaceous hydathodes—do occur in some populations of *A. anfractuosa*, but not together, and not in Mesoamerica. Because this clear distinction can be made, at least locally, I prefer to maintain *A. alan-smithii* as distinct from *A. anfractuosa* until further work can be done on the variation between populations of the latter.

Ascogrammitis anfractuosa (Kunze ex Klotzsch) Sundue**, comb. nov.**

Polypodium anfractuosum Kunze ex Klotzsch, Linnaea 20: 375. 1847. *Ctenopteris anfractuosa* (Kunze ex Klotzsch) Copeland [as "*anfratuosa*"], Phillip. J. Sci. 48: 431. 1956. *Grammitis anfractuosa* (Kunze ex Klotzsch) Proctor, Rhodora 63: 35. 1961. *Melpomene anfractuosa* (Kunze ex Klotzsch) A. R. Sm. & R. C. Moran, Novon 2: 429. 1992. *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A. R. Sm., Amer. Fern J. 93: 86. 2003. Type: Venezuela. Mérida: *Moritz 330* (holotype: B n.v.; isotypes: B n.v., MO, two sheets; photo of the holotype: F). (Figs. 3, 13 D, H–K)

Polypodium monticola Klotzsch, Linnaea 20: 377. 1847. Type: Perú, Huánuco, Muña, *H. Ruíz Lopez 58* (lectotype, chosen by Tryon & Stolze, 1993: B n.v.; photo of lectotype: F; fragment: NY).

Polypodium saxicola Baker ex Jenman, J. Bot. 15: 264. 1877. ["*saxicolum"*] *hom. illeg. non* Swartz, 1817. Type: Jamaica, *G. S. Jenman 84*, March 1877 (holotype: K, n.v.; isotypes: NY, two sheets).

Polypodium induens Maxon, Bull. Torrey Bot. Club 32: 5. 1905. TYPE: Jamaica. Highest slopes of John Crow Peak, on tree trunk, 5500–6000 ft, 18 Apr 1903, *W. R. Maxon 1324* (lectotype, **here**

designated: US). Syntypes: Jamaica, Near Morce's Gap, on moist rocks, 1500 m, 18 Apr 1903, *W. R. Maxon 1214* (US), Highest slopes of John Crow Peak, on tree near summit, 5500–6000 ft, 18 Apr 1903 *W. R. Maxon 1332* (US); vicinity of Morce's Gap, rich wooded slope, 1500 m, 23 Jun 1904, *W. R. Maxon 2770* (NY, US); [without definite locality, ex herb. Botanical Dept. Jamaica], 1885 (US).

Plants epiphytic or epipetric, producing large colonies; roots proliferous; rhizome 0.5–0.7 mm wide; branch buds absent; rhizome scales 0.5–0.7 × 0.2–0.3 mm, ovate, clathrate, blackish in mass, the cell walls reddish, the lumina slightly occluded, the apex acute, the margins usually entire, sometimes with 1–2 setae on either side, the setae 0.1–0.2 mm long; fronds 5–10 × 0.9–1.4 cm, hemidimorphic, erect, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 0.5–2 cm long, with a single vascular bundle, castaneous, narrowly alate throughout, the wings up to 0.1 mm wide, moderately setose, the setae 1.0 mm long, sparsely hairy, the hairs 1-furcate; rachis blackish, with the dark color visible on both sides of the lamina, the abaxial side moderately setose the setae 1.0 mm long, sparsely hairy, the hairs 1-furcate, the adaxial rachis moderately setose, the setae 0.3–0.5 mm long, spreading; laminae chartaceous, elliptic, acute at both ends, 1-pinnatisect, with 10–25 segment pairs; medial segments 5–7 × 2–3 mm, oblong, sessile, the basiscopic side usually slightly decurrent, the acroscopic side somewhat surcurrent or not, the apex rounded, the margins moderately setose, the setae 0.5 mm long, reddish, spreading, often more abundant toward the segment apex, the abaxial lamina provided with reddish spreading setae, sterile portions of the abaxial lamina moderately setose, the setae 0.2–0.6 mm long, fertile portions of the abaxial lamina moderately to densely setose, the setae up to 1.2 mm long, the adaxial lamina usually glabrous, sometimes sparsely to moderately setose, the setae 0.5 mm long; segment costae blackish, usually visible abaxially, but not adaxially; veins not readily visible; hydathodes slightly cretaceous or not, white, never stained red; sori inframedial, somewhat confluent at maturity, up to three per segment, confined to the distal portion of the lamina; receptacular setae present.

Distribution.—West Indies, southern Mexico to Bolivia; 1500–2500 m.

Additional specimens examined. MEXICO. **CHIAPAS:** Yajalon, slopes of Ahk'ubal Nab, above Yajalon, 1200 m, 6 Apr 1973, *Breedlove34598* (MO); Mun. de Rayon, Selva Negra 10 km above Rayon Mezcalapa along rd. to Jitotol, 1700 m, 27 Jan 1973, *Breedlove & Smith 32644* (F, NY); southeast side of Cerro Tres Picos and the ridges near summit, 18.0663° N, 96.3961° W, 2100-2500 m, 11 Dec 1972, *Breedlove & Thorne 30159* (NY); Los Llanos, 21°1’36”N, 98°38’35”W, *Munch 170* (US). **HIDALGO:** Tlalchinol, Km 168.5 (fed. 105) entre Tlalchinol y

Huejtla, 1200 m, 14 May 2000, *Tejero-Díez 4073* (NY). **OAXACA:** Teotitlán, Mun. San José de Tanango, San Martín Caballero, 1590 m, 1 Feb 1995, *Geith 95-M046* (NY); Sierra de Juárez, Km 85 ruta 175, Tuxtepec-Oaxaca, 1800 m, 19 Nov 2005, *Kessler 13507* (UC); Sierra de Juárez, Km 85 ruta 175, Tuxtepec-Oaxaca, 1800 m, 19 Nov 2005, *Kessler 13517* (NY); Ixtlán, 65 km N of Ixtlán, 44 km S of Valle Nacional, 6400 ft, 25 Jul 1971, *Mickel 5562* (NY); Ixtlán, 65–68 km N of Ixtlan, 41–44 km S of Valle Nacional, 6200 ft, 28 Oct 1969, *Mickel & Hellwig 4292* (NY, US); Ixtlán, 7 km S of Vista Hermosa, 71 km N of Ixtlán de Juarez on Rte. 175, 5400 ft, 23 Sep 1972, *Mickel & Purdue 6771* (NY).

GUATEMALA. **ALTA VERAPAZ:** Coban, 5 Aug 1920, *Johnson 533* (US); hills about 5 km E of San Juan Chamelco, 1600 m, 8 Feb 1969, *Williams & Wilson 40732* (F). **EL PROGRESO:** Hills N of Finca Piamonte, bw. Fina Piamonte and summit of Volcan Santa Luisa, 15°26'N, 90°16'W, 2850 m, 5 Feb 1942, *Steyermark 43610* (F, US). **EL QUICHE:** Mountain slopes S of Nebaj, 25 Jun – 17 Aug 1964, *Proctor 25071* (US); 1 mi. N of Nebaj, 4 Aug 1964, *Spross 117* (F). **SANTA ROSA:** Santa Rosa, 3000 m, Apr 1892, *Heyde et Lux 3254* (NY, US). **ZACAPA:** Sierra de las Minas, below Finca Alejandra, 2000 m, 14 Oct 1939, *Steyermark 30020* (F, US); slopes of Monte Virgen, around summit of mountain, Río Repollal, 12–13 Jan 1942, *Steyermark 42665* (F, US).

HONDURAS. **COMAYAGUA:** Summit of the range above El Achote, above the plains of Siguatepeque, 1850 m, 28 Jul 1936, *Yunker et* *al. 6197* (NY, US). **El Paraíso:** Montaña de Yuscaran, 1800 m, 31 Dec 1943, *Rodríguez 1945* (F). **Francisco Morazán:** Cerro de Uyuca, 4 Jul 1952, *Howard 39* (US); La Tigra, 20 km NE de Tegucigalpa, 2000 m, 13 May 1984, *Lopez 188* (NY); mountains above San Juancito, 2000 m, 22 Feb 1949, *Merril et al. 15678* (F pp, US); San Juancito Mtns, La Tigra cloud forest, 2100 m, 4 Feb 1968, *Molina & Molina 21463* (F, GH, NY, UC, US); Montaña Uyuca, 14°55'N, 88°7'W, 1800 m, 7 Jun 1962, *Molina 10673* (F, NY); Cerro de Uyuca, 10–20 Mar 1951, *Morton 7176* (NY, US); Cerro de Uyuca, 10–20 Mar 1951, *Morton 7182* (MO, US); Eastern slopes of Pena Blanca, San Juancito Mountains, 22 Mar 1951, *Morton 7313* (US); western slopes of Pena Blanca, San Juancito Mountains, 25 Mar 1951, *Morton 7458* (US); western slopes of Pena Blanca, San Juancito Mountains, 25 Mar 1951, *Morton 7515* (US); eastern slopes of Pena Blanca, San Juancito Mountains, 22 Mar 1951, *Morton 7524* (UC, US); Uyuca, 1238 m, 9 Sep 1943, *Rodríguez 756* (F); Cerro de Uyuca, 1600 m, 2 Mar 1947, *Standley 4902* (F); along trail from Las Flores to La Labranza, Oct–Dec 1948, *Standley 15653* (F); Mt. Uyuca, 2000 m, 20 Aug 1946, *Williams & Molina 10287* (US); Mt. Uyuca, 2000 m, 20 Aug 1946, *Williams & Molina 10387* (F, GH, MO, UC); Mt. Uyuca, 2000 m, 5 Dec 1946, *Williams & Molina 11142* (US); mountains SW of San Juancito, 2000 m, 21 May 1947, *Williams & Molina 12790* (US); mountains above San Juancito, 2200 m, 20 Feb 1948, *Williams & Molina 13688* (F, US); Montaña La Tigra, cerca de Juancito, 2000 m, 5 Oct 1953, *Williams &*

Molina 18869 (US); 7 km N of El Mochito, on the E slopes of Mt. Santa Bárbara, 23 Nov 1991, *Moran 5670* (MO, UC). **Intibuca:** Rd. between Jesús de Otoro and La Esperanza, 1800 m, 2 Nov 1974, *Horwatch 150* (F).

EL SALVADOR. **Morazán:** El Zancudo, 1900 m, 28 Mar 1979, *Seiler 987* (F). **Santa Ana:** Cordillera Miramundo, mountain of Montecristo, 27–31 Jan 1966, *Molina et al. 16807* (F, NY); Bosque Montecristo, 2100 m, 16 Sep 1977, *Seiler 95* (F, NY); Bosque Montecristo, 2200 m, 10 Oct 1978, *Seiler 648* (F, GH, NY).

COSTA RICA. **Alajuela:** Between Las Nubes and La Palma, 30 Jan 1938, *Knight, W. 2* (US); Vera Blanca, north slope of Central Cordillera, Jul–Sep 1937, *Skutch 3229* (GH, MO, NY, US); region of Zarcero, 8 Sep 1937, *Smith 85* (F); Viento Fresco, 13 Feb 1926, *Standley & Torres 47752* (US). **Cartago:** Volcán Irazú and Volcán Turrialba, rd. from Payacas to Hacienda Central, 31 Mar 1982, *Barringer et al. 2277* (F); W slope of Cerro Duan, ca. 3 km above Guataba, E of Río Grande de Orosi, 15 Jan 1987, *Hill et al. 17854* (NY); Santa Clara de Cartago, 1 Jan 1924, *Lankester 902* (US); Forest beyond El Empalme, at Km 55, along the Pan-American Hwy, 2400 m, 9 Sep 1964, *Lems s.n.* (NY); Vicinity of Coliblanco, 1950 m, 30 Apr–2 May, 1906, *Maxon 278* (NY, US); Santa Clara de Cartago, 1950 m, 20 Jul 1923, *Maxon 8232* (US); Santa Clara de Cartago, 1950 m, 20 Jul 1923, *Maxon & Harvey 8142* (US); Interamerican Hwy. vic. of Villa Mills and 1 km NW (Vic. of Hotel La Georgina), 24 Mar 1967, *Mickel 2165* (NY); Tapantí, ca 15 km S of Paraiso, 1150 m, 3

Jul 1967, *Mickel 2352* (NY); Along Pan American Hwy, Rte 2, near Km 66, 8°58’3”N, 82°46’15”W, 3000 m, 11 Aug 1982, *Moran 2377* (MO); Canton de Paraiso, Cuenca del Reventazón. Estación de Biologia Tropical Río Macho y alrededores, 9°27’25”N, 83°32’55”W, 27 Sep 1996, *Rojas 3128* (MO, NY,UC); Road from Cartago to San Isidro del General (Pan American Hwy, Rt. 2), Km 67, 16 km SE of Empalme, 2550 m, 30 Jan 1986, *Smith & Beliz 2109* (MICH, MO, NY, UC); Río Birris, southern slope of Volcán de Irazú, *Standley 35403* (US); Estrella, 20 mi S of Cartago, 17 May 1928, *Stork 1969* (NY, UC); Interamerican hwy., slope below hotel La Georgina, along senderos los Quetzales en el Roblero, 3093 m, 27 Jan 2008, *Sundue et al. 1689* (INB, NY). **GUANACASTE:** 2 km NE de Tilaran, 850 m, 4 Dec 1963, *Jiménez 1341* (F). **HEREDIA:** Alto Río Patria, rt 113 above San Rafael and San José de la Montaña, 9°57’N, 83°48’W, 2 Jul 1983, *Barringer & Christenson 3419* (F); NW slope of Volcán Barba, ca. 2 km (by rd.) NE of Los Cartagos, 2075 m, 16 Mar 1986, *Grayum & Yatskievych 6623* (MO); Volcán Barba, S of the principal peak above Porrosati, 16 Apr 1971, *Lellinger 1735* (F, US); 0.5–1.0 km W of the Río Las Vueltas (Río Patria) 0.5 km NE of Cerro Chompipe, ca. 11 km NNE of Heredia, 1950 m, 7 Jul 1970, *Lellinger & White III 997* (US); N of Heredia, ca. 1 km beyond Porrosati, 2100 m, 18 Aug 1970, *Lellinger & White 1694* (F, US); along the cart-road from Vera Blanca (between Poas and Barba Volcanoes) to La Concordia, 23 Jul 1923, *Maxon & Harvey 8434* (US); along the cart-road from Vara Blanca (between Poas and Barba Volcanoes) to La Concordia, 23 Jul 1923, *Maxon & Harvey 8448* (US); Along the cart-road from Vara Blanca (between Poas and Barba Volcanoes) to La Concordia, 27 Jul 1923, *Maxon & Harvey 8487* (GH, UC, US); Ranch Flores (Barba), 8°57.25'N, 82°50'W, 2043 m, 15 Feb 1890, *Pittier 2000* (CR, NY , US); Cerros de Zurqui, NE of San Isidro, 9°51'N, 84°7'W, 3 Mar 1926, *Standley& Valerio. 50466* (US). **LIMÓN:** Cordillera Talamanca, Atlantic slope, canyon of the Río Sini, 9°8'N, 82°58'W, 15 Sep 1984, *Davidse & Herrera 29122* (MO); Cordillera de Talamanca, Atlantic slope, Valle de Silencio, area just N of Cerro Hoffman, 4 km W of the Costa Rican-Panamanian border, 8 Sep 1984, *Davidse et al. 28598* (MO, UC); Talamanca, Cordillera Talamanca, along quebrada Kuisa (tributary of Río Lori) near crossing of Ujarras-San José Cabecar trail, 10°9'N, 84°9'W, 2100 m, 13 Mar 1993, *Grayum 10303* (MO); Talamanca, Parque Internacional La Amistad, cordillera de Talamanca, Valle de Silencio, 2450 m, 16 Apr 1996, *Moraga et al. 334* (MO). **PUNTARENAS:** Upper Río Buru, 9°20.5'N, 83°14'W, 2010 m, 19 Aug 1983, *Gómez 21778* (MO, UC); Coto Brus, Z. P. Las Tablas, 1960 m, 18 Feb 1998, *Navarro 905* (MO, NY); Coto Brus, Cordillera de Talamanca, Las Alturas de Coton, Estación Biológica Las Alturas, sendero a Cerro Enchandi, 9°46'N, 83°51'W, 19 Dec 1993, *Rojas 703* (MO). **SAN JOSÉ:** 10 km N of San Rafael de Heredia on Volcán Barba, 1950 m, 9 Jul 1967, *Bishop 826* (UC); 10 km N of San Rafael de Heredia on Volcán Barba, 9°13'N, 82°59'W, 1950 m, 30 Jul

1967, *Bishop 857* (MO, UC); Potreros of Rancho Redondo, 21 Nov 1929, *Dodge & Thomas 7889* (GH); San Cristóbal Norte, 2000 m, Oct 15, 1969, *Gómez 2400* (F); 10 km N of San Rafael de Heredia on Volcán Barba, 1950 m, 30 Jul 1967, *Lellinger 786* (MO, US); S of Cartago, ca. 4 km S of El Empalme near La Chonta, 2500 m, 14 Aug 1970, *Lellinger & White 1582* (US); Ca. 10 km N of San Rafael de Heredia on Volcan Barba, 1950 m, 13 Jul 1967, *Mickel 2664* (NY, US); Vicinity of La Hondura (4 km S to 1 km N on Rte 220) between Volcán Irazú and Volcán Barba, 9° 7’15”N, 82°57’55”W, 25 Mar 1967, *Mickel 2195* (NY); Perez Zeledon, Parque Nacional Chirripo, Cordillera de Talamanca, 26 Jul 1996, *Rojas 2820* (MO); Las Nubes, 23 Feb 1924, *Standley 38367* (US); Las Nubes, 20–22 Mar 1925, *Standley 38566* (US); Las Nubes, 20–22 Mar 1926, *Standley 38667* (US); Las Nubes, 20–22 Mar 1924, *Standley 38749* (US); Zurqui, 13 Feb 1926, *Standley & Valerio 48052* (US); Cerro Daser (Azulillo), 6 km W of rte. 4, 5 km S of Asseri, 2050 m, 19 Mar 1973, *Stolze 1416* (F, UC); Forests de Santa Rosa, 1800 m, Apr 1898, *Tonduz 12197* (US); Forests de Santa Rosa du Copey, 8°33’29”N, 83°43’24”W, Apr 1898, *Tonduz 12197* (CR); La Carpintera, 1800 m, 15 Dec 1923, *Torres R., R. 66* (US); La Carpintera, 1800 m, 16 Dec 1923, *Torres 69a* (US).

PANAMÁ. **BOCAS DEL TORO:** Cordillera de Talamanca, headwaters of the Río Culubre, 6 km NW of the peak of Cerro Echandi on the Costa Rican-Panamanian border, 2–3 Mar 1984, *Davidse 25257* (MO, UC); SE slopes of Cerro Echandi, 1 Mar 1984, *Gomez 22228* (MO, UC).

CHIRIQUI: Guadalupe, Cerro Punta, finca Maduro, 2000 m, 23 Apr 1982, *Caballero 126* (F, MO); El Boquete, Feb 1918, *Cornman 1042* (MO, UC); vicinity of El Boquete, 22 Feb 1918, *Cornman 1042* (US); vicinity of El Boquete, 28 Mar 1918, *Cornman 1241* (US); vicinity of El Boquete, 13 Apr 1918, *Cornman 1326* (US); Cerro Pate de Macho, ca. 5 mi. ME of Boquete, along trail to continental divide which leads to Finca Serrano (Francisco Serrano), Pacific slope, 9°5'N, 82°50.5'W, 23 Nov 1979, *Croat 48567* (MO); Boquete, Bajo Chorro, 24 Jan 1936, *Davidson 195* (MO); Valley of the Río Caldera, from El Boquete to the Cordillera, 8°47'N, 82°22'W, 5–19 Feb 1918, *Killip 5194* (GH, UC, US); S slopes of Cerro Pate Macho along Río Palo Alto, 11 Nov 1981, *Knapp et al. 2008* (MO); between Alto de las Palmas and top of Cerro de la Horqueta, 18 Mar 1911, *Maxon 5486* (GH, NY, US); upper Caldera River, near "Camp I," Holcomb's trail, above El Boquete, 22–24 Mar 1911, *Maxon 5714* (US); vicinity of Camp Aguacatal, eastern slope of Chiriquí Volcano, 10–13 Mar 1911, *Maxon 5291* (GH, NY, US); Bajo Grande, ca. 3 km E of town of Cerro Punta, 2200 m, 23 Feb 1974, *Nee 9976* (MO); Valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, 8°48'N, 82°23.5'W, 27 Jun – 13 Jul 1935, *Seibert 196* (GH, MO, NY, US); along trail between N fork of Río Palo Alto and Cerro Pate Macho, ca. 6 km NE of Boquete, 6 Feb 1986, *Smith et al. 2388* (MO, NY, UC); vicinity of Casita Alta, Volcán de Chiriquí, 28 Jun – 2 Jul 1938, *Woodson et al. 829* (GH, MO, NY, US).

CUBA. **SANTIAGO DE CUBA:** Oriente: Pico Turquino, Sierra Maestra, 10–26 Jun 1936, *Acuña 9991* (MO).

JAMAICA. **ST. ANDREW:** Vicinity of Cinchona, below Morce's Gap, 2–10 Sep 1906, *Britton s.n.* (US); vicinity of Cinchona, 2–10 Sep 1906, *Britton s.n.* (NY); Chesterdale, Near Newcastle, in the Blue Mountains, 15–30 Mar 1909, *Carhart s.n.* (NY); vicinity of Cinchona, 2–10 Sep 1906, *Underwood 3157* (NY). **ST. THOMAS:** Along trail between Portland Gap and Blue Mt. Peak, 22 Jan 1967, *Evans 2613* (MO); John Crow Peak, 5 Dec 1914, *Harris s.n.* (NY); Morce's Gap, Nov – Dec 1915, *Farr s.n.* (NY); trail from Morce's Gap to Vinegar Hill, 6 Mar 1920, *Maxon & Killip 711* (F, NY, US); Morce's Gap and vicinity, 1500 m, 14 Mar 1920, *Maxon & Killip 1077a* (US); near Morce's Gap, 5000 m, 18 Apr 1903, *Maxon 1214* (US); trail from Morce's Gap to Vinegar Hill, 21 Mar 1920, *Maxon & Killip 1302* (F, NY, US); highest slopes of John Crow Peak, 18 Apr 1903, *Maxon 1324* (US); highest slopes of John Crow Peak, 18 Apr 1903, *Maxon 1332* (US); vicinity of Morce's Gap, 1500 m, 23 Jun 1904, *Maxon 2770* (NY, US); "Main Ridge Gap" and vicinity (W of Mossman's Peak), 15 Jul 1926, *Maxon 10221* (F, NY, US); "Main Ridge Gap" and vicinity (W of Mossman's Peak), 15 Jul 1926, *Maxon 10240* (NY, US); summit of Blue Mtn. Peak, 7–9 Jul 1926, *Maxon 10567* (US); Blue Mtns, summer 1895, *Moore s.n.* (MO); summit of Blue Mtn. Peak, 30 Dec 1954, *Proctor 9704* (MO); Morce's Gap, 2 Feb 1903, *Underwood 540* (NY); John Crow Peak, 2 Feb 1903, *Underwood 773*

(NY); Mabes River, below Vinegar Hill, 9 Feb 1903, *Underwood 1273* (NY); Vinegar Hill, *Underwood 1369* (NY); Morce's Gap, 18 Apr 1903, *Underwood 2346* (NY); John Crow Peak, 6000 m, 18 Apr 1903, *Underwood 2448* (NY); John Crow Peak, 18 Apr 1903, *Underwood 2451* (NY); summit of Blue Mt, 20–21 Apr 1903, *Underwood 2489* (NY). **Parish unknown:** Maybess, 26 Jul 1907, *Fisher 151* (NY); *Hart s.n.* (MO); *Jenman, s.n.* (NY).

DOMINICAN REPUBLIC. **AZUA:** Cordillera Central, prov. de Azua, San Juan, Sabana Nueva, 1950 m, 16 Sep 1929, *Ekman 13585* (F, NY); 26 Mar 1905, *Fuertes s.n.* (NY); between Valle Nuevo and Azua, 24 Dec 1964, *Jones & Norris 1113* (NY). **INDEPENDENCIA:** Sierra de Neiba, entre Cerros de Plan Ciquen y Loma El Hoyaza, 34 km de La Descubierta en la carretera de la frontera a Aniseto Martínez y Hondo Valle, 18°17’N, 71°43’W, 1800 m, 15 Dec 1982, *Zanoni et al. 24947* (NY). **LA ESTRELLETA:** Sierra de Neiba, 31–34 km by rd. NNW of La Descubierta, 11–14 km N of Ángel Félix, 18°41’N, 71°47’W, 21 Feb 1983, *Mickel et al. 8754* (NY). **LA VEGA:** Loma del Campana Río, Ciénaga de la Culata, Constanza, 24 Sep 1969, *Lioger 16069* (NY); Cordillera Central, La Nevera, 41.7–43.7 km N of Central Park of San José de Ocoa on the rd. to Costanza, 22 Feb 1982, *Mickel et al. 8267* (NY); Cordillera Central, La Nevera, 41.7–43.7 km N of Central Park of San José de Ocoa on the rd. to Costanza, 22 Feb 1982, *Mickel et al. 8270* (NY); Cordillera Central, La Nevera, 41.7–43.7 km N of Central Park of San José de Ocoa on the rd. to

Costanza, 22 Feb 1982, *Mickel et al. 8292* (NY); Cordillera Central, Parque Nacional J. A. Bermúdez, "La Laguna", aprox. 4 horas a pie desde La Ciénaga (de Manabao) en el sendero al Pico Duarte, 2000 m, 13 Jan 1987, *Zanoni et al. 37502* (NY). **PEDERNALES:** Sierra de Baoruco, 44 km desde Perdernales, en el camino a Los Arroyos y Duverge o 6 km nore del puesto Militar de Los Arroyos, 19° 2'N, 70° 32'W, 6 May 1982, *Zanoni et al. 20416* (NY). **SAN JOSÉ DE OCOA:** La Nevera San José de Ocoa, 2100 m, 20 Jan 1975, *Lioger & Lioger 22356* (NY, US). **Prov. unknown:** Bañaderos del Valle, headwaters of Bao River, Cordillera Central, 1700 m, 1–7 Oct 1968, *Lioger 12807* (NY, US).

PUERTO RICO. **PONCE:** Barrio Anón, along Río Inabón at brink of high falls, 22 Jan 1984, *Proctor 40084* (SJ n.v.).

GUADELOUPE. **BASSE-TERRE:** Basse Terre, comm, Matouba, Trace Victor Hugues, summit area of Grande Decouverte, at La Vigie, 1130 m, 19 Mar 2005, *Christenhusz, Katzer 4158* (UC). **Comm. unknown:** 16°3'N, 61°40'W, 24 Sep 24, 1943, *Questel 3228* (US).

HAITI. **DEPT. OUEST:** Massif de la Selle, gr. Crete a Piquants, Port au Prince, Malanga, 1200 m, 16 Dec 1926, *Ekman 7373* (NY); Massif de la Selle, Dept. Sud'est, Mare Blanche, 12.7 km E of Seguin on road to Mare Rouge, 1840 m, 13 Mar 1983, *Mickel et al. 9394* (NY, US); Summit of Morne Guimby, above Morne Des Commissaires, 16 Sep 1955, *Proctor 10844* (US).

COLOMBIA. **ANTIOQUIA:** La Unión, Faldas del Cerro San Miguel, 2500 m, 6 Jan 1984, *Atehortúa 1124* (US); Medellín, Santa Elena, Oct 1918, *Henri-Stanislas 1683* (US); Cordillera Central, bosque bajo de la cumbre cerca de Boquerón, camino entre Medellín y Palmitas, 10°11'N, 83°54'W, 19 Dec 1945, *Hodge 6951* (GH); Savenetas, eastern slopes of the highland of Santa Rosa, 5°40'5"N, 75° 44'21.3"W, Dec 1891, *Lehmann 7365* (US); Támesis, Vereda San Antonio, Quebrada San Antonio, sector Organera (cuevas de la quebrada), 5°47'59.98"N, 75°47'27.83"W, 2360 m, 25 Feb 2005, Rodríguez *et al. 5195* (NY); Jericó, Reserva La Nubes, sector Valle de las Palmas, 5°47'59.98"N, 75°47'27.83"W, 11 Dec 2004, Rodríguez *et al. 4746* (NY); Jericó, Reserva La Nubes, sector Valle de las Palmas, 11 Dec 2004, Rodríguez *et al. 4755* (NY); cerca a Santo Domingo, 1200 m, 7 May 1949, *Scolnik et al. 19an445* (US). **CAUCA:** Timbío-Paispampa Hwy., 2000 m, 23 Nov 1946, *Haught 5288* (US); El Tambo, Centro de Investigaciones Biológicas El Tambito, 1500 m, 21 Jun 1995, *Ramírez et al. 7794* (UC). **CUNDINAMARCA:** Fusagasugá, 15 Sep 1920, *Popenoe 1095* (US). **HUILA:** Cordillera Central, Cordillera del Buey, from Finca Loyola over páramo down to San Antonio, 2300 m, 14 Dec 1975, *Bishop 1989* (UC); Cordillera Central, Cordillera del Buey, hike from Finca Loyola over the páramo down to San Antonio (2100 m according to resident), east slope, 2300 m, 14 Dec 1975, *Bishop 1989* (UC). **RISARALDA:** Mun. Santuario, PNN Tatamá, camino que lleva al páramo de Tatamá, subiendo hacia

Morro Zancudo, 0°11’N, 78°51’W, 2368 m, 17 Apr 2007, *Sundue & Vasco 1232* (HUA, NY, UC). **VALLE DEL CAUCA:** Cordillera Occidental, vertiente occidental, monte La Guarida, filo de la cordillera sobre La Carbonera (entre Las Brisas y Albán), 16 Oct 1946, *Cuatrecasas, J. 22141* (US); La Cumbre, Cordillera Occidental, 14–19 May 1922, *Killip 5841* (US); Tocota, 3°24’N, 76°30’W, 1800 m, 16 Aug 1883, *Lehmann 3010* (US). **Dept. unknown:** Salto de Guadalupe, 1600 m, 27 Jul 1947, *Hodge 6961* (US).

VENEZUELA. **AMAZONAS:** Río Negro, Cerro de Neblina, 5.1 km NE Pico Phelps (=Neblina), 21.5 km E Neblina Base Camp, 9°14’N, 70°11’W, 1730 m, 30 Nov 1984, *Bell 374* (UC); Río Negro, W of Neblina Camp 7, S slopes of Canyon Grande, 1850 m, 30 Nov 1984, *Kral 71973* (UC). **BOLIVAR:** Roscio, a lo largo del camino que va de la base de la cumbre del Cerro Roraima, 0°50’4”N, 65°58’10”W, 27 Mar 1984, *Aymard & Luteyn 2459* (NY, UC); Mount Roraima, southwest-facing quebrada near Rondon Camp, 26 Sep 1944, *Steyermark 58710* (F, GH, US); Mt. Roraima, ascent of ledge along southwest facing side, 5°11’59.1”N, 76°2’29.7”W, 27 Sep 1944, *Steyermark 58731* (NY, US); Chimanta Massif, vicinity of camp 4, SW edge of Apacara-Tepui, 5°18’N, 62°9’W, 15 Apr 1953, *Steyermark 75401* (US); Piar, Macizo del Chimanta, sector centro-noreste del Chimanta-Tepui, cabeceras orientales del Caño Chimanta, 0°46’56” S, 77°46’51”W, 2000 m, 26–29 Jan 1983, *Steyermark et al. 128039* (UC). **CARABOBO:** Valencia, Cerro El Amparo y la fila al noreste, E de Valencia, cabeceros del Río Tocuyito, 9°12'13"N, 70°10'W, 23 May 23 2000, *Meier & Borjas 7229* (NY). **MERIDA:** Andrés Bello, Municipo Zerpa, La Carbonera, Bosque San Eusebio, 10°15'N, 68°7'30"W, 18 Jan 1982, *Marin et al. 132* (F). **TRUJILLO:** Bocono, Páramo de Guaramacal, SE of television towers, 0°55'N, 66°0'W, 2000 m, 28 Apr 1988, *Dorr et al. 4984* (NY); entre las antenas de relevo en el Páramo de Guaramacal y la Vega de Guaramacal, 9°41'N, 70°7'W, 23–24 Jul, 1984, *Ortega et al. 2044* (UC); Carache, Entre Carache y Agua de Obispo, 9°12'N, 70°10'W, 2600 m, 2 Nov 1987, *Rivero & Diaz 1422* (UC); Bocono, 22 km SE of Bocono, road to Guaramacal, 2300 m, 25–26 Nov 1982, *Smith et al. 1569* (UC).

GUYANA. **CUYUNI-MAZARUNI:** Mt. Roraima, upper slope, 10 Dec 1884, *Mt. Roraima Expidition 181*(US); Mt. Roraima, 16 Dec 1884, *Mt. Roraima Expidition 281* (US); Mt. Roraima, Rondon Camp, 3 Dec 1927, *Tate 504* (NY, US).

ECUADOR. **COTOPAXI:** Tenefuerte, Río Pilalo, Km 52–53, Quevado-Latacunga, 1°25' S, 78°26'W, 19 Jul 1982, *Dodson & Embree 13394* (US); Sigchos, 0°58'42"S, 79°6'22"W, 3044 m, 21 Jul 2003, *Ramos et al. 6372* (MO); Pujili, Reserva Ecológica Los Ilinizias, sector II, sector Chuspitambo, al occidente de Choasilli, Cordillera Occidental, 3°59.457' S, 79°7.974'W, 1900 m, 5 Aug 2003, *Silverston-Sopkin et al. 9809* (UC); Pujili, Reserva Ecológica Los Ilinizias, sector II, sector Chuspitambo, al occidente de Choasilli, Cordillera Occidental, 1725 m, 8

Aug 2003, *Silverston-Sopkin et al. 9934* (UC). **IMBABURA:** San Pablo on the Río Pamplona, Selva Alegra, SW of Volcón Cotocachi, 30 Nov 1943, *Ownbey 2616* (US pp); vicinity of Río Verde, ca. 5 km SW from the village of Mani, Río Cachaco, 1°27’S, 78°4’W, 1300 m, 2 Jun 1980, *Sperling & Bleiweiss 5024* (GH, QCA, US). **NAPO:** Along rd. between Baeza and Archidona, 16 km S of turn off to Loreto and Cocoa, 1°28’S,78°6’W, 985 m, 19 Apr 2003, *Croat et al. 87817a* (MO); Quijos, within 5 km of the town of Baeza, 4°29’S, 79°7’W, 1900 m, 8 Aug 1992, *Fay & Fay 3897* (UC); Cascada San Rafael, Km 101 via Lago Agrio (14 km by road SW of Reventador), 1°27’S, 78°15’W, 21–24 Feb 1985, *Foster 85-153* (UC); Ca. 50 km NE of Baeza, Cascada de San Rafael, along Río Quijos, 1350 m, 22 Feb 2005, *Moran et al. 7567* (NY); Cerro Huacamayos, on road Baeza - Tena, Ca. 34 km from Baeza, 5°7’28.1”N, 76°2’30.6”W, 2000 m, 9–10 Aug 1980, *Øllgaard, et al. 35900* (AAU); Yanayacu Biological Field Station, W of Cosanga, aprox. 15 km S of Baeza, 0°35.962’ S, 77°55.42’W, 2133 m, 5 Dec 2006, *Sundue & Schuettpelz 1075* (NY, UC); Yanayacu Biological Field Station, W of Cosanga, aprox. 15 km S of Baeza, 4°9’S, 78°38’W, 2106 m, 6 Dec 2006, *Sundue & Schuettpelz 1086* (NY, UC); Quijos, Reserva Ecológica Antisana, Cordillera de lo Guacamayos, sector oriental, cruce del oleoducto de la compañia ARCO, entre El Mirador y camino de La Virgen, 2300 m, 12–14 Jan 1999, *Vargas & Narvaez 3531* (MO, NY, UC). **PASTAZA:** Mera - Shell Mera, ca. 2 km E of Mera, at bridge over Río

Alpayacu, 1°28'S, 78°6'W, 1100 m, 21 Jan 1992, *Øllgaard 99568* (QCA); Mera - Shell Mera, ca. 2 km E of Mera, at bridge over Río Alpayacu, 1°28'S, 78°6'W, 1100 m, 21 Jan 1992, *Øllgaard 99581* (QCA); Mera - Shell Mera, ca. 2 km E of Mera, at bridge over Río Alpayacu, 0°46'N, 78°28'W, 1100 m, 21 Jan 1992, *Øllgaard 99575* (QCA); ca. 5 km E of Mera, on road to Shell Mera, 0°10'N, 78°46'W, 1050 m, 30 Jul 1980, *Øllgaard et al. 35598* (AAU); 2 km W of Shell on Shell-Mera road, 1°28'S, 78°5'W, 1100 m, 21 Jan 1992, *Stolze & Stolze 1678* (UC). **PICHINCHA:** Quito-Santo Domingo vis Chiriboga (old rd. Km 94), 0°14' S, 78°48'W, 1060 m, 17 May 1981, *Dodson et al. 10929* (US); Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old rd. Quito-Santo Domingo, 0°14' S, 78°48'W, 1900 m, 6 Jul 1991, *Fay & Fay 3052* (QCA); Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old rd. Quito-Santo Domingo, 0°14'S, 78°48'W, 1900 m, 10 Jul 1991, *Fay & Fay 3163* (QCA); Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old rd. Quito-Santo Domingo, 0°14'S, 78°48'W, 1900 m, 10 Jul 1991, *Fay & Fay 3193* (QCA); Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old rd. Quito-Santo Domingo, 0°14'S, 78°48'W, 1900 m, 9 Jul 1991, *Fay & Fay 3227* (QCA); Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old rd. Quito-Santo Domingo, 0°14'S, 78°48'W, 1900 m, 10 Jul 1991, *Fay & Fay 3284* (QCA); Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old rd. Quito-Santo Domingo, 1900 m, 10 Jul 1991, *Fay & Fay 3286*

(QCA); ca. 2 km NW of Mindo, Hacienda San Vicente, 10–14 Feb 1985, *Foster 85-2* (UC); Road Chiriboga - Santo Domingo, just below Chiriboga, 2°27’N, 77°5’W, 1900 m, 2 Jun 1979, *Holm-Nielsen 18144* (AAU); Mindo Cloudforest Reserve, 1 km N of Milpe, on rd. Quito-Pto. Quito, 0°0’5”S, 78°39’15”W, 1150 m, 11 Sep 2004, *Lehnert & Kessler 1206* (UC); Carretera Nanegalito - San Tadeo, Km 30, 0°7’N, 78°38’W, 1850 m, Jan 1995, *Navarrete 908* (QCA); Maquipucuna Reserve, at Río Umachaca, 0°58’45” S, 79°6’53”W, 1300 m, 20 Feb 1997, *Øllgaard & Navarrete 2297* (QCA); Road Pacto-La Delicia-La Esperanza, Km 19.5, 0°17’S, 78°46’W, 1150 m, 1 Dec 1996, *Øllgaard, et al. 2235* (AAU); Road El Paraíso - Saguanagal, 3 km from El Paraíso, 0°41’S, 77°50’W, 1500 m, 2 May 1982, *Øllgaard, et al. 37794* (AAU); Reserva Maquipucuna, sendero tranquillo, 22 Aug 2001, *Smith et al. 2800* (UC); 0°14’S, 78°48’W, *Sodiro s.n.* (UC); Quito, Estación Biológica Río Guajalito, Km 59 of old rd. from Quito to Santo Domingo, 0°14’S, 78°48’W, 1800 m, 18 Nov 2006, *Sundue & Martin 1031* (NY); Quito, Estación Biological Río Guajalito, Km 59 of old rd. from Quito to Santo Domingo, 0°7.346’S, 78°37.919’W, 1800 m, 18 Nov 2006, *Sundue & Martin 1035* (NY, UC); Maquipucuna Biological Field Station, ca. 5 km E of Nanegalito and ca. 25 km N of Quito, 0°7.5’N, 78°38’W, 1371 m, 24 Nov 2006, *Sundue & Martin 1050* (NY, UC); Quito, Hacienda El Carmen, guava grove along trail to Hacienda Espárragos, ca. 5 km airline SE of Nanegal, 0°7.29’N, 78°38’W, 1300 m, 13 Sep 1989, *Webster & Addison*

27573 (QCA); Quito, Parroquia Nanegal, Bosque Protectora Maquipucuna, 0°6’N, 78°37.5’W, 0 m, 10 Jul 1992, *Webster et al. 29317* (UC); Bosque Protector Maquipucuna, E side of Río Tulambi, 0°6’12”N, 77°35’15”W, 5 Sep 1993, *Webster et al. 30299* (UC). **SANTIAGO-ZAMORA:** Between Campanas and Arenillas, along Río Tintas, 10 leagues SE of El Pan, 3°58’S, 79°4’W, 2195 m, 13 Jul 1943, *Steyermark 53612* (US). **TUNGURAHUA:** Banos, up the valley of Río Bascun, on E side of river, 0°27’5”S, 77°53’0”W, 2300 m, 4 Jul, 1992, *Fay & Fay 3586* (NY, UC); W of Río Guambi, ca. 7 km along road and trails S of Río Negro, 1780 m, 31 Mar 1998, *Øllgaard & Navarrete 3014* (QCA); Río Mapoto at confluence with R. Pastaza, 0°35’4”S, 78°49’54”W, 1225 m, 21 Mar 1939, *Penland & Summers 207* (F, US). **ZAMORA-CHINCHIPE:** Reserva Tapichalaca, N slope of Cerro Tapichalaca, 2465 m, 31 Oct 2003, *Lehnert 1035* (GOET, UC); P. N. Podocarpus, along new Loja-Zamora rd., 4 km E of the pass "El Tiro", 3°59.349’S, 79°5.713’W, 2630 m, 18 Dec 2006, *Sundue 1176* (NY); P. N. Podocarpus, park entrance "San Francisco," on new Loja-Zamora rd., 0°35.962’S, 77°55.42’W, 2151 m, 14 Dec 2006, *Sundue 1128* (NY); Along rd. between Paquisha to Chinapintza, 0°38’ S, 77°51’W, 17 Nov 2004, *van der Werff et al. 19569* (MO, UC); Area of Estación Científica San Francisco, 2000 m, 9 Jan 2004, *Werner 734* (UC).

PERU. **AMAZONAS:** Bongara, Pomacochas, ridge above Quebrada Santa Rosa lying across Lago Pomacochas from Village, 4 Apr 1944, *Hodge 6156* (US); Chachapoyas, Cerros Calla Calla, east side, 10 km above Leimebabma on the road to Balsas, 9°40’S, 76°5’W, 2700 m, 29 Mar 1964, *Hutchinson & Bennett 4754* (F, NY); Pcia. Pongara, Distr. Yambras-bamba, along road above Cpto. Buenas Aires, at Km 53.6, ca. 40 km N of Jumbilla, 2 Mar 1967, *Tillet 673-231* (F, GH, US); In monte Campana, prope Tarapoto, Peruviae Orientalis, 5°40’27”S, 77°40’35”W, Aug 1856, *Spruce 4642* (NY); Leimebamba, 2400 m, 30 Dec 1962, *Woytowski 7840* (GH). **CAJAMARCA:** 5°17’3”S, 79°16’W, *Bues 1945* (US); Tabaconas, Santuario Nacional, Tabaconas-Namballe, 5°45’S, 77°29’W, 16 Nov 1998, *Campos & Tenorio 5047a* (MO); Jaen, Ridges of the valley of Río Manchara, E of Tabaconas, 19 Nov 1943, *Hodge 6102* (US). **CUSCO:** San Miguel, Urubamba valley, 1800 m, 9 Jun 1915, *Cook & Gilbert 1168* (US). **HUANUCO:** Huánuco, Huánuco - Tinga María, Km 40, abra de carpish, 23 Aug 2002, *Lehnert 291* (GOET pp); Huánuco, Tingo María - Huánuco, 43 km antes Huánuco, carpish, 10°22.9’S, 75°35.4’W, 1000 m, 26 Aug 2002, *Lehnert 312* (GOET pp, UC pp); Huánuco, Tingo Maria - Huánuco, 43 km antes Huánuco, carpish, Aug 26, 2002, *Lehnert 315* (GOET pp); Huánuco, within 5 km of Carpish, pass on the Huánuco-Tingo María road, about half way between Acomayo and Chinchao, 35 km NE of Huanuco, 2500 m, 11 Sep 1956, *Tryon & Tryon 5310* (F, GH, US). **PASCO:** Oxampampa, Oxampampa-Santa Barbara, "rodal" at the end of the road, 1500 m, 28 Aug 2002, *Lehnert 329* (UC). **SAN MARTÍN:** Rioja, Km 399 of Carretera Marginal, trail to Quebrada Venceremos and Río Serranoyacu, 67 km E of Pomacochas, 8 km W of bridge over Río Serranoyacu, 13 Jun 1986, *Knapp & Alcorn 7776* (F, NY); Rioja, Carretera Moyobamba - Pedro Ruiz, Km 404, 9°43.5'S, 76°5.66'W, 2 Aug 2002, *Lehnert 212* (GOET, UC); Rioja, Along road Rioja-Pedro Ruiz, 5°40'26"S, 77°40'35"W, 1170 m, 23 Mar 1998, *van der Werff et al. 15535* (UC); Along road Rioja-Pedro Ruiz, about bridge Serranoyacu, 5°15'S, 60°42'W, 1170 m, 5 Mar 2001, *van der Werff et al. 16773* (MO, NY, UC).

BOLIVIA. **COCHABAMBA:** Prov. Ayopaya, Comunidad Pampa Grande, cruzando el Río del mismo nombre, 16°40'S, 66°28'W, 2150 m, 9 Jun 2002, *Jiménez 1396* (LPB, UC); Prov. Ayopaya, Comunidad Pampa Grande, cruzando el Río del mismo nombre, 16°40'S, 66°28'W, 2150 m, 9 Jun 2002, *Jiménez 1397* (UC); Prov. Ayopaya, Comunidad Pampa Grande, cruzando el Río del mismo nombre, 17°8'S, 65°38'W, 2150 m, 9 Jun 2002, *Jiménez, I. 1399* (LPB); Prov. Ayopaya, Comunidad Pampa Grande, al inicio del sendero Pampa Grande-Carmen Pampa, 6°12'S, 67°53'W, 2110 m, 9 Aug 2002, *Jiménez 1443* (UC); Prov. Carrasco, Km 116 antigua carretera Cochabamba a Villa Tunari, 17°8'S, 65°37'W, 2400 m, 6 Jul 1996, *Kessler 7029* (LPB, UC); Prov. Carrasco, Km 123 antigua carretera Cochabamba a Villa Tunari, 16°23'S, 67°48'W, 2100 m, 9 Jul 1996, *Kessler 7146* (LPB, UC); 6°12'S, 67°53'W, Feb 1984, *Windisch 2363* (AAU). **LA PAZ:** Prov. Nor Yungas, Estación Biológica de Tunquini, senda cafetal al camino de la mina, 6°12'S, 67°53'W, 2500 m, 3 Aug 2001, *Bach et al. 1349* (LPB, UC); Prov. Nor Yungas, Estación

Biológica de Tunquini, Bajo Hornui, senda del campo de Dn. Pedro al camino de la mina, 16°40’S, 66°28’W, 2400 m, 26 Jul 2000, *Garcia et al. 4466* (LPB, UC); Prov. Nor Yungas, Cerro Hornui, alrededores de la 2nd Estación climatológía, 17°8’S, 65°38’W, 2700 m, 12 Dec 2000, *Jiménez & Quisbert 2* (LPB, UC); Prov. Nor Yungas, Estación Biológica de Tunquini, Bajo Hornuni, senda del Campo de Don Pedro al Camino de la mina, 16°11’S, 67°53’W, 2350 m, 8 Aug 2000, *Jiménez et al. 398* (LPB); Prov. Nor Yungas, km 8 Chuspipata a Coroico, 16°24’S, 67°47’W, 2650 m, 19 Sep 1997, *Kessler 12128* (LPB, UC); Prov. Nor Yungas, km 10 Chuspipata a Coroico, 16°17’S, 68°48’W, 2500 m, 20 Sep 1997, *Kessler 12199* (LPB, UC); Nor Yungas, Carretera Chuspipata - Yolosa; entre Chuspipata y Sacramento Central, 2580 m, 10 Nov 2002, *Lehnert 499* (GOET, LPB, UC); Mapiri, Apr 1886, *Rusby 382* (NY).

Ascogrammitis anfractuosa has a much wider geographic distribution than its congeners, and distinctive morphological variants exist throughout its distribution. Specimens from the West Indies typically have rhizome scales with entire margins, and about half of the specimens examined had at least a few 0.2 mm long reddish setae on the adaxial laminae. West Indian plants often have a minute cretaceous deposit on the hydathode; none had conspicuous deposits. The syntypes of *Polypodium induens* exhibit these characters. If the West Indian plants were recognized as a species, this name would apply.

The Mesoamerican material is nearly uniform and agrees well with the type from Venezuela. One relatively common variation among Mesoamerican specimens is the presence of 1–2 setae that are 0.1 mm long along the margins of the rhizome scales. Plants with this character have been collected in Panama (*Woodson et al. 829*), Costa Rica (*Mickel 2664*), and Honduras (*Merill et al. 15678),* whereas most Mesoamerican material has entire rhizome scales. An uncommon variation among Mesoamerican material is the prescence of cretaceous hydathodes. Although most Mesoamerican material has non-cretaceous hydathodes, cretaceous deposits have been seen on specimens from two localities, in Panama (*Killip 5194*) and Costa Rica (*Barringer et al. 2277*).

Several regional variations occur in South America. Material corresponding to the Venezuelan type is primarily restricted to the eastern flank of the Andes. In contrast, plants from the western flanks in Ecuador (*Moran et al.* 7567) and Colombia (*Sundue & Vasco 1232*) differ by rhizome scales with 1–2 marginal setae. Plants with conspicuously cretaceous hydathodes and entire rhizome scales are found on both sides of the Andes in Ecuador (*Fay & Fay 3586*) and Peru (*Tryon & Tryon 5310*), and with a single disjunct specimen known from Cochabamba, Bolivia (*Windisch 2363*). Many of these plants were growing on rocks. Lax, long-leaved plants with adaxially setose laminae have been collected along the Shell – Mera road in Ecuador (e.g., *Stolze & Stolze. 1678*; *Øllgaard 99568, 99575, 99581*; *Øllgaard et al. 35598*). With the exception of the specimen mentioned above, Bolivian collections (*Jiménez 1396*; *Kessler et al. 12128*) differ from the type by larger fronds and rhizome scales with setose margins. One specimen (*van der Werff et al., 16674*), from the Huancabamba Depression, stands out for its very small fronds that are densely setose on both sides of the laminae. Further investigation may warrent the recognition of some of these entities as taxa.

Ascogrammitis angustipes (Copel.) Sundue, **comb. nov.** *Ctenopteris angustipes* Copel., Phillipp. J. Sci. 84: 404. 1956. *Terpsichore angustipes* (Copel.) A. R. Sm., Novon 3: 485. 1993. Type: Colombia. Valle del Cauca: El Silencio, Yanaconas, dense forest, on tree, 1900–2200 m, 28 Feb 1939, *E. P. Killip & H. Garcia 33843* (holotype: US).

(Fig. 6, 15 E–H)

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 1.3–1.5 mm wide; branch buds absent; rhizome scales 1.5–3.5 × 0.4–0.5 mm, lanceolate, the lumina slightly iridescent, clear to partially occluded, the apex attenuate, the margins setose, the setae 0.1 mm long, reddish; fronds 20–26 × 2.5–3.5 cm, hemidimorphic, arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 3.5–5 cm × 0.5–0.8 mm, with a single vascular bundle, brown to castaneous, narrowly marginate throughout or nearly so, moderately setose, the setae 1–1.5 mm long, sparsely hairy, the hairs 1-furcate; rachis with castaneous sclerenchyma visible on both sides of the lamina, the abaxial side sparsely to moderately setose, the setae 0.5 mm long, sparsely hairy, the hairs simple, 0.1 mm long, the adaxial side sparsely to moderately setose, the setae 0.5 mm long; laminae chartaceous, narrowly elliptic, 1-pinnatisect throughout, with 40–50 pairs of segments, the base attenuate with up to 12 pairs of reduced segments; medial segments 12–15 × 3–5 mm, oblong, widest at the base, the base slightly decurrent and slightly surcurrent, the apex rounded, the margins entire, glabrous or provided with simple 0.1 mm long hairs, sterile portions of the abaxial lamina surface sparsely to moderately setose, the setae 0.2–0.4 mm long, fertile portions of the abaxial lamina moderately setose, the setae up to 0.8 mm long; adaxial lamina surface wtih a few scattered setae along the segment costa, otherwise glabrous; segment costae with castaneous sclerenchyma visible abaxially, partially visible adaxially; veins not readily visible; hydathodes cretaceous; sori inframedial, 4–8 per segment, confined to the distal portion of the lamina; receptacular setae present.

Distribution.—Colombia, western side of the Andes; (1500–)1900–2723 m.

Additional specimens examined. COLOMBIA. **ANTIOQUIA:** Mun. de Caldas, Along Río Medellín, disturbed and secondary vegeatation below Alto de Morrogil, 5°7’ 28.1”N, 76°2’ 30.6”W, 1500–1600 m, 27 Jan 1984, *Juncosa 1987* (UC); Mun. Támesis, Vereda San Antonio, Quebrada San Antonio, sector Organera (cuevas de la quebrada), 16°19’N, 67°56’W, 2360 m, 10 Jul 2005, *Rodríguez 5182* (HUA, NY); Mun. Támesis, Vereda San Antonio, Quebrada San Antonio, sector Organera (cuevas de la quebrada), 16°12’N, 67°53’W, 2360 m, 25 Feb 2005, *Rodriquez et al. 5128* (HUA). **RISARALDA:** Mun. Pueblo Rico, Vereda Tatamá, zona amortiguadora PNN Tatamá, Parcela Los Incorados, 6°5’N, 75°32’W, 2263 m, 15 Apr 2007, *Sundue & Vasco 1208* (HUA, NY); Mun. Santuario, PNN Tatamá, camino que lleva al páramo de Tatamá, subiendo hacia Morro Zancudo, 2723 m, 17 Apr 2007, *Sundue & Vasco 1237* (HUA, NY); Pueblo Rico, Vereda Montebello, cerca a Los Cajones, subiendo hacia la base militar, 5°40’5.7”N, 75°44’21.3”W, 2240 m, 14 Apr 2007, *Vasco & Sundue 650* (HUA, NY); Pueblo Rico, Vereda Montebello, cerca a Los Cajones, subiendo hacia la base militar, 5°15’2.9”N, 76°6’19.9”W, 2300 m, 14 Apr 2007, *Vasco & Sundue 702* (HUA, NY, UC).

Ascogrammitis angustipes is distinguished by laminae proximally 1-pinnatisect with up to 12 pairs of reduced segments, hydathodes cretaceous, pinna margins that lack setae, petioles moderately setose and not marginate throughout, 4–8 sori per segment. It is a variable species. The type collection, which is a unicate, differs from all other material by having essentially the same density of setae present on fertile and sterile portions of the blade. *Sundue & Vasco 1208* differs from other material by having 2.0 mm long setae in the fertile portion of the blade. *Rodríguez 5821* differs by the 1-furcate hairs of the petioles having a setiform branch 1.0 mm long, and by the segment margins which are provided with sparse to moderately dense indument that is composed of an irregular combination of 0.1 mm long simple hairs, 0.2–0.4 mm long setae, 1-furcate hairs with a 0.3 mm long setiform branch.

Ascogrammitis athyrioides (Hooker) Sundue, **comb. nov.** *Polypodium athyrioides* Hook., Sp. Fil. 4: 224. (1862). *Ctenopteris athyrioides* (Hooker) Copeland, Phillip. J. Sci. 84: 406. 1956. *Grammitis athyrioides* (Hook.) C. V. Morton, Contr. U. S. Natl. Herb. 38: 255. 1973. *Terpsichore athyrioides* (Hook.) A. R. Sm., Novon 3: 488. 1993. TYPE: Peru. Cuzco: Pangoa [San Martín de Pangoa], *A. Mathews 1103* (holotype: K, photo: F of holotype). (Figs. 1 C, 4, 15 A–D)

Polypodium yungense Rosenst., Fedde, Repert. Spec. Nov. Regni Veg. 5: 236. 1908. *Ctenopteris yungensis* (Rosenst.) Copel., Phillip. J. Sci. 84: 407. 1956. *Xiphopteris yungensis* (Rosenst.) Crabbe, British Fern Gaz. 9: 319. 1967. TYPE: Bolivia. La Paz: Prov. Nor Yungas, Unduavi, 3400 m, 12 Feb 1907, *O. Buchtien 891* (holotype: B? n.v., isotype: US).

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 1.5–3 mm wide; branch buds absent; rhizome scales 2.5 × 0.5 mm, lanceolate, blackish, castaneous in age, concolorous, the lumina clear but narrow and appearing occluded, the margin setose, the setae 0.1–0.2 mm long, reddish, the apex attenuate; fronds 40–68 × 4–6.5 cm, monomorphic, pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 2.5–14 cm long, 0.5–0.8 mm wide, with a single vascular bundle, castaneous or brown, terete, moderately setose, the setae 1.5–2 mm long, moderately hairy, the hairs, 1-furcate, ca. 0.1 mm long; rachises moderately setose abaxially and adaxially, the setae 1.5 mm long, sparsely hairy, the hairs 1-furcate, 0.1 mm long, ca. 0.1 mm long; laminae chartaceous, 1-pinnate-pinnatifid, sometimes young fronds simply 1-pinnate; medial segments 1.8–4 × 0.3–0.6 cm, narrowly triangular, ascending, often falcate, or sometimes merely spreading, widest at the base, the base decurrent, larger segments with an acroscopic auricle, the apex acute, the margin glabrous, the abaxial lamina surfaces essentially glabrous, with scattered simple hairs, ca. 0.1 mm long; segment costae blackish, the dark sclerenchyma visible on both the abaxial and adaxial sides of the blade; veins on the abaxial side of the lamina or not, not visible on the adaxial side of the lamina; hydathodes cretaceous; sori medial, situated in the lobes of the segments, up to 13 pairs per segment, receptacular setae absent.

Distribution.—Peru and Bolivia, eastern slopes of the Andes; 3000–3450(3600) m.

Additional specimens examined. BOLIVIA. **COCHABAMBA:** Prov. Chapare, Candelaria, 16°18'S, 67°52'W, 3360 m, 6 Jun 1995, *Fernández 632* (UC); Prov. Ayopaya, comunidad Pampa Grande, sendero a Incacasani Grande, 17°10'S, 65°54'W, 3200 m, 18 Sep 2002, *Jiménez 1692* (UC); Prov. Chapare, carretera nueva a Santa Cruz, pasando la represa de Corani, 14°41'S, 68°58'W, 3180 m, 28 Sep 2002, *Jiménez 1753* (UC); Prov. Chapare, ca. 4 km al N de Maycamayu, ca. 5 km de Sacaba, 17°12'S, 65°41'W, 3400 m, 13 Aug 1991, *Kessler 2926* (LPB); Prov. Carrasco, km 100 antigua carretera Cochabamba a Villa Tunari, 17°12'S, 65°41'W, 3250 m, 26 Jun 1996, *Kessler 6723a* (UC); Carrasco, km 130 antigua carretera Cochabamba a Villa Tunari, 15°10'S, 68°53'W, 2000 m, 13 Jul 1996, *Kessler 7231* (UC); Prov. Chapare, Llantas Aduana, 3100 m, 9 Mar 1929, *Steinbach 9554* (F, GH, MO, NY, UC, US); Prov. Chapare, 10°22'S, 75°27'W, 3100 m, 2 Sep 1929, *Steinbach 9720* (GH). **LA PAZ:** Prov. Nor Yungas, ca. de 30 km después de la cumbre hacia Unduavi, 16°12'S, 67°53'W, 3380 m, 2 Sep 1980, *Beck 2844* (F, LPB); Prov. Nor Yungas, pasando Unduavi antes de llegar a Cotapata, subiendo la senda antigua hacia Coroico, 19°38'S, 63°43'W, 3500 m, without date, *Beck 21496* (LPB, UC); Prov. Nor Yungas, Unduavi, 16°19'S, 57°54'W, 3300 m, Nov 1910, *Buchtien 2754* (NY); Prov. Nor Yungas, Unduavi, 17°19'S, 65°56'W, 3300 m, Nov 1910, *Buchtien 2756* (UC, US); Prov.

Nor Yungas, etween Sorata and Mapiri, without date, *Cárdenas 1002* (GH); Prov. Franz Tamayo, Pusupunku, a 30 km al NE de Pelechuco, 14°40'S, 68°55'W, 3600 m, 16 Oct 1999, *García & Beck 4079* (NY); Prov. Sud Yungas, Unduavi, cerca. a la Mina Lourdes, 16°18'S, 67°52'W, 3450 m, 25 Nov 1995 *Gonzales 1541* (UC); Prov. Sud Yungas, Unduavi, cerca. a la Mina Lourdes, 16°18'S, 67°52'W, 3450 m, 25 Nov 1995 *Gonzales, J. 1552* (LPB); *Gonzales, J. 1576* (LPB, UC); Tablas, 16°12'S, 67°53'W, 3400 m, 1 May 1911, *Herzog 2190* (US); Prov. Nor Yungas, Coscapa, sobre el sendero prehispánico Sillutinkara, 16°40'S, 66°28'W, 3200 m, 1 Oct 2001, *Jiménez 543* (LPB, UC); Prov. Franz Tamayo, PN-ANMI Madidi, senda Pelechuco-Mojos, localidad Tambo Quemado (lugar para acampar), bajando por el sendero, poco después del 2º Río, 17°12'S, 65°58'W, 3470 m, 29 Apr 2003, *Jiménez 1774* (LPB, UC); Prov. Saavedra, km 15 Charazani a Chullina, 16°12'S, 67°53'W, 3400 m, 5 Jul 1997, *Kessler, M. 10622* (UC); Prov. Nor Yungas, Trocha al Valle de Coscapa, P.N. Cotapata, 16°17'S, 67°54'W, 3450 m, 9 Sep 1997, *Kessler 11714* (UC); Prov. Nor Yungas, Río Coscapa Trail, following the trail to the Río Coscapa from its inception on the Yungas Highway ca. 3 km NE of Unduavi to the ridge line, 16°35'S, 67°44'W, 3450 m, 30 Apr 1988, *Lewis 88339* (MO, UC); Prov. Nor Yungas, P. N. Cotapa, Unduavi, sendero Sillutincara, ca. de 1 km subiendo de la carretera, 16°17'28"S, 67°53'28"W, 3300 m, 30 May 2007, *Fuentes et al. 11943* (NY). **SANTA**

CRUZ: Prov. Cordillera, Lagunillas, 16°19’S, 57°54’W, 3000 m, 7 Mar 1950, *Brooke 6166* (F, NY).

PERU. **AMAZONAS:** Chachapoyas, Cerros Calla Calla, 26 km above Leimebamba on road to Balsas, Km 403, 6°43.3’S, 77°53’W, 3360 m, 16 Oct 1964, *Hutchinson & Writght 6988* (UC, US [frag]); Chachapoyas, Leymebamba-Balsas, 25 km from Leymebamba, 3300 m, 8 Jul 2002, *Lehnert 261* (GOET, UC); Chachapoyas, Upper slopes of Puma-urcu ESE of Chachapoyas, 1 Jun 1962 *Wurdack 703* (GH, US); **CUSCO:** Vilcabamba, July, 1934, *Bues 2116* (US). **HUANUCO:** Muna, 23 May - 4 Jun 1923, *Bryan 550b* (F, US); Muña, trail to Tambo de Vaca, 5–7 Jun 1923, *Macbride 4305pp* (F, NY pp, US), *Macbride 4329pp* (F, NY pp, US); 6 miles S of Mito, 15 Aug 1922, *Macbride & Featherstone 1862* (F, US). **JUNÍN:** Satipo, Cordillera Vilcabamba, Río Ene slope, near summit of divide, 17°9’S, 65°38’W, 3320 m, 14 Jun 1997, *Boyle et. al. 4389* (USM); **PASCO:** Oxapampa, Parque Nacional Yanachaga-Chemillen, Abra Yanachaga, 3°28’S, 79°36’W, 2900 m, 1 Aug 2003, *Vásquez et al. 28446* (MO). **SAN MARTÍN:** Mariscal Cáceres, Chocos, Río Abiseo Nat. Park, 3550 m, 16 Jun 1988, *León 1898* (UC). **WITHOUT PRECISE LOCALITY:** 8000–10,000 ft, Oct 1920, *Bues 1039* (US); 12,000 ft, Oct 1920, *Bues 1259* (US); 9,000 ft, 1923, *Bues 1391* (US); 10,000 ft, 1923, *Bues 1547* (US); Río Lachac, 7,000 ft, *Bues 1822* (US).

Ascogrammitis athyrioides differs from its congeners by pinnatifid segments—a character seen even in juvenile material.

Ascogrammitis clathrata (Sundue & M. Kessler) Sundue, **comb. nov.**

Terpsichore clathrata Sundue & M. Kessler, Org. Divers. Evol. 8: 163. 2008. Type: Bolivia. La Paz: Prov. Nor Yungas, Parque Nacional Cotapa, Estación Biológica de Tunquini, caminos alrededor de la estación biológica, 1500 m, bosque de los Yungas siempreverde disturbado, 16°11’ S, 67°52’W, 17 Jul 2000, *T. Krömer & C. Acebey 1237* (holotype: UC, isotype: LPB). (Figs. 5, 17 D–G)

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 2–2.5 mm wide; branch buds present; rhizome scales 4.5 × 0.5 mm, narrowly lanceolate, clathrate, the lumina clear, the cell walls dark red to blackish, the apex long-attenuate, the margin setose, the setae 0.1 mm long, pale reddish; fronds monomorphic, 26–32 × 5–7.5 cm, presumably arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petiole 5–6.5 cm × 0.6–1.2 mm, with a single vascular bundle, terete, non-marginate or narrowly marginate distally, brown to castaneous, sparsely setose, the setae 0.5 mm long, sparsely hairy, the hairs 1-furcate; rachis abaxially moderately setose, the seta 0.2 mm long, sparsely hairy, the hairs 1-furcate, 0.1 mm long, adaxially densely setose, the setae 0.2 mm long; laminae chartaceous, 1-pinnatisect throughout or basally 1-pinnate, the segments widely spaced, patent; medial segments 24–37 × 3–4 mm, oblong, the base slightly expanded, the apex acute, the margins entire, moderately provided wide simple hairs; abaxial lamina surface moderately to densely setose, the setae evenly distributed, 0.3–0.5 mm long, erect; adaxial lamina surfaces glabrous except for scattered hairs along the segment costae; segment costae with dark sclerenchyma visible on both sides of the lamina; veins visible on the abaxial side of the lamina, not visible on the adaxial side of the lamina; hydathodes non-cretaceous; sori inframedial, 14–22 per segment, distributed evenly throughout the frond; receptacular setae present.

Distribution.—Bolivia, known only from the type locality despite intensive collecting of epiphytic plants in that area; 1500 m (Sundue & Kessler, 2008).

Ascogrammitis clathrata is distinguished by its large 1-pinnate fronds, large rhizome scales (up to 4.5 × 0.5 mm), and evenly setose abaxial surface of the lamina. The specific epithet refers to the clathrate rhizome scales.

Ascogrammitis clavigera Sundue ex A. R. Sm., **sp. nov.** Type: Venezuela. Trujillo: Dtto. Boconó, 22 km SE of Boconó, road to Guaramacal, ca. 9°12’N, 70°10’W, 2300 m, 25–26 Nov 1982, *A. R. Smith, B. Stergios, G. Aymard & D. Taphorn 1572* (holotype: UC, isotypes: FLAS, n.v., PORT, n.v.). (Fig. 5, 14 D–E)

Ascogrammitis pichinchae similis, sed ab ea laminis 1-pinnatifidis et foliis minus dense setosis differt.

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 2.5–4 mm wide; branch buds present; rhizome scales 4–5 × 0.5 mm, lanceolate, blackish in mass, the cell walls reddish, the lumina clear, narrow and so appearing occluded, the apex attenuate the margin setose, the setae 0.1 mm long, reddish; fronds 23–30 × 4.5 cm, monomorphic, presumably arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 4.5–10 cm × 0.7–1 mm, with two vascular bundles, brown, narrowly marginate to the base, sparsely setose, the setae 1.5 mm long, sparsely hairy, the hairs 1-furcate; rachis with dark sclerenchyma visible on both sides of the blade, the abaxial side sparsely hairy, the hairs 1-furcate, 0.1 mm long, the adaxial side moderately to densely setose, the setae 0.5–1 mm long; laminae chartaceous, elliptic, proximally 1-pinnate, medially and distally 1-pinnatisect, with 32–40 segment pairs the base with 2–5 pairs of reduced segments; medial segments narrowly triangular, 1.8–2.4 cm long, ca. 2 mm wide medially, widest at the base, the base 5 mm wide, decurrent, the apex acute, the margins entire, bearing scattered simple hairs, ca. 0.1 mm long; the abaxial lamina surface essentially glabrous, sometimes with a few scattered setae along the veins, 0.5 mm long, the adaxial lamina surface with scattered 0.3 mm long setae along the segment costae, otherwise glabrous; segment costae with dark sclerenchyma visible on both sides of the blade; veins visible abaxially, sometimes slightly darkened, more often the veins the same color as the lamina tissue; hydathodes not cretaceous; sori inframedial, confined to the distal portion of the lamina, 8–11 per segment; receptacular setae absent.

Distribution.— Venezuela, subpáramo woodlands; 2500–3000 m.

Additional specimens examined. VENEZUELA. **MÉRIDA:** San José de Acequias, La Centella, 2700–2800 m, 25 Apr 1999, *Schneider 2400* (UC). **TRUJILLO:** Boconó, Parque Nacional Guaramacal, road from Boconó to Guaracamal, SE of Guaracamal. N slope of mountain, 2200–2500 m, 16 Jul 1995, *Dorr et al. 8154* (UC); Boconó, Páramo de Guaramacal, 9°12'N, 70°9'W, 2800 m, 22 Nov 1984, *Ortega & van der Werff 2236* (MO, NY, UC); Boconó, montañas y páramo de Guaracamal, 2500–3000 m, 22 Nov 1984, *Ortega & van der Werff 2263* (MO); Boconó, Páramo de Guaramacal, 2500–3000 m, 3 Feb 87, *van der Werff et al. 8799* (MO); Boconó, Páramo de Guaramacal, 4°29'27.9"N, 73°40'58.6"W, 2500–3000 m, 3 Feb 1987, *van der Werff et al. 8822* (MO).

Ascogrammitis clavigera is distinguished by 1-pinnatisect laminae, rhizome scales with narrow lumina that appear occluded and blackish in mass, non-cretaceous hydathodes, and sparse covering of setae throughout. *Ascogrammitis athyrioides*, *A. tungurahua*, *A. pichinchae*, and *A. colombiensis* have similar scales to *A. clavigera*, but these plants all differ by fully 1-pinnate laminae and being more densely setose throughout. The specific epithet was originally chosen by Alan Smith who applied the name to herbarium specimens; it means "bearing clubs", in reference to the clavate ascomes of *Acrospermum*.

Ascogrammitis colombiensis Sundue, **sp. nov.** Type: Colombia. Meta: San Juanito, Parque Nacional Natural Chingaza, cañón del Río Guácharo, Lago Chingaza, bosque muy húmedo montano alto, pendiente oriental de la cordillera Oriental, 4°31'52.8"N, 73°44'55"W, 3188 m, 3 May 2007, *M. Sundue & A. Vasco G. 1331* (holotype: NY, isotypes: HUA, UC.)

(Figs. 6, 13 C, 16 D–F)

Ascogramitis pichinchae similis, sed ab ea marginibus pinnarum sine setis et hydathodis non cretaceis differt.

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 2.5–3 mm wide; branch buds present; rhizome scales 2.5–3.5 × 0.6–0.8 mm, lanceolate, the cell walls blackish, the lumina clear to partially occluded, narrow and appearing fully occluded, the apex attenuate, the margins sparsely setose, the setae 0.1 mm long, reddish;

fronds 21–32 × 3.0–4.5 cm, hemidimorphic, arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petiole 5.5–12 cm × 0.7–1 mm, with two vascular bundles, terete, very narrowly marginate distally, castaneous, sparsely setose, the setae 0.5–2 mm long, sparsely hairy, the hairs 1-furcate; rachis with castaneous sclerenchyma visible on both sides of the lamina, the abaxial side sparsely setose, the setae 0.5–2 mm long, sparsely hairy, the hairs 1-furcate, the adaxial side moderately setose, the setae 0.5 mm long, laminae chartaceous, elliptic, proximally 1-pinnate, medially and distally 1-pinnatisect, with 40–60 pairs of segments, the base attenuate with 3–6 pairs of reduced segments, the apex subcaudate, pinnatifid; medial segments 1.5–2 × 0.4–0.5 cm, oblong to narrowly triangular, slightly ascending, widest at the base, the base very slightly decurrent and surcurrent, the apex acute, the margins entire, sparsely provided with simple hairs toward the segment apex, sometimes the apex provided with a single seta, 0.5 mm long; sterile portions of the abaxial lamina surface glabrous, fertile portions of the abaxial lamina surface moderately setose, the setae 0.5–1 mm long; adaxial lamina surface sparsely setose along segment costae, the setae 0.5 mm long, otherwise glabrous; segment costae with castaneous sclerenchyma visible on both sides of the lamina; veins not readily visible; hydathodes not cretaceous; sori inframedial, 8–10 per segment, confined to the distal portion of the lamina; receptacular setae present.

Distribution.—Colombia, Eastern Cordillera; (2580–)2900–3500(–3700) m.

Additional specimens examined. COLOMBIA. **CUNDINAMARCA:** Los bosques below Páramo de Guasca, 17°50'N, 64°42.2'W, 10,700 ft, 13 Mar 1939, *Alston, 7442* (MO); Páramo de Guasca, 4° 32.026'N, 73° 42.963'W, 11500 ft m, 13 Mar 1939, *Alston 7476* (MO); Mun. de Junín, Vereda San Antonio, 19.7 km w of Gachetá, on road from Guasca, 2580 m, 13 Jul 1994, *Dassler 94-7-13-1* (OS); E slope of the Río Blanco, 14 km WSW of Junín, 40 km NE of Bogotá, 2900 m, 19 Apr 1944, *Grant 9062* (US). **META:** Mun. San Juanito, PNN Chingaza, cañón del Río Guacharo, encenillo, 4°32.026'N, 73°42.963'W, 3109 m, 3 May 2007, *Sundue & Vasco 1334* (HUA, NY, UC); Mun. San Juanito, PNN Chingaza, cañón del Río Guácharo, encenillo, 4°31'52.8"N, 73°44'55"W, 3109 m, 3 May 2007, *Sundue & Vasco 1335* (HUA, NY, UC); Mun. San Juanito, PNN Chingaza, cañón del Río Guácharo, 4° 29.275'N, 73° 41.527'W, 2767 m, 3 May 2007, *Sundue & Vasco 1306* (NY); Mun. San Juanito, PNN Chingaza, cañón del Río Guácharo, 2767 m, 3 May 2007, *Sundue & Vasco 1312* (NY, UC); Mun. San Juanito, PNN Chingaza, cañón del Río Guácharo, 4°29'27.9"N, 73°40'58.6"W, 2984 m, 3 May 2007, *Sundue & Vasco 1316* (NY, UC); Mun. San Juanito, PNN Chingaza, cañón del Río Guácharo, Lago Chingaza, 4°49'N, 73°46'W, 3188 m, 3 May 2007, *Sundue & Vasco 1331* (NY).

Ascogrammitis colombiensis is distinguished by 1-pinnate laminae, non-cretaceous hydathodes, and lack of setae along the segment margins. *Ascogrammitis pichinchae*, which is distributed to the south of *A. colombiensis*, is similar but differs by having moderately and evenly setose segment margins. *Ascogrammitis clavigera* is distributed in the Venezuelan Andes north of *A. colombiensis.* It is similar, but differs by the abaxial lamina surface essentially glabrous, with scattered setae 0.5 mm long. *Ascogrammitis angustipes*, from the western slope of Colombia's western cordillera, could also be confused with *A. colombiensis*. That species differs by having cretaceous hydathodes and 1-pinnatisect laminae. The specific epithet is derived from Colombia, where species is endemic.

Ascogrammitis cuencana (Hieron.) Sundue, **comb. nov.** *Polypodium cuencanum* Hieron., Bot. Jahrb. Syst. 34: 505. 1904. *Grammitis cuencana* (Hieron.) C. V. Morton, Contr.U. S. Nat. Herb. 38: 111. 1967. *Ctenopteris cuencana* (Hieron.) Copel., Philipp. J. Sci. 84: 396. 1956. Type: Ecuador.Azuay: near Chagal and Yerbabuena, Cordillera Occidental of Cuenca, *F. C. Lehmann 5728* (holotype: B?; isotype: US pro parte, all of the material except for the plant in the lower right hand corner).

(Fig. 16 G–J)

Plants epiphytic or epipetric, singular or forming small colonies; roots not prolific; rhizome 1–1.5 mm; branch buds absent; rhizome scales 2.5–3.5 × 0.7 mm, lanceolate, clathrate, the cell walls black, the lumina partially occluded, faintly iridescent, yellowish, the margins setose, the setae reddish; fronds 15–17.5 × 0.8–1.6 cm, hemidimorphic, erect, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 1.7–3.5 cm × 0.5–0.7 mm wide, with a single vascular bundle, castaneous, moderately setose, the setae 0.5–1 mm long, sparsely pubescent, the hairs 1-furcate; laminae chartaceous, narrowly elliptic to linear, 1-pinnatisect, the base attenuate with many pairs of gradually reduced segments, the apex acute; 33–45 segment pairs; medial segments triangular, sessile, decurrent and slightly sursumcurrent, 4–7 mm long, 3–4 mm wide at the base, ca. 2 mm wide medially, the apex acute or sometimes rounded, the margins entire, occasionally with a single seta at the segment apex, abaxial lamina surfaces moderately to densely setose, the setae 2.0 mm long, the adaxial lamina surfaces glabrous; segment costae with castaneous sclerenchyma visible abaxially, not readily visible adaxially; veins not readily visible; hydathodes cretaceous; sori 3–7 per segment, inframedial, somewhat confluent at maturity, confined to the distal portion of the frond.

Distribution.—Western Cordillera of Ecuador from 2200–2400 m, and from 2600–2800 m in the Central Cordillera of Colombia. The type and both collections from the Mindo area of Pichincha were of epiphytic plants, whereas other collections were epipetric.

Additional specimens examined. COLOMBIA. **CALDAS:** Pinares, above Salento, Cordillera Central, 2600–2800 m, 2–10 Aug 1922, *Pennell 9620* (GH).

ECUADOR. **COTAPAXI:** Around Pilaló, 79°2'W, 0°57' S, dry crack in rock, 2400 m, 5 July 1968, *Holm-Nielsen & Jeppesen 1376* (AAU, F). **PICHINCHA:** Lloa valley, W of Quito, 15 km below Lloa, on roadbank, ca. 2200 m, 2 Feb 1981, *Balslev 1934* (NY); Bellavista, entre Tandayapa y Mindo, vieja carretera Quito-Puerto Quito, 2300 m, *Lehnert & Kessler 1164* (GOET, UC); Bella Vista Biological Field Station, ca. 5 km S of Tandayapa, and 25 km NW of Quito, 0.00807°S, 78.68971°W, 2264 m, 8 Dec 2006, *Sundue & Schuettpelz 1091* (NY, UC).

Ascogrammitis cuencana most closely resembles *A. anfractuosa* and could easily be mistaken for that species. It differs by having non-proliferous roots and pinna costae with dark sclerenchyma visble on the lower surface. The pinna costae of *A. anfractuosa* are usually obscured by the parenchyma, but sometimes the dark sclerenchyma may be partially visible. *Ascogrammitis cuencana* also differs by having larger fronds and rhizome scales.

Ascogrammitis david-smithii (Stolze) Sundue, **comb. nov.** *Grammitis david-smithii* Stolze, Fieldiana, Bot. n. s., 32: 109. 1993. *Terpsichore david-*

smithii (Stolze) A. R. Sm., Novon 3: 488. 1993. TYPE: Peru. Pasco: Prov. Oxapampa, 2–4 km N of Mallampampa, 10°32' S, 75°45'W, 2200–2400 m, epiphyte, 22 Jan 1984, *D. N. Smith & J. Canne 5837* (holotype: F; isotype: MO). (Fig. 7, 16 A–C)

Terpsichore youngii B. León & A. R. Sm., Amer. Fern J. 93: 84–86. 2003.

TYPE: Peru. Cuzco: Prov. Quispicanchis, montane forest facing San Lorenzo, epiphyte, pendulous, 2300–2350 m, 6 Jul 2000. *B. León & K. R. Young 4487* (holotype: USM, n.v.; isotype: UC).

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 2–3 mm wide, branch buds absent; rhizome scales 2.5–3 × 0.3–0.6 mm, lanceolate, the apex attenuate, clathrate, the lumina iridescent, clear to partially occluded, the margin setose, 0.1 mm long, the setae reddish or hyaline, often mixed on a single scale; fronds 18–37 × 3–4 cm, hemidimorphic, arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 3–11 cm × 0.7–1 mm, with a single vascular bundle, castaneous, sparsely setose, the setae 1.0–1.5 mm long, sparsely hairy, the hairs 1-furcate, 0.1 mm long; rachis with dark sclerenchyma visible on both sides of the blade, abaxially moderately setose, the setae 0.5–1 mm long, adaxially densely setose, the setae 0.5–1(–1.5) mm long; laminae narrowly elliptic, 1-pinnate nearly throughout, the apex 1-pinnatisect, the base acute, with 1–6 pairs of reduced segments, the apex attenuate; 38–52 segment pairs; medial segments oblong, 0.9–2.5 cm × 1.6–3 mm, sessile, not or only slightly wider at the base, the base even-sided, the apex acute, the margin entire, sparsely hairy, the hairs simple, 0.1 mm long; the abaxial lamina surface glabrous in sterile portions of the frond, moderately to densely setose in fertile portions of the frond, the setae 0.3–1 mm long, the adaxial lamina surface glabrous, or sometimes with scattered setae along the segment costae, 0.2–0.4 mm long; segment costae with castaneous sclerenchyma visible on both sides of the lamina; veins not readily visible; hydathodes cretaceous; sori elongate, inframedial, 7–14 per segment confined to the distal portion of the lamina; receptacular setae present.

Distribution.—Central Peru to central Bolivia; eastern slopes of the Andes; 2100–3200 m.

Additional specimens examined. BOLIVIA. **COCHABAMBA:** Prov. Ayopaya, ca. 10 km al NW de Independencia, 16°17’ S, 67°50’W, 3200 m, 9 May 1998, *Beck 14474* (LPB); Prov. José Carrasco Torrico, Siberia Este, Monte Hotel, 17°50’37”S, 64°41’40”W, 2700 m, 22 Sep 2003, *Fernández et al. 2511* (MO); Prov. Ayapoya, San Cristobal, 16°41’40” S, 66°42’32”W, 2890 m, 27 Oct 2005, *Fernández et al. 4250* (NY); Prov. Ayopaya, Bosque de Pichagani, 17°30’S, 65°17’W, 3200 m, 5 Jul 1990, *Hennipman 8138* (LPB); Prov. Carrasco, Sehuencas, Km 18, 16°12’S, 67°53’W, 2100 m, 30 Apr 1993, *Ibisch 930102* (NY); Prov. José

Carrasco Torrico, a 3 km aproximadamente desde el campamento Locotal, en direccion NO, a lo largo de la antigua senda de Kara Huasi a Pojo, 17°49’S, 64°40’W, 2200 m, 2 Feb 2000, *Jiménez 337* (UC); Prov. Ayapoya, San Cristobal, ladera del cerro Jucumarini Punta, arriba del pueblo, 17°13’S, 65°49’W, 2910 m, 10 Jun 2002, *Jiménez 1215* (LPB, UC); Ayapoya, San Cristobal, ladera del cerro Jucumarini Punta, arriba del pueblo, 16°38’S, 66°41’W, 2750 m, 13 Jun 2002, *Jiménez 1246* (LPB, UC); Prov. Ayapoya, San Cristobal, ingresando por el sendero que se desvía de la senda San Cristobal-San Miguel, hacia el Río Junta Mayu, luego bajando por el mismo, 17°48’S, 64°41’W, 2440 m, 19 Jun 2002, *Jiménez 1352* (LPB, UC); Prov. Ayopaya, Comunidad Pampa Grande, al inicio del sendero Pampa Grande-Carmen Pampa, 17°13’S, 65°49’W, 2110 m, 9 Aug 2002, *Jiménez 1452* (LPB, UC); Prov. Ayapoya, Comunidad Pampa Grande, al inicio del sendero Pampa Grande-Carmen Pampa, 16°39’S, 66°43’W, 2110 m, 8 Sep 2002, *Jiménez 1452* (UC); Prov. Chapare, Paracti, carretera nueva a Santa Cruz, subiendo 1/2 km aproximadamente a partir del puente por el Río Malaga, 17°50’S, 64°42.2’W, 2130 m, 28 Sep 2002, *Jiménez 1709* (LPB, UC); Prov. José Carrasco Torrico, 5 km de Siberia hacia Karahuasi, 17°50’S, 64°42.2’W, 2200 m, 15 Oct 1996, *Kessler et al. 9049* (UC); Prov. José Carrasco Torrico, 5 km de Siberia hacia Karahuasi, 17°49’37”S, 64°41’18”W, 2200 m, 15 Oct 1996, *Kessler et al. 9059* (LPB, UC); Prov. Ayapoya, 10 km Cocopata - Cotacajes, 17°47’19”S, 64°47’18”W, 3000 m, 9 May 1997, *Kessler et al. 9401* (UC); Ayopaya, km 10 Cocapata a Cotacajes, 16°38’S, 66°41’W, 2700 m, 11 May 1997, *Kessler 9485* (LPB); Prov. Ayapoya, 10 km Cocopata - Cotacajes, 16°38’S, 66°41’W, 2700 m, 11 May 1997, *Kessler et al. 9511* (UC). **La Paz:** Prov. Franz Tamayo, PN-AMNI Madidi, senda Keara-Mojos entre Lagunillas y Fuertecillos, 10°22’33”S, 75°38’37”W, 2120 m, 6 Nov 2001, *Jiménez 894* (LPB, UC); Prov. Nor Yungas, Estación Biológica Tunquini, 16°48’S, 67°15’W, 1710 m, 24 Aug 1998, *Portugal 289* (LPB); Inquisivi, comunidad Choquetanga - valle Chimu, valle lateral al Río Chimu, 16°7’S, 68°5’W, 3000 m, 26 Jan 1994, *Salinas 2460* (LPB); Murillo, 30.5 km N (below) of dam at Lago Zongo Trail up Río Jachcha Cruz, 17°50’S, 64°42.2’W, 2200 m, 17 Dec 1982, *Solomon 9112* (LPB). **Santa Cruz:** Prov. Manuel M. Caballero, Siberia entre El Empalme y locotal, 16°40’S, 66°28’W, 2100–2850 m, 8 Apr 2004, *Arroyo et al. 2741* (NY); Prov. Manuel M. Caballero, 28 km desde Comarapa camino a la Siberia, 16°39’S, 66°43’W, 2600 m, 15 Aug 1991, *Arroyo et al. 62pp* (LPB, NY, UC); Prov. Manuel M. Caballero, entre Comarapa y Siberia, 17°50’S, 64°38’W, 2600 m, 18 Mar 2003, *Lehnert 697pp* (LPB, UC); Prov. Manuel M. Caballero, Siberia, a 27 km de Comarapa, 14°36’S, 68°56’W, 2499 m, 28 Nov 2003, *Núñez 448* (NY); Manuel M. Caballero, Bosque de ladera, 16° 39’S, 66° 43’W, 2555 m, 23 Mar 2004, *Núñez 542* (MO); Prov. Caballero, 1.5 km down from Empalme (on Comarapa-Cochabamba highway) on road to Khara Huasi, 17°50’37”S, 64°41’40”W, 2475 m, 2 Aug 2003, *Sundue 785* (NY, USZ);

Prov. Manuel M. Caballero, 1.5 km down from Empalme (on Comarapa-Cochabamba highway) on road to Khara Huasi, 17°46’12”S, 64°45’62”W, 2475 m, 2 Aug 2003, *Sundue et al. 782pp* (NY, USZ).

PERU. **CUZCO:** Machu Picchu, along trail to Winay Waina, 10°32’S, 75°21’W, 2300 m, 21 Jan 1976, *Bishop 2506* (UC); Urubamba, Dist. Machu Picchu, bosque prima Río en la quebrada, 2349 m, 13 Apr 2003, *Valenzuela et al. 1749* (NY, UC). **JUNÍN:** Chanchamayo, Río Rondayacu, 45 km from San Ramón, 10°32’S, 75°21’W, 1881–1950 m, 15 Oct 1982, *Smith et al. 2607* (MO). **PASCO:** Oxapampa, 2-4 km north of Mallampampa, 13°13’S, 72°33’W, 2200–2400 m, 22 Jan 1984, *Smith & Canne 5837* (F); Oxampampa, San Alberto, 11°20’S, 72°20’W, 2400 m, 18 Jul 2003, *van der Werff 18622* (MO); Oxampampa, San Alberto, 10°32’S, 75°45’W, 2400 m, 18 Jul 2003, *van der Werff et al. 18599pp* (UC); Oxampampa, San Alberto, 2400 m, 18 Jul 2003, *van der Werff et al. 18622* (UC); Oxampampa, Dist. Huancabamba, Sector Milpo, 10°22’33”S, 75°38’37”W, 2900 m, 15 Mar 2004, *Vásquez et al. 30123* (MO); Oxampampa, Dist. Huancabamba, Sector Milpo, 10°32’S, 75°21’W, 2900 m, 15 Mar 2004, *Vásquez et al. 30123* (MO).

Ascogrammitis david-smithii is distinguished by its fully 1-pinnate laminae densely setose abaxially and segments parallel sided at the base, not expanded. Northern plants tend to have longer setae (up to 1.5 mm long) on the abaxial side of the rachis.

Terpsichore youngii is placed here in synonymy. In the protologue of that species, León and Smith (2003) noted the similarity between *A. david-smithii* and *T. youngii*. The type of *T. youngii* differs from *A. david-smithii* only by rhizome scales with elongate, curved, hyaline setae. In contrast, the rhizome scales of *A. david-smithii* have short, straight setae along the margin of the scale that are a mixture of hyaline and reddish in color. No other specimen has scale marginal setae that match *León & K. R. Young 4487*. The variation is best interpreted as variation within *A. david-smithii*.

Ascogrammitis dilatata (Sundue & M. Kessler) Sundue**, comb. nov.**

Terpsichore dilatata Sundue & M. Kessler, Org. Divers. Evol. 8:163. 2008. Type: Bolivia. Santa Cruz: Prov. Manuel Maria Caballero, 4 km al sureste de la comunidad de Siberia, 17°49’57” S, 64°43’11”W, 2920 m, 9 Apr 2004, *R. Núñez C. 644*. (holotype: NY; isotypes UC, USZ).

(Figs. 8, 12 B, 12 D)

Lellingeria carrascoensis M. Kessler & A. R. Sm., Org. Divers. Evol. 8: 167. 2008. Type: Bolivia, Cochabamba: Prov. Carrasco, Colomi, 17°13’S, 65°53’W, 3100 m, 30 Dec 1998, *M*. de *Boer 1161* (holotype: LPB, n.v., isotype: UC).

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome ca. 1.5 mm wide; branch buds absent; rhizome scales 1.5–3 × 0.2–0.3 mm, lanceolate, the cell walls dark red, the lumina iridescent, transparent to partially occluded, the apex attenuate, the margins setose, the setae 0.2 mm long, reddish; fronds 21–27 × 2–5 cm, hemidimorphic, arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 4–12 cm × 0.5–1 mm, with a single vascular bundle, distally marginate, castaneous, very sparsely setose, the setae 0.5–1 mm, sparsely hairy, the hairs 1-furcate; rachis with castaneous sclerenchyma visible on both sides of the lamina, the abaxial side very sparsely setose, the setae 0.5–1 mm, sparsely hairy, the hairs 1-furcate, 0.1 mm long, the adaxial side moderately setose, the setae 0.5–0.7 mm long; laminae 1-pinnatisect throughout, chartaceous, the base attenuate, with 4–8 pairs of reduced segments the basal segments widely spaced but narrowly connected, apparently never fully pinnate; medial segments 1.5–2.5 cm × 2.5–4 mm, slightly ascending, narrowly triangular to oblong, the base expanded, decurrent and surcurrent, the apex acute, the margins sparsely provided with simple, two-celled hairs, ca. 0.1 mm long, or sometimes the hairs replaced sporadically by setae, 0.5 mm long, the abaxial lamina surface glabrous to sparsely provided with 0.1 mm long simple hairs and 0.5 mm long setae, the fertile portions of the lamina more densely setose, the adaxial surface of the lamina with scattered setae along the segment costae, the setae 0.5 mm long; segment costae with castaneous sclerenchyma visible on both sides of the lamina; veins not readily visible on either side of the lamina; hydathodes cretaceous, the secretion often abraded; sori inframedial, up to 12 pairs per segment, confined to the distal portion of the lamina; receptacular setae present.

Distribution.—Southern Peru to Santa Cruz, Bolivia, eastern slopes of the Andes; 2500–3200 m.

Additional specimens examined. BOLIVIA. **COCHABAMBA:** Prov. Chapare, 54 km hacia Villa Tunari, 17°9'S, 65°38'W, 2750 m, 30 Apr 1979, *Beck 1424a* (F); Prov. Ayapoya, San Cristobal, subiendo por el sendero que va a San Miguel, 16°15'S, 67°50'W, 3220 m, 6 Jun 2002, *Jiménez 1156* (LPB, UC); Ayopaya, comunidad Pampa Grande, sendero a Incacasani Grande, 16°17'S, 67°49'W, 3200 m, 18 Sep 2002, *Jiménez 1689* (UC); Prov. Ayapoya, comunidad Pampa Grande, sendero a Incacasani Grande, 17°46'S, 64°48'W, 3200 m, 18 Nov 2002, *Jiménez 1689* (UC); Prov. Ayopaya, Comunidad Pampa Grande, sendero Incacasani Grande, 14°38'S, 68°57'W, 2650 m, 14 Sep 2002, *Jiménez & Moguel 1609* (LPB); Prov. Carrasco, Km 108 antigua carretera Cochabamba a Villa Tunari, 9°33.94'N, 83°43.348'W, 2950 m, 22 Jun 1996, *Kessler 6567* (UC); Prov. José Carrasco Torrico, 108 Km antigua carretera Cochabamba-Villa Tunari, 16°12'S, 67°53'W, 2950 m, 22 Jun 1996, *Kessler et al. 6567* (UC); Prov. José Carrasco Torrico, 108 Km antigua carretera Cochabamba-Villa Tunari, 2950 m, 23 Jun 1996, *Kessler* *et al. 6621* (UC); Prov. José Carrasco Torrico, 104 Km antigua carretera Cochabamba-Villa Tunari, 17°9'S, 65°38'W, 3150 m, 25 Jun 1996, *Kessler et al. 6682* (UC); Prov. José Carrasco Torrico, 110 Km antigua carretera Cochabamba-Villa Tunari, 17.1284°S, 65.5321°W, 2800 m, 29 Jun 1996, *Kessler et al. 6801* (UC); Prov. José Carrasco Torrico, 8 km de Enpalme hacia Siberia, 17°49'S, 64°40'W, 2900 m, 22 Oct 1996, *Kessler et al. 9193* (UC); 23 km from Colomi on the road to Tunari, 17°49'57"S, 64°43'11"W, 2870 m, 7 Feb 1978, *King 7695* (MO); 23 km from Colomi on the road to Tunari, 16°17'S, 67°50'W, 8900 ft, 7 Feb 1978, *King & Bishop 7695a* (MO). **La Paz:** Prov. Nor Yungas, Estación Biológica de Tunquini, Bajo Hornuni, senda del Campo de Don Pedro al Camino de la mina, 17°49'13"S, 64°40'45"W, 3000 m, 14 Sep 2000, *Bach et al. 1051* (LPB); Prov. Nor Yungas, Chuspipata, 5 km via Unduavi, 3150 m, 2 Apr 1982, *Beck 7600* (F, LPB); Prov. Nor Yungas, Cotapa, roadside behind gas station, 16°40'S, 66°28'W, 3225 m, 27 Jul 1989, *Fay & Fay 2449* (UC, US); Prov. Nor Yungas, Off the La Paz-Yolosa Road, along road, about 1 km east of Cotapata gas station, and on a trail on left (from La Paz), roughly north, 17°49'43"S, 64°43'5"W, 3200 m, 8 Aug 1990, *Fay & Fay 2961* (MO); Prov. Nor Yungas, Roadside bank between Cotapata and Chuspipata, south-facing La Paz-Caranavi road, 17°47' S, 64°47'W, 3200 m, 15 Aug 1990, *Fay & Fay 3033* (LPB); Prov. Franz Tamayo, PN-ANMI Madidi, senda Keara-Mojos, Chunkani, 17°49'S, 64°41'W, 2930 m, 11 Oct 2001, *Jiménez 954* (LPB, UC); Prov. Franz Tamayo, PN-ANMI

Maddidi, senda Keara-Mojos, abajo de Chunkani, 2870 m, 11 Aug 2001, *Jiménez & Gallegos 912C* (LPB); Prov. Nor Yungas, Coscapa, sobre el sendero prehispánico Sillutinkara, 17°49'S, 64°40'W, 3100 m, 7 Jan 2001, *Jiménez & Vidaurre 528* (UC); Prov. Nor Yungas, Trocha al Valle de Coscapa, P.N Cotapata, 16°17'S, 67°50'W, 3250 m, 11 Sep 1997, *Kessler et al. 11813* (UC); Prov. Nor Yungas, Trocha al Valle de Coscapa, P.N. Cotapata, 17°11'S, 65°40'W, 3000 m, 12 Sep 1997, *Kessler et al. 11872* (UC); Prov. Nor Yungas, Chuspipata, sendero a la mina San Juan, 16°15'S, 67°51'W, 2900 m, 26 Nov 2002, *Lehnert 380* (UC); Prov. Nor Yungas, Chuspipata, sendero a la mina San Juan, 2900 m, 26 Nov 2002, *Lehnert 381* (UC); Prov. Nor Yungas, 1 km W of Chuspipata Elfin forest with *Clusia*, *Weinmannia* and *Myrica*, 14°38'S, 68°57'W, 3140 m, 24 Mar 1982, *Solomon, J. C. 7261* (US). **SANTA CRUZ:** Prov. Manuel María Caballero, Astillero, 15 Aug 2003, *Fernández 2202* (MO); Prov. Caballero, Serrania Siberia, entre Torrecillas e Pojo, 13 km de Torrecillas, 16°40'S, 66°28'W, 2470 m, 14 Dec 2002, *Labiak et al. 2856* (LPB); Prov. Caballero, Serrania Siberia, entre Torrecillos e Pojo, 33 km de Torrecillas, 16°12'S, 67°53'W, 2630 m, 14 Dec 2002, *Labiak et al. 2864* (LPB); Prov. Caballero, Comarapa, serrania Siberia, entre Torrecillas e Pojo, 33 km de Torrecillas, 16°12'S, 67°53'W, 2630 m, 14 Dec 2002, *Labiak et al. 2867* (RB); Prov. Caballero, Comarapa, serrania Siberia, entre Torrecillas e Pojo, 36 km de Torrecillas, 17°50'15"S, 64°42'31"W, 2800 m, 14 Dec 2002, *Labiak et al. 2871* (RB); Prov. Manuel M.

Caballero, Entre Comarapa y Siberia, pasando Torecillos, 16°12’S, 67°53’W, 2700 m, 18 Mar 2003, *Lehnert 702* (UC); Prov. Manuel M. Caballero, Entre Comarapa y Siberia, pasando Torecillos, 17°49’17”S, 64°40’44”W, 2550 m, 18 Mar 2003, *Lehnert 708* (UC); Prov. Manuel M. Caballero, Comarapa, 16°15’S, 67°51’W, 2460 m, 13 Apr 2003, *Núñez 57* (NY); Prov. Manuel M. Caballero, Siberia, a 25 km de Comarapa, 2495 m, 3 Nov 2003, *Núñez 333* (MO, UC).

PERU. **CUSCO:** Urubamba, Macchu Picchu, on a hillside above the Río Mandor, 4 km from Km 114 of the Urubamba railroad, 17°9’S, 65°38’W, 2750 m, 24 Sep 1982, *Peyton & Peyton 1331* (MO).

Ascogrammitis dilatata can be distinguished by its 1-pinnatifid laminae and dilated segment bases that are both strongly decurrent and surcurrent. The basal segments are usually remote from each other and the lamina tissue connecting these segments is very narrow, ca. 0.2 mm wide. Some specimens, primarily from the northern portion of its range, have longer hairs (ca. 0.2 mm) along the segment margins and some of these hairs are replaced by 0.5 mm long setae. *Ascogrammitis dilatata* was originally described from specimens referred to as *A. david-smithii*, but that species differs by having fully 1-pinnate laminae, and segments that are parallel-sided, not expanded at the base. *Ascogrammitis david-smithii* further differs by the setae of the abaxial lamina distributed evenly, versus confined to sori and fertile veins in *A. dilatata*.

Lellingeria carrascoensis is also placed here in synonymy. The type, *De Boer, M. 1161*, was included as a paratype in the protologue of *A. dilatata* (Sundue & Kessler, 2008). It does not belong in *Lellingeria* as evidenced by the presence of setae, 1-furcate hairs along the petiole and rachis that lack an acicular cell, and rhizome scales with reddish instead of hyaline marginal setae. It also has pinna costae with dark sclerenchyma visible on the lower surface and cretaceous hydathodes--two uncommon characters in *Lellingeria*. Chloroplast sequence data further supports its placement in *Ascogrammitis* (Sundue Thesis chapter 2). Kessler & Smith (2008) reported *De Boer, M. 1161* as a mixed unicate containing *L. carascoensis* and an undescribed species of *Terpsichore*. This is confusing, because the holotype at LPB which I have seen a photograph of, contains only a single plant. The isotype of *De Boer, M. 1161* (UC), which they apparently did not see, is not mixed either.

Ascogrammitis loxensis Sundue, **sp. nov.** Type: Ecuador. Loja: Parque Nacional Podocarpus, Bombuscaro park entrance, ca. 7 km SSW of the Loja-Vilcabomba rd., 0°35.96' S, 77°55.42'W, 1003 m, 17 Dec 2006, *M. Sundue & F. A. Werner 1164* (holotype: NY, isotypes: QCA, QCNE, UC).

(Figs. 9, 13 A)

A congeneris foliis venetis 1-pinnatisectis segmentis 48- ad 55-jugatis, basi attenuata segmentis reductis 16- ad 20-jugatis, marginibus segmentorum esetosis et hydathodis cretaceis differt.

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 2.5 mm wide; branch buds absent; rhizome scales 2.3–4.2 × 0.3–0.6 mm, lanceolate, clathrate, the cell walls black, the lumina iridescent, transparent to slightly occluded, the apices attenuate, the margins setose, the setae 0.2 mm long, red; fronds hemidimorphic, (15–)21–34 × (1.6–)2.1–5 cm, arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 0.6–3 cm × 1–1.3 mm, with a single vascular bundle, terete, non-marginate, castaneous, moderately setose, the setae 1.0 mm long, sparsely hairy, the hairs simple or 1-furcate; rachis with castaneous sclerenchyma visible on both sides of the lamina, abaxially with scattered, setae 0.5 mm long, adaxially moderately setose, the setae 0.3–0.5 mm long; lamina chartaceous, green to blue-green in color, deeply 1-pinnatisect, with 48–55 segment pairs, elliptic, the base attenuate with 16–20 pairs of gradually reduced segments, the apex gradually reduced and usually forming a pinnatifid and semi-caudate apex, the segments oblong, widest at the base, the bases surcurrent, sometimes slightly decurrent as well, the apex acute, the margin entire, bearing minute hairs and scattered setae, the setae 0.5 mm long, the medial segments 1.6–1.9 cm × 1.8–3.5 mm measured in the middle, up 3.5–4.5

mm wide at the base, the smaller basal segments 0.5–2 × 3 mm, deltate to narrowly hemi-elliptical, the abaxial lamina surfaces sparsely to moderately setose, the setae more abundant on fertile portions of the lamina, 0.3 mm long, erect, the setae associated with sori longer, up to 1.0 mm long, the adaxial lamina surface glabrous; segment costae with the castaneous sclerenchyma visible on both sides of the blade; veins not visible; hydathodes cretaceous; sori slightly longer than wide, inframedial, confined to the distal portion of the lamina, 11–12 pairs per segment; receptacular setae present.

Distribution and ecology.—Ecuador and northern Peru, primarily along the eastern slope of Ecuador's Eastern Cordillera; partially disturbed forests; 1000–2150(–4000 m).

Additional specimens examined. ECUADOR. **MORONA SANTIAGO:** Junction of Ríos Itzintza and Chupiasa, 0°7' S, 77°36'W, 3500 ft, 17 Nov - 5 Dec 1944, *Camp 1394* (NY). **NAPO:** East of Santa Barbara along road to La Bonita, 2°40'S, 78°0'W, 3000 m, 17 May 1982, *Boom 1432* (QCA); Along road between Lago Agrio and Baeza, in vicinity of Km marker 100, 43.2 km W of Lumbaqui, 20.4 Km E of Estación Bomba Cepe Saltado, 70.9 Km E of Baeza turn off 4°3.5'S, 78°57.5'W, 1460 m, 29 Apr 1984, *Croat 58706* (QCA); Cerro Antisana, 5600 ft, 29 Aug 1960, *Grubb et al. 1369* (NY); Río Borja, Km 4, riverside forest, 5°41'S, 77°48'W, 1780 m, 21 Sep 1980, *Holm-Nielsen et al. 26638*

(AAU); Valley of Río Oyacachi, ca 10 km along rd. W of El Chaco, trail along river to Río San Juan Grande, 0°21'39.25"S, 78°13'15.98"W, 1760-1800 m, 12 Mar 1996, *Øllgaard & Navarrete 1641* (AAU); Yanayacu Biological field station, W of Cosanga, approx. 15 km S of Baeza, 0°35.962'S, 77°55.42'W, 2133 m, 5 Dec 2006, *Sundue & Schuettpelz 1073* (NY, QCA, UC); Yanayacu Biological field station, W of Cosanga, approx. 15 km S of Baeza, 4°4.685'S, 78°57.827'W, 2133 m, 5 Dec 2006, *Sundue & Schuettpelz 1078* (NY, QCA, UC); Yanayacu Biological field station, W of Cosanga, approx. 15 km S of Baeza, 0°35.962'S, 77°55.42'W, 2106 m, 6 Dec 2006, *Sundue & Schuettpelz 1084* (NY, QCA, UC); Yanayacu Biological field station, W of Cosanga, approx. 15 km S of Baeza., 4°9'S, 78°38'W, 2106 m, 6 Dec 2006, *Sundue & Schuettpelz 1088* (NY, QCA, UC). **PASTAZA:** Rd. N of El Topo (Río Negro - Mera), Km ca. 9, 4°28'S, 79°9'W, 1450 m, 23 Jan 1992, *Øllgaard et al. 99638* (AAU). **PICHINCHA:** Páramo de Guamani, rd. Pifo - Papallacta, just W of the pass, 3°55'S, 78°35'W, 4000 m, 18 Jan 1992, *Stolze & Stolze 1663* (F, NY). **ZAMORA-CHINCHIPE:** Zamora, Within 3 km of the town of Zamora, 0°30'S, 78°0'W, 1000 m, 17 July 1994, *Fay & Fay 4446* (MO, UC); Lodge "Copalinga," 3 km from Bombuscaro Ranger Station of Podocarpus National Park, 900-1300 m, 15 Sep 2004, *Lehnert 1233pp* (UC); Lodge "Copalinga," 3 km from Bombuscaro Ranger Station of Podocarpus National Park, 3°59.349'S, 79°5.713'W, 900-1300 m, 15 Sep 2004, *Lehnert 1235* (UC); P. N. Podocarpus, Rd. Yangana - Valladolid, Km 21, 0°17'S, 77°51'W, 2700–2800 m, 24 Jan 1989, *Madsen 85650* (AAU); Rd. Loja-Zamora, 38.6 km from pass, 0° 27'S, 77° 47'W, 1200 m, 15 Feb 1991, *Moran & Rohrbach 5394* (MO); Ca. 4 km E of Pasquisha, 4°0'S, 79°0'W, 1250 m, 6 Feb 1989, *Øllgaard et al. 90445* (AAU); P. N. Podocarpus, Park entrance "Sanfrancisco," on new Loja-Zamora rd., 0°35.962'S, 77°55.42'W, 2151 m, 14 Dec 2006, *Sundue 1125* (NY, QCA); Along rd. between Paquisha to Chinapintza, 1°21'S, 78°12'W, 1000–1400 m, 17 Nov 2004, *van der Werff 19568* (UC).

PERU. **AMAZONAS:** San Martín, Near the border with Dept. San Martín, 5°41'S, 77°48'W, 2000 m, 3 Mar 2001, *van der Werff 16676* (MO); San Martín, Montane forest on sandstone or limestone, 17°49'S, 64°32'W, 1950 m, 4 Mar 2001, *van der Werff 16700* (MO, NY, UC).

Ascogrammitis loxensis is distinguished by its attenuate base with 16–20 reduced segments, cretaceous hydathodes, and segment margins that lack setae. When fresh the laminae are conspicuously bluish-green. This has been noted by myself and other collectors. Some specimens have the 0.1 mm long hairs of the segment margins unevenly mixed with setae.

Ascogrammitis nana (Sundue & M. Kessler) Sundue**, comb. nov.** *Terpsichore nana* Sundue & M. Kessler, Org. Divers. Evol. 8: 163. 2008. Type*:* Bolivia. Dept. Santa Cruz, Prov. Manuel María Caballero, along the Comarapa-Cochabamba highway, 2.5 km (by road) NE of El Empalme, 12.5 (by road) NW of Torrecillas, 17°49.5’ S; 64°41.3’W, 2520 m, 7 Aug 2003, *M. Sundue*, *M. Nee*, *& R. Núñez C. 866* (holotype: NY; isotypes: LPB, USZ). (Fig. 10)

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome ca. 1 mm wide, lacking branch buds; rhizome scales 1.5–3 × 0.2–0.3 mm, dull, the cell walls blackish, the lumina mostly occluded and blackish, some lumina partially occluded and castaneous, the margin setose, the setae 0.1 mm long, reddish; fronds 14–20 × 1.2–2.8 cm, hemidimorphic, erect, usually bearing the mycelia and ascomes of *Acrospermum*; petiole 3–6 cm × 0.5–0.8 mm, castaneous, with a single vascular bundle, distally marginate, moderately setose, the setae 1.5–2 mm long, sparsely hairy, the hairs 1-furcate; rachis with dark sclerenchyma visible on both sides of the lamina, moderately setose, the setae 1.5–2 mm long, sparsely hairy, the hairs 1-furcate; laminae chartaceous, proximately 1-pinnate, medially and distally 1-pinnatisect, with 35–40 segment pairs, the base with 2–3 pairs of reduced segments; medial segments 8–12 × 2.5 mm, spreading to slightly ascending, widest at the base, the base slightly decurrent and surcurrent, the apex acute, often provided with 1–2 setae, 1.0 mm long, the margin entire, slightly revolute, glabrous; abaxial lamina surface moderately and evenly setose, the setae 0.8 mm long, erect, fertile portions of the abaxial lamina more densely setose than sterile portions; segment costae with dark sclerenchyma visible on both sides of the lamina; veins usually not visible on either side of the lamina, sometimes visible on the abaxial side of the lamina; hydathodes cretaceous; sori inframedial, confined to the distal portion of the lamina; receptacular setae absent.

Distribution.—Peru and Bolivia, eastern slopes of the Andes, 2500–3200 m.

Additional specimens examined. PERU. **HUANUCO:** Cani, pueblo 7 mi. NE of Mito, 10°32’3”S, 75°21’2”W, 16–26 Apr 1923, *Bryan 383* (F).

BOLIVIA. **COCHABAMBA:** Prov. Ayopaya, San Cristobal, subiendo por el sendero que va a San Miguel, 3100 m, 6 Jun 2002, *Jiménez 1106a pp* (UC); Prov. Chapare, Tunari, 3000 m, 4 May 1892, *Kuntze s.n.* (NY). **LA PAZ:** Prov. Nor Yungas, Coscapa, sobre el sendero prehispánico Sillutinkara, 17°50’ S, 64°44’W, 3200 m, 1 Nov 2001, *Jiménez 554* (UC); Sud Yungas, 3.1 km SE of Unduavi bridge (below) on old road, 17°49.5’S, 64°41.3’W, 3000 m, 6 Nov 1982, *Solomon 8656* (LPB, MO, NY). **SANTA CRUZ:** Caballero, Amboro National Park, Cerro Bravo area; ca. 10 map km N of Comarapa, 17°50’S, 64°43’W, 2500 m, 20 Jun 1995, *Abbott 17066pp* (MO); Caballero, Siberia, laguna movible, bosque nublado alrededor de la laguna y al frente de la laguna, 16°12’S, 67°53’W, 2750 m, 10 Apr 2004, *Arroyo 2762* (NY); Caballero, Siberia, a

2.5 km de la carretera bajando por el camino Saipina,16°19’S, 67°53’W, 2650 m, 30 Nov 2002, *Núñez C 29* (NY).

Ascogrammitis nana is distinguished by its basally 1-pinnate laminae, small fronds (14–20 × 1.2–2.8 cm), and narrow scales (0.2–0.3 mm wide) with a mixture of partially and fully occluded lumina. Other distinguishing features are the moderately densely setose petioles provided with 1.5–2 mm long setae, and segment margins glabrous except for having 1–2 apical setae. Most similar species differ by having 0.1 mm long hairs along the segment margins.

Ascogrammitis oxapampensis Sundue**, sp. nov.** Type: PERU. Pasco: Prov. Oxapampa, road to Chacos, 10°35’S, 75°6’W, 2400-2700 m, 17 Jul 2003, *H. van der Werff, R. Vasquez, B. Gray, R. Ortiz & N. Davila 18537* (holotype: UC; isotype: MO). (Fig. 5, 15 J–M)

Ab *Ascogrammitis david-smithii* petiolo dense brevi-setuloso et squamis rhizomatum marginibus et superficiebus ambabus setosis differt.

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 1–2 mm wide; branch buds absent; rhizome scales 1.5–3.5 × 0.4–0.5 mm, lanceolate, appearing blackish in mass, clathrate, the lumina clear and iridescent to partially occluded, the margin as well as the abaxial and adaxial faces of the scales setose, the setae reddish, 0.15 mm long, the apex attenuate; fronds 19–38 × 2–4.6(–6) cm, presumably arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 4–8 cm × 0.6–1.5 mm, with a single vascular bundle, brown to castaneous, terete, densely setose, the setae 0.2(–0.3) mm long; rachis with brown to castaneous sclerenchyma visible on both sides of the blade, the abaxial side moderately setose, the setae 0.2–0.5 mm long, the adaxial side densely setose, the setae 0.2 mm long; laminae deeply 1-pinnatifid, narrowly elliptic, widest in the middle, gradually reduced both proximally and distally, with 22–50 pairs of segments; medial segments spreading, oblong, 2.2–2.5 mm wide in the middle, widest at the base, the base 3.5–5 mm wide, sessile, dilate, decurrent and surcurrent, the apex acute, the margin entire, slightly involute, provided with 0.1 mm long simple hairs, especially distally, the abaxial lamina surface moderately setose when fertile, the setae 0.2 mm long, setae associated with sori longer, 0.5 mm long, the adaxial lamina surfaces glabrous; segment costae blackish, the sclerenchyma visible on both sides of the blade; veins not readily visible; hydathodes cretaceous; sori slightly longer than wide, usually 8–12 pairs per segment, inframedial, confined to the distal portion of the lamina; receptacular setae present.

Distribution.—Northern Peru, particularly the Oxapampa region of Pasco; 2300–2900 m.

Additional specimens examined. PERU. **AMAZONAS:** Rd. Chachapoyas-Mendoza, a little past Molinopampa, 10°35'S, 75°6'W, 2400 m, 15 Mar 1998, *van der Werff et al. 15007* (NY). **PASCO:** Oxapampa, Sector Abra Esperanza, 10°32'32"S, 75°21'17"W, 2807 m, 22 Oct 2004, *Mellado & Beccera 2015* (MO); Oxapampa, Sector Quebrada San Alberto, 2657 m, 24 Oct 2004, *Mellado & Beccera 2066* (MO); Oxampampa, San Alberto, Cordillera de Yanachaga, 10°37'S, 75°17'W, 2400 m, 6 Mar 1986, *van der Werff, H. 8451pp* (MO, NYpp, UC); Oxampampa, Chacos, 10°37'S, 75°17'W, 2500 m, 22 Jun 2003, *van der Werff 17706* (UC); Oxapampa, San Alberto, Cordillera de Yanachaga, 2300–2500 m, 6 Mar 1986, *van der Werff et al. 8452* (MO); Oxapampa, P. N. Yanachaga-Chemillen, Abra Yanachaga, 2900 m, 1 Aug 2003, *Vásquez et al. 28474pp* (MO pp, UC pp).

Ascogrammitis oxapampensis is distinguished from its congeners by rhizome scales with setae on the surfaces and margins. These setae are infrequent and often difficult to observe. It can also be distinguished by petioles densely setose, the setae 0.2(–0.3) mm long, spreading, and orange. Most other species of *Ascogrammitis* bear reddish setae 1–2.5 mm long on their petioles.

Ascogrammitis pichinchae (Sodiro) Sundue**, comb. nov.** *Terpsichore pichinchae* (Sodiro) A. R. Sm., Novon 3: 488. 1993. *Polypodium* *pichinchae* Sodiro, Crypt. Vasc. Quit. 329. 1893. *Ctenopteris pichinchae* (Sodiro) Copeland, Phillip. J. Sci. 84: 455. 1956. *Grammitis pichinchae* (Sodiro) C. V. Morton, Contr. U. S. Natl. Herb. 38:111. 1967. TYPE: Ecuador. Pichincha: Mt. Pichincha, *L. Sodiro s.n.*, (holotype: QPLS?; isotype: not located, photo at AAU of possible isotype in Q).

(Fig. 11)

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 0.8–2.0 mm; branch buds absent; rhizome scales 3 × 0.3–0.5 mm, lanceolate, blackish, the lumina occluded, the apex attenuate, the margin setose, the setae 0.1 mm long, reddish; fronds 23–37 × 2.6–3.6(–6) cm, arching to pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles brown to castaneous, 2–9 cm long, 0.6–1.2 mm wide, moderately seotse, the setae 1–2.5 mm long, sparsely hairy, the hairs 1-furcate, 0.1 mm long; rachis with castaneous sclerenchyma visible on both sides of the lamina, the abaxial side moderately setose, the setae 0.5–2 mm long, the adaxial side moderately setose, the setae 0.7 mm long; laminae chartaceous, 1-pinnatisect, basally 1-pinnate, elliptic and widest in the middle, or oblanceolate and widest above the middle, with 25–50 segment pairs; medial segments narrowly deltate, widest at the base, 3 mm wide medially, 5 mm wide at the base, sessile, the apex acute, the margin essentially entire but slightly undulate, moderately and evenly setose, the setae 0.5–1 mm long, fertile portions of the abaxial lamina surface with scattered setae along the segment costae and veins, the setae up to 1.2 mm long, otherwise glabrous, the adaxial lamina surface glabrous; segment costae with the dark sclerenchyma visible on both sides of the lamina; veins visible, but not darkly colored; hydathodes cretaceous, but the deposit often abraded; sori infamedial, usually 5–7 pairs per segment, distributed evenly throughout the frond; receptacular setae present.

Distribution.—Ecuador and Colombia, Cordillera Real of Ecuador, and the Western, Cordillera and the Central and Eastern Cordillera of Colombia; 3200–3800 m.

Additional specimens examined. COLOMBIA. **CALDAS:** Cordillera central, Parmo de Letras, above cienega, SW of Letras, 3700 m, 4 Dec 1958, *Barclay & Juajibioy 6301* (MO); Páramo de Ruiz, 25 km SE of Manizales, 22 Nov 1961, *Tryon & Tryon 6148* (GH, US). **HUILA:** Cordillera Central, Cordillera del Buey (West slope), from Finca Loyola above Valencia to Páramo de las Pampas, 3200–3400 m, 13 Dec 1975, *Bishop 1952* (UC); Cordillera Central, Cordillera del Buey (west slope), from Finca Loyola above Valencia to Páramo de las Pampas, 3°51’N, 73°59’W, 3200–3400 m, 13 Dec 1975, *Bishop 1953* (UC); Cordillera Central, Cordillera del Buey (west slope), from Finca Loyola above Valencia to Páramo de las Pampas, 3200–3400 m, 13 Dec 1975, *Bishop 1955* (UC); Cordillera Central, Cordillera del Buey (west slope), from Finca Loyola above Valencia to Parmao de las Papas, 3200–3400 m, 12

Dec 1975, *Bishop 1956* (UC). **META:** main north affluent of Río Grande, S of Cordillera de las Cruces, south slopes of páramo de Sumapaz, 3130 m, 20 Aug 1943, *Fosberg 20861* (US); Macizo de Sumapaz, cabeceras de la quebrada El Buque, 3460 m, 7 Jul 1981, *Díaz-Piedrahita 2626* (MO). **QUINDÍO:** Cordillera central, Río Corubeina, 1300 m, 5 Mar 1875, *André K129* (F, NY). **TOLIMA:** Summit above "Volcancitos", old Quindío Trail, 3300–3500 m, 2 Aug 1922, *Killip & Hazen 9488* (GH, NY).

ECUADOR. **CARCHI:** Montufar, within 3 km of Colonia Huaquena, 0°35'N, 77°42'W, 3600 m, 26 Jun 1994, *Fay & Fay 4286pp* (AAU pp, MO); Montufar, Within 3 km of Colonia Huaquena, 0°25'S, 78°10'W, 3500 m, 30 Jun 1994, *Fay & Fay 4339pp* (AAU, MO pp, NY, UC pp); Estación Biológica La Guandera, 0°23' S, 78°1'W, 3310 m, 18 Feb 2004, *Moran et al. 6863* (NY, US); Reserva Guanderas, ca. 3 km E of Mariscal Sucre, 1°11'S, 78°12'W, 3400–3700 m, 12 Nov 1998, *Navarrete & Øllgaard 3036* (AAU); road from El Playon de San Francisco to Cerro Mirador, 3300 m, 11 Aug 1990, *Øllgaard et al. 98177* (AAU); about 1/2 hr. E of Huaca, past Colonia Huacena, 0°36'N, 77°42'W, 3200–3400 m, 18 Feb 1989, *van der Werff & Palacios 10622* (AAU, MO, UC); Montufar, Guandera reserve, ca. 6 km E of *Fernández* Salvador, 3°42'S, 79°17'W, 3500 m, 2 Jul 1996, *Wilson 2816* (UC). **CHIMBORAZO:** Rd. ca 10 km NE of Alao, at Cuspipacha, 0°5'N, 78°1' 30W, 3500 m, 6 May 1982, *Øllgaard et al. 38137* (AAU). **IMBABURA:** Lago San Marcos, Cayambe, 0°25'S, 78°10'W, 11,200 ft, 28 Nov 1961, *Cazalet &*

Pennington 5378 (GH, UC, US); Hacienda Yura Cruz, 10 km N of Ibarra, 3700–3800 m, 25 May 1973, *Holm-Nielsen et al. 6493* (AAU, MO); Road Ibarra-Mariano Acosta, E of the pass, 0°18'N, 78°1'W, 3500–3550 m, 9 Aug 1976, *Øllgaard & Balslev 8589* (AAU, F, GH, UC); Pimampiro Canton, Ibarra-Mariano Ascosta, Loma Yanalpacunga, 3400 m, 3 Mar 1992, *Palacios & Tipaz 9898* (AAU, MO, UC); 8 km E of Ibarra, along rd. between Yuracruz and Mariano Ascota 3500 m, 17 Nov 1981, *Sperling 5269* (NY, QCA). **LOJA:** Loja-Saraguro, at Loma del Oro turnoff towards Fierro Urcu, 9 km from turnoff, 3°41'S, 79°20'W, 3550 m, 30 Dec 1998, *Jørgensen & Madsen 65795* (AAU); Road Pichig-Fierro Urco, ca. Km 10, 1°8' S, 78°18'W, 3000–3500 m, 20 Jan 1990, *Madsen 86751* (AAU). **NAPO:** Quijos, Rd from Quito to Papallacta, 2 km E of the pass, above the laguna de Papallacta, 0°22'N, 78°5'W, 3800 m, 8 Dec 1990, *Fay & Fay 2639* (MO); Quijos, Road from Quito to Papallacta, 2 km E of the pass, above the Laguna de Papallacta, 0°35.5'N, 77°42'W, 3800 m, 8 Dec 1990, *Fay &. Fay 2644* (AAU, MO, UC); N side of Cerro Sumaco, loma NW of campsite, 0°36'S, 77°39'W, 3100–3150 m, 28 Apr 1979, *Holm-Nielsen et al. 17405* (AAU); Cordillera de los Llanganatis, NE side of Laguna Encantada, 0°36'N, 77°39'W, 3430 m, 16 Mar 1983, *Holm-Nielsen et al. 41786* (AAU); S side of Cerro Sumaco, 1°9'S, 78°18'W, 2900–3050 m, 1–2 May 1979, *Lojtnant & Molau 13133* (AAU); Near Papallacta, 0°35'N, 77°42'W, 3000 m, 1 Dec 1923, *Mille s.n.* (NY 2-sheets, US); Oyacachi, 5 km después el paso, 0°12' S, 78°7'W, 3500 m, 28 Dec 1996, *Navarrete*

1385 (AAU); Oyacachi, 5 km después el paso, 0°12’N, 78°6’W, 3500 m, 28 Dec 1996, *Navarrete 1388* (AAU); Oyacachi, Yarupaccha, 0°36’N, 77°41’W, 3620–3680 m, 16 Jan 1996, *Navarrete 1428* (AAU); Carretera Baeza-Quito, 5 km después de Cuyuja, Hacienda Flor del Bosque, 0°19’S, 78°7’W, 3200 m, 1 Sep 1994, *Navarrete 373* (AAU, QCA); Llanganati, North facing slope towards the Río Golpe, just north of Chosa Aucacocha, 0°34’S, 77°43’W, 3500 m, 15 May 1982, *Øllgaard et al. 38632* (AAU); Llanganati, North-facing slope towards the Río Golpe, just north of Chosa Aucacocha, 1°8’S, 79°18’W, 3600 m, 16 May 1982, *Øllgaard et al. 38693* (AAU); Road to Quito-Baeza, 5 km NW of Laguna Papallacta (Páramo de Guamani), 0°20’N, 78°0’W, 3700–3750 m, 18 Jul 1976, *Øllgaard & Balslev 8069* (AAU, GH, NY); Llanganati, along Río Topo, SE of Aucacocha, 1°48’S, 78°26’W, 3370–3420 m, 18 May 1982, *Øllgaard & Holm-Nielsen 38755* (AAU). **PICHINCHA:** Rd. Olmedo - Laguna San Marcos, W of the pass, 0°12’N, 78°6’W, 3600 m, 10 Jul 1980, *Øllgaard et al. 34360* (AAU). **SUCUMBÍOS:** Cerro "El Mirador," 4 km al SW de la población de "Cocha Seca," subiendo por el sector de "Chozas Viejas," 3300–3500 m, 29 Feb 1992, *Gavilanes & Funk 837* (USM).

Ascogrammitis pichinchae is most easily recognized by its narrowly deltate segments with moderately and evenly setose margins.

Ascogrammitis pichinchensis (Hieron.) Sundue, **comb. nov.** *Polypodium pichinchense* Hieron., Bot. Jahrb. Syst. 34: 506. 1904. 1956. *Grammitis pichinchensis* (Hieron.) C. V. Morton, Contr. U. S. Nat. Herb. 38: 111. 1967. *Terpsichore pichinchensis* (Hieron.) A. R. Sm., Novon 3: 488. 1993. *Polypodium ecuadorense* C. Chr., Index. Fil. 524. 1906. Nom. superfl., an illegitimate renaming of *P. pichinchense* Hieron. *Ctenopteris ecuadorensis* (C. Chr.) Copel., Phillip. J. Sci. 84: 434. 1956. TYPE: Ecuador. Pichincha: western side of Pichincha, 1862, *W. Jameson s.n.* (lectotype: designated by C. V. Morton, 1967: B, n.v.; possible isolectotypes: B, n.v., BM, n.v., NY, US 2-sheets; photo of lectotype B virtual herbarium, F).

(Fig. 9, 13 B, 14 A–C)

Plants epiphytic, singular or forming small colonies, sometimes epipetric or on soil banks; roots not prolific; rhizome 0.4–0.6 mm wide; branch buds absent; rhizome scales 1.5–2.5 × 0.3–0.4 mm, lanceolate, clathrate, the cell walls black, the lumina clear, sometimes the lumina very narrow and so appearing occluded, the margin sparsely setose, the setae 0.2 mm long, the apex attenuate; fronds 6–36 × 0.6–1.7 cm, hemidimorphic, pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petioles 1.5–4.5 cm × 0.2–0.4 mm, with a single vascular bundle, castaneous, terete, non-marginate, moderately setose, the setae 1.5–2 mm long, sparsely hairy, the hairs 1-furcate; rachises with castaneous sclerenchyma visible on both the abaxial and adaxial sides of the lamina, or the sclerenchyma not visible on the adaxial side, moderately setose, the setae 1.5–2 mm long, sparsely hairy, the hairs 1-furcate; laminae membranaceous, deeply 1-pinnatifid to 1-pinnate, nearly linear, even sided, with 21–85 pairs of segments; medial segments 3–9 × 1.8–3.5 mm, oblong, slightly ascending, the base decurrent, the apex rounded, the margin slightly undulate, setose, the setae 0.5–1 mm long, the abaxial and adaxial lamina surfaces moderately setose, the setae 0.5–1 mm long, fertile portions of the lamina more densely setose than sterile portions; segment costae with the dark sclerenchyma sometimes visible abaxially, not readily visible adaxially; veins not readily visible on either side of the lamina; hydathodes cretaceous; sori inframedial, confined to distal portions of the frond, 3–4 pairs per segment; receptacular setae present.

Distribution.—The Western Cordillera of northern and central Ecuador; (2800–)3000–3500(–3700) m. *Fay & Fay 3105, 3113, 3285,* report elevations of 1900 m, 1000 m lower than any other record. Whether this represents a labeling error or a disjunct population is unclear. No other collections of *A. pichinchensis* have been made at that locality, the Río Guajalito Reserve, despite it being frequently visited by collectors.

Additional specimens examined. ECUADOR. **CARCHI:** Valle de Maldonado, km 53 on the road Tulcán-Maldonado, 3150–3250 m, 17–18 May 1973, *Holm-Nielsen et al. 5656* (MO, NY); Road Tulcán-Maldonado, 53 km from Tulcán, 0°49’N, 78°2’W, 3200 m, July 1976, *Øllgaard & Balslev 8267* (NY); Road Tulcán-Maldonado, 49 km from Tulcán, 0°33’S, 78°42’W, 3200–3350 m, 1 August 1976, *Øllgaard & Balslev 8331* (NY). **CHIMBORAZO:** Chimborazo-Cañar border, western escarpment, near Tipococha, 0°5’N, 78°30’W, 9,800–10,400 ft, 6–9 Jun 1945, *Camp 4075pp* (F, GH pp, MO, NY). **COTOPAXI:** Along Quevedo-Latacunga road, between Pilalo and Pujili, 3400 m, 26 Nov 2004, *Lehnert 1577* (UC); Sigchos, al SW del Cerro Azul, 3207–3340 m, 26 Jul 2003, *Ramos et al. 6601* (UC); Quebrada Faldiguera, Hacienda El Pongo, E side of Iliniza, 3270 m, February 13, 1990, *Ulloa 92952* (AAU, QCA). **IMBABURA:** Volcán Imbaburra, about 7 km E of Otovalo, 0°40’N, 78°47’W, 3200 m, 3 Dec 2006, *Sundue Martin & Shear 1070* (NY, UC); Pimampiro, Ibarra-Mariano Ascota, Loma Yanalpacunga, 0°27’S, 78°28’W, 3400 m, 3 Mar 1992, *Palacios & Tipaz 9884* (MO). **PICHINCHA:** Below San Juan towards Chiriboga, 0°20’N, 78°3’W, 3250 m, 29 Apr 1955, *Asplund 16106* (NY); Old Rd. Quito - Santo Domingo, 12–16 km W of Chillogallo, 3200–3300 m, 22 Jan 1981, *Balslev Luteyn & Clements 1629* (AAU); N slopes of Pasochoa, S of Quito, 0°5’S, 78°33’W, 3000–3500 m, 1 Feb 1981, *Balslev 1848* (AAU, NY); Camino Yanacocha en faldas N de Cerro Pichincha, 0°5’S, 78°33’W, 3700 m, 3 Jun 1982, *Balslev 2700* (NY); Camino Yanococha al lado NW de Cerro Pichincha, 3700 m, 30 Sep 1982, *Balslev & Steere 3267* (NY); Quito, Parroquia Calacali, reserva Geobotanica del Pululahua, 0°14’S, 78°48’W, 3000–3300 m, 2 Feb 1992, *Ceron 18127* (MO, UC); Quito, Río Guajalito

Reserve, 10 km W of Chiriboga, km 59 of Old Rd. from Quito to Santo Domingo de los Colorados, 0°14'S, 78°48'W, 1900 m, 15 Jun 1991, *Fay & Fay 3105* (AAU, UC); Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old rd. Quito-Santo Domingo, 0°14'S, 78°48'W, 1900 m, 15 Jun 1991, *Fay & Fay 3113* (AAU, QCA); Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km 59 of old rd. Quito-Santo Domingo, 0°50'N, 78°3'W, 1900 m, 10 Jul 1991, *Fay & Fay 3285* (QCA); *Jameson 137* (NY (Frag.); Quito, 1846, *Jameson s.n.* (GH); [Quito], *Jameson s.n.* (NY); Nor-Oeste del Pasochoa, colecciones en el crater, 3400 m, 29 Nov 1980, *Jaramillo 3869* (QCA); Along-Partidero linea ferrea-param El Pongo, 0°59'S, 78°58'W, 21 Mar 1981, *Jaramillo & Cachago 4664* (AAU, QCA); Pasochoa, 3000 m, *Mille s.n.* (GH); Mt. Atacazo, 0°50'N, 78°3'W, 1500–2800 m, 1916, *Mille s.n.* (GH, NY); Rd. and trail from Chaupi - W of pass btw. Iliniza and Corazon, 0°18'N, 78°1'W, 3780–3930 m, 15 Mar 1995, *Øllgaard et al. 1187pp* (AAU pp, QCA); Machachi, Reserva Ecologica Los Ilinizas, 0°36.04'S, 78°50.55'W, 3378 m, 18 Aug 2003, *Ramos 7392* (MO, UC); Bosque Protector Pasochoa, 30 km SE de Quito, 26 Apr 1987, *Rodríguez 603* (QCA); Bosque Protector Pasochoa, 30 km SE de Quito, 9 May 1987, *Rodríguez 641* (QCA); Bosque Protector Pasochoa, 30 km SE de Quito, 9 May 1987, *Rodríguez 646* (QCA); Sep 1899, *Sodiro s.n.* (NY); *Sodiro s.n.* (UC); In Mte. Atacazo, 1500–2800 m, 1916, *Mille, L. sn.* (NY); Sep 1899, *Sodiro 33* (NY); Bosque Protector Pasochoa, 30 km SE of Quito, 0°28'S, 78°40'W, 2850–3900 m, October

16, 1988, *Paz 78* (QCA), *Sodiro 136* (AAU); 35 km from Quito on rd. to Santo Domingo, 10,000 ft, 11 Apr 1945, *Weatherwax 325* (MO);. **TUNGURAHUA:** Cordillera Oriental, Tungurahua, 3000 m, Oct 1907, *Rimbach 37* (GH); ad ped m. Tungurahua, 0°16.247'N, 78°12.397'W, 1857–9, *Spruce 5372* (NY). **Province unknown:** Andinis, 300 m [3000?] *Mille s.n.* (US); La Bonita, NE face of forested slope, 3500 m, 17 Oct 1981, *Sperlling 5267* (NY).

Ascogrammitis pichinchensis is distinguished by its membrancaceous laminae, rounded segments, and setae present along segment margins and on both sides of the laminae. Like its congeners, the costae are provided with dark sclerenchyma, but in *A. pichinchensis* the costae are obscured beneath a layer of parenchyma and therefore not clearly visible on the lower surface of the frond.

Ascogrammitis tungurahuae Sundue**, sp. nov**. Type: Ecuador. Tungurahua: 3000 m, Oct 1912, *A. Rimbach 131* (holotype: US; isotype: P).

(Fig. 17 A–C)

Ab *Ascogrammitis athyrioides* marginibus segmentorum integris apice setosis et lamina abaxialiter modice setosa differt.

Plants epiphytic, singular or forming small colonies; roots not prolific; rhizome 1.2 mm wide; branch buds absent; rhizome scales 2.2–3.5 × 0.4–0.5 mm, lanceolate, the cell walls blackish, the lumina transparent but very narrow and appearing occluded, the margin sparsely setose, the setae 0.1 mm long, the apex attenuate; fronds 27–60 × 2–4.5 cm, pendent, monomorphic, pendent, usually bearing the mycelia and ascomes of *Acrospermum*; petiole 6–12 cm × 0.6–0.8 mm, brown to castaneous, terete, sparsely setose, the setae 2–2.5 mm long, sparsely hairy, the hairs 1-furcate, 0.1 mm long; rachis with castaneous sclerenchyma visible on both sides of the lamina, the abaxial side sparsely to moderately setose, the setae 0.7–1 mm long, the adaxial side moderately setose, the setae 0.7–1.5 mm long; laminae chartaceous, narrowly elliptic to oblong, 1-pinnate proximally and distally, 1-pinnatisect distally, with 35–50 pairs of segments, the base attenuate, with 5–8 pairs of reduced and distant segments, the apex attenuate; medial segments 1–2.5 cm × 2.3–4 mm, narrowly triangular, widest at the base, the base slightly decurrent, the apex narrowly rounded to acute, the margin entire to sparsely denticulate, provided with scattered simple hairs, 0.1 mm long, the apex with 1–3 setae, 0.5–1 mm long, the abaxial surface sparsely to moderately setose, the setae 0.5–1.2 mm long, also with scattered simple hairs, 0.1 mm long, the adaxial surface with a few scattered setae along the pinna costae, 0.5–1 mm long, otherwise glabrous; pinna costae with dark sclerenchyma visible on both sides of the lamina; veins visible on the abaxial side of the lamina, not visible on the adaxial side of the lamina; hydathodes cretaceous; sori inframedial, apparently confined to the distal portion of the lamina, 3–6 per segment; receptacular setae present.

Distribution.—Ecuador, Mt. Tungurahua, forested slopes; ca. 3000 m. Rimbach's locality for the type is "Western Cordillera of Riobamba, western slope." This might refer to the western slope of Mt. Tungurahua above Riobamba, or to the slopes of Mt. Chimborazo west of Riobamba since Mt. Chimborazo is considered to be part of the Western Cordillera whereas Mt. Tungurahua is not.

Additional specimens examined. ECUADOR. **CHIMBORAZO:** Western Cordillera of Riobamba, western slope, 3300 m, *Rimbach 22* (GH, US). **TUNGURAHUA:** Tungurahua, Oct 1912, *Rimbach 127a*; Tungurahua, Oct 1912, *Rimbach 131a* (US); in sylvis [illegible] Tungurahua, Aug 1903, *Sodiro s.n.* (US). **Prov. unknown:** Río [illegible], 3200 m, 1912, *Rimbach 113a* (US).

Ascogrammitis tungurahuae resembles *A. athyrioides* by having rhizome scales with narrow lumina that appear blackish in mass, and long pendent fronds. In fact, *A. tungurahuae* could easily be mistaken for A. *athyrioides* that had entire or very shallowly-lobed rather than pinnatifid segments. Upon closer examination, *A. tungurahuae* differs from *A. athyrioides* by the sparse to moderately dense covering of setae on the abaxial side of the lamina, simple hairs along the segment margins, and setae on segment apices. These two species occur at similar elevations, but their distribution is separated by the Huancabama Depression. *Ascogrammitis tungurahuae* has not been collected since 1912. Widespread deforestation in the area, and major eruptions including lava flows on Mt. Tungurahua from 1916–1918 (Ruiz et al., 2006) may have greatly restricted the population.

The recognition of *Ascogrammitis tungurahuae* has probably been delayed because of its confusion with *Terpsichore attenuatissima* (Copel.) A. R. Sm. These species are not closely related, but misidentification of specimens is frequent and repeated in the literature. *Terpsichore attenuatissima* belongs to the clade which includes species such as *T. semihirsuta* and *T. alsopteris* (Sundue dissertation Chapter 2) as evidenced by concolorous orange to castaneous rhizome scales with turgid cells, veins with dark sclerenchyma visible on the abaxial lamina surface, and round sori. *Terpsichore attenuatissima* is based on a Sodiro collection that, like *A. tungurahuae*, is from Mt. Tungurahua. Three Sodiro collections at US have been identified as *T. attenuatissima*, but one of these is actually referable to *T. tungurahuae*. The holotype of *T. attenuatissima* (*Sodiro s.n.*, US), bears the US accession number 1431876 cited by Copeland. The second Sodiro collection bears the same collection date (Aug 1904) and locality (silvis v. Tungurahua) as the holotype, and can be considered a possible isotype of *T. attenuatissima.* The third collection, which is referable to *A. tungurahuae*, bears an earlier date of Aug 1903. Thus despite some confusion, the type of *T. attenuatissima* does not appear to be a mixed collection. Copeland (1956) cited *Rimbach 22* and *113a*, and Smith (1999) cited *Rimbach 22* (US pp) as *T. attenuatissima*, but these plants are in fact *T. tungurahuae* as evidenced by their blackish, clathrate scales, lack of dark sclerenchyma along their veins, and elliptic sori. *Rimbach 113a* is a mixed collection containing two plants of *A. pichinchae* [center and right] and one plant of *A. tungurahuae* [left], and this may explain Morton's (1967) citation of Rimbach *127a*, *131*, and *131a* as that species. Jørgensen (1999) cited *Rimbach 22* (US) as "pp," but the material that I have seen of *Rimbach 22* at US is uniformly referable to *A. tungurahuae*.

Excluded names:

Terpsichore kegeliana (Kunze) A. R. Sm., Novon 3: 487. 1993. *Polypodium kegelianum* Kunze, Linnaea 21: 210. 1848. *Ctenopteris kegeliana* (Kunze) K. U. Kramer, Amer. Fern J. 64: 114. 1974. *Grammitis kegeliana* (Kunze) Lellinger, Amer. Fern J. 74: 58. 1984. Type: Suriname. Sornaukreek, *H. A. H. Kegel 1072* (GOET). = *Ceradenia*, possibly an older name for *C. pruinosa* (Maxon) L. E. Bishop.

Terpsichore kegeliana is the last species not placed into a group within *Terpsichore* by Smith (1993). Other species that were not placed to group do in fact belong to *Ascogrammitis* and are treated here. All other names in *Terpsichore* are now accounted for meaning that they clearly belong to a well defined genus or clade. For further reference, readers should see Smith (1993), Ranker et al. (2004), Sundue et al. (dissertation chapter 2), Sundue & Kessler (2008), and Labiak & Matos (2007)

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Appendix I

Index to collectors' names and numbers. Number in parentheses refer to the species number below.

List of Species

1. *Ascogrammitis alan-smithii* (A. Rojas) Sundue

2. *A. anfractuosa* (Kunze ex Klotzsch) Sundue

3. *A. angustipes* (Copel.) Sundue

4. *A. athyrioides* (Hooker) Sundue

5. *A. clathrata* (Sundue & M. Kessler) Sundue

6. *A. clavigera* Sundue ex A. R. Sm.

7. *A. colombiensis* Sundue

8. *A. cuencana* (Hieron.) Sundue

9. *A. david-smithii* (Stolze) Sundue

10. *A. dilatata* (Sundue & M. Kessler) Sundue

11. *A. loxensis* Sundue

12. *A. nana* (Sundue & M. Kessler) Sundue

13. *A. oxapampensis* Sundue

14. *A. pichinchae* (Sodiro) Sundue

15. *A. pichinchensis* (Hieron.) Sundue

16. *A. tungurahuae* Sundue

LIST OF COLLECTORS NAMES AND NUMBERS

The number in parentheses refers to the species numbers assigned in the taxonomic treatment (List of Taxa, above). Boldface indicates types.

Abbott, 17066 (12)

Acuña, 9991 (2)

Alston, 7442, 7476 (7)

Alverson & Flores, 3101 (1)

Andre, K129 (14)

Antonio, 2578 (1)

Arroyo et al., 62pp (9); 2741 (9); 2762 (12)

Asplund, 16106 (15)

Atehortúa, 1124 (2)

Aymard & Luteyn, 2459 (2)

Bach et al., 1051 (10); 1349 (2)

Balslev, 1848 (15); 1934 (8); 2700 (15)

Balslev & Steere, 3267 (15)

Balslev et al., 1629 (15)

Barclay & Juajibioy, 6301 (14)

Barringer & Christenson, 3419 (2)

Barringer et al., 2277 (2)

Beck, 2844 (4); 7600 (10); 14474 (9); 21496 (4); 1424a (10)

Bell, 374 (2)

Bello & Mendez, 2663 (1)

Bishop, 826 (2); 857 (2); 1952 (14); 1953 (14); 1955 (14); 1956 (14); 1989 (2); 2506 (9)

Boom, 1432 (11)

Boyle et al., 4389 (4)

Breedlove, 34598 (2)

Breedlove & Smith, 32644 (2)

Breedlove & Thorne, 30159 (2)

Britton, sn, sn (2)

Brooke, 6166 (4)

Bryan, 383 (12); 550b (4)

Buchtien, **891** (4); 2754 (4); 2756 (4)

Bues, 1039 (4); 1259 (4); 1391 (4); 1547 (4); 1822 (4); 1945 (2); 2116 (4)

Caballero, 126 (2)

Camp, 4075 (15); E1394 (11)

Campos & Tenorio, 5047a (2)

Cardenas, 1002 (4)

Carhart, sn (2)

Cazalet & Pennington, 5378 (14)

Ceron, 18127 (15)

Christenhusz & Katzer, 4158 (2)

Cook & Gilbert, 1168 (2)

Cornman, 1042, 1241 (2); 1326 (2)

Croat, 23166, 33054, 33898 (1); 48567 (2), 54917 (6), 58706 (11)

Croat et al., 87817a (2)

Cuatrecasas, 22141 (2)

Dassler, 94-7-13-1 (7)

Davidse, 25257 (2)

Davidse & Herrera, 29122 (2)

Davidse et al., 28598 (2)

Davidson, 195 (2)

De Boer, **1161** (10)

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Dodson & Embree, 13394 (2)

Dodson et al., 10929 (2)

Dorr et al., 4984 (2); 5010, 8154 (6)

Ekman, 7373, 13585 (2)

Espinoza, 322 (1)

Evans, 2613 (2)

Farr, s.n. (2)

Fay & Fay, 2449 (10); 2639, 2644 (14); 2961, 3033 (10); 3052 (2); 3105, 3113 (15); 3163, 3193, 3227, 3284 (2); 3285 (15); 3286, 3586, 3897 (2); 4286, 4339 (14); 4446 (11)

Fernández, 632 (4)

Fernández et al., 2202 (10); 2511, 4250 (9)

Fisher, 151 (2)

Fosberg, 20861 (14)

Foster, 85-153, 85-2 (2)

Fuentes et al., 11943 (4)

Fuertes, sn (2)

García & Beck, 4079 (4)

García et al., 4466 (2)

Gavilanes & Funk, 837 (14)

Gómez, 2400, 21778, 22228 (2)

Gonzales, 1541, 1552, 1576 (4)

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Hart, s.n. (2)

Haught, 5288 (2)

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Ingela, 95-M046 (2)

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Jaramillo, 3869 (15)

Jaramillo & Cachago, 4664 (15)

Jenman, **84**, s.n. (2)

Jiménez M., A., 1341 (2)

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1396, 1397, 1399, 1443 (2); 1452 (9); 1689 (10); 1692 (4); 1709 (9); 1753, 1774 (4)

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Juncosa, 1987 (3)

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Kuntze, s.n. (12)

Labiak et al., 2856, 2864, 2867, 2871 (10)

Lankester, 902 (2)

Lehmann, 3010 (2); **5728** (8); 7365 (2)

Lehnert, 212 (2); 261 (4); 291, 312, 315, 329 (2); 380, 381 (10); 499 (2); 697 (9); 702 (10); 708 (10); 1035 (2); 1233, 1235 (11); 1577 (15)

Lehnert & Kessler, 1164 (8); 1206 (2)

Lellinger, 786, 1735 (2)

Lellinger & White III, 997 (2); 1311 (1); 1582, 1694 (2)

Lems, s.n. (2)

Lent, 1760 (1)

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Mille, s.n. (14); s.n. (15)

Molina, 10673 (2)

Molina & Molina, 21463 (2)

Molina et al., 16807 (2); 17522, 17728 (1)

Moore, s.n. (2)

Moraga et al., 334 (2)

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Øllgaard et al., 38632, 38693 (14); 1187 (15); 2235 (2); 34360 (14); 35598, 35900, 37794 (2); 38137 (14); 90445 (11); 98177 (14); 99638 (11)

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Ortega et al., 2044 (2)

Ownbey, 2616 (2)

Palacios & Tipaz, 9884 (15); 9898 (14)

Paz, 78 (15)

Penland & Summers, 207 (2)

Pennell, 9260 (8)

Penneys, **469** (1)

Peyton & Peyton, 1331 (10)

Pittier, 2000 (2)

Pizarro, 9 (4)

Popenoe, 1095 (2)

Portugal, 289 (9)

Proctor, 9704, 10844, 25071 (2)

Questel, 3228 (2)

Ramirez et al., 7794 (2)

Ramos, 7392 (15)

Ramos et al., 6372 (2); 6601 (15)

Rimbach, 22 (16); 37 (15); 113a (14); 127a, **131**, 131a (16)

Rivero & Díaz, 1422 (2)

Rodríguez, J., 603, 641, 646 (15)

Rodríguez, J. V., 756, 1945 (2)

Rodríguez, W. D., 5182 (3)

Rodríguez, W. D. et al., 4746, 4755, 5195 (2); **5128** (3)

Rojas, 703 (2); 2430 (1); 3128 (2); 4279 (1)

Rojas et al., 2820 (2)

Ruíz, **58** (2)

Rusby, 382 (2)

Salinas, 2460 (9)

Santiago, 2626 (14)

Schneider, 2400 (6)

Scolnik et al., 19an445 (2)

Seibert, 95, 196, 648, 987 (2)

Silverston-Sopkin et al., 9809, 9934 (2)

Skutch, 3229 (2)

Smith, A. R. & Beliz, 2109 (2)

Smith, A. R. et al., 1569 (2); **1572** (6); 2388, 2800 (2)

Smith, Austin, 85 (2)

Smith, D. N. & Canne, **5837** (9)

Smith, D. N. et al., 2607 (9)

Sodiro, 33, 136, s.n. (15); s.n. (2); **s.n.** (14); s.n. (16)

Solomon, 7261 (10); 8656 (12); 9112 (9)

Sperling, 5267 (15); 5269 (14)

Sperling & Bleiweiss, 5024 (2); 5165 (16)

Spross, 117 (2)

Spruce, 4642 (2); 5372 (15)

Standley, 4902

Standley, 15653, 35403, 38367, 38566, 38667, 38749 (2)

Standley & Torres, 47752 (2)

Standley & Valerio, 44598, 44610 (1); 48052, 50466 (2)

Steinbach, 9554, 9720 (4)

Steyermark, 30020, 42665, 43610, 53612, 58710, 58731, 75401 (2)

Steyermark et al., 128039 (2)

Stolze, 1416 (2)

Stolze & Stolze, 1663 (11); 1678 (2)

Stork, 1969 (2)

Sundue, 1125 (11); 1128, 1176 (2)

Sundue & Martin, 1031, 1035, 1050 (2)

Sundue & Schuettpelz, 1073 (11); 1075 (2); 1078, 1084 (11); 1086 (2); 1088 (11); 1091 (8)

Sundue & Vasco, 1208 (3); 1232 (2); 1237 (3); 1306, 1312, 1316, **1331**, 1334, 1335 (7)

Sundue & Werner, **1164** (11)

Sundue et al., 782, 785 (9); **866** (12); 1070 (15); 1689 (2)

Tate, 504 (2)

Tejero-Díaz, 4073 (2)

Tillet, 673-231 (2)

Tonduz, 12197 (2)

Torres, 66, 69a (2)

Tryon & Tryon, 5310 (2); 6148 (14)

Ulloa, 92952 (15)

Underwood, 540, 773, 1273, 1369, 2346, 2448, 2451, 2489, 3157 (2)

Valenzuela et al., 1749 (9)

van der Werff & Palacios, 10622 (14)

van der Werff et al., 8451, 8452 (13); 8799, 8822 (6); 15007 (13); 15535; 16676, 16700 (11); 16773 (2); 17706, **18537** (13); 18599, 18622 (9); 19568 (11); 19569 (2)

Vargas & Narvaez, 3531 (2)

Vasco & Sundue, 650, 702 (3)

Vasquez et al., 28446 (4); 28474 (13); 30123 (9)

Weatherwax, 325 (15)

Webster & Addison, 27573 (2)

Webster et al., 29317, 30299 (2)

Werner, 734 (2)

Williams & Molina, 10287, 10387, 11142, 12790, 13688, 18869, 40732 (2)

Wilson, 2816 (14)

Windish, 2363 (2)

Woodson Jr. et al., 829 (2)

Woytowski, 7840 (2)

Wurdack, 703 (4)

Yunker et al., 6197 (2)

Zanoni et al., 20416, 24947, 37502 (2)

Distribution of *Ascogrammitis* by country.

Endemics are in boldface.

MEXICO, GUATEMALA, HONDURAS, EL SALVADOR, CUBA, JAMAICA, HAITI, DOMINICAN REPUBLIC, GUADELOUPE, GUYANA: *A. anfractuosa*

COSTA RICA: *A. alan-smithii, A. anfractuosa*

PANAMA: *A. alan-smithii; A. anfractuosa*

VENEZUELA: *A. anfractusa,* ***A. clavigera***

COLOMBIA: *A. anfractuosa,* ***A. angustipes****,* ***A. colombiensis****, A. pichinchae*

ECUADOR: *A. anfractuosa, A. loxensis, A. pichinchae, A. pichinchensis, A. tungurahuae*

PERU: *A. anfractuosa, A. athyrioides, A. david-smithii, A. loxensis, A. nana,* ***A. oxapampensis***

BOLIVIA: *A. anfractuosa, A. athyrioides,* ***A. clathrata****, A. david-smithii,* ***A. dilatata****, A. nana*

FIG. 1. A. *Ascogrammitis loxensis*, spore 400×, ca. 45 µm diam. (*Sundue & Schuettpelz 1078*, NY). **B.** *Ascogrammitis clavigera*, scale bar = 10 µm, spore (*Jiménez*, 1215, UC). **C–D.** *Ascogrammitis athyrioides*, **C**. 1-furcate, 3-celled hair, the longer branch is setiform, scale bar = 10 µm. **D.** Dictyostele with leaf gaps on the dorsal side. The ventral side lacks perforations, scale bar = 1 mm (*Kessler et al. 10622*, UC). **E.** *Acrospermum maxonii* on *Ascogrammitis pichinchae*, hyphae stained with lactophenol blue, scale bar = 100 µm (*Moran et al. 6863*, NY).

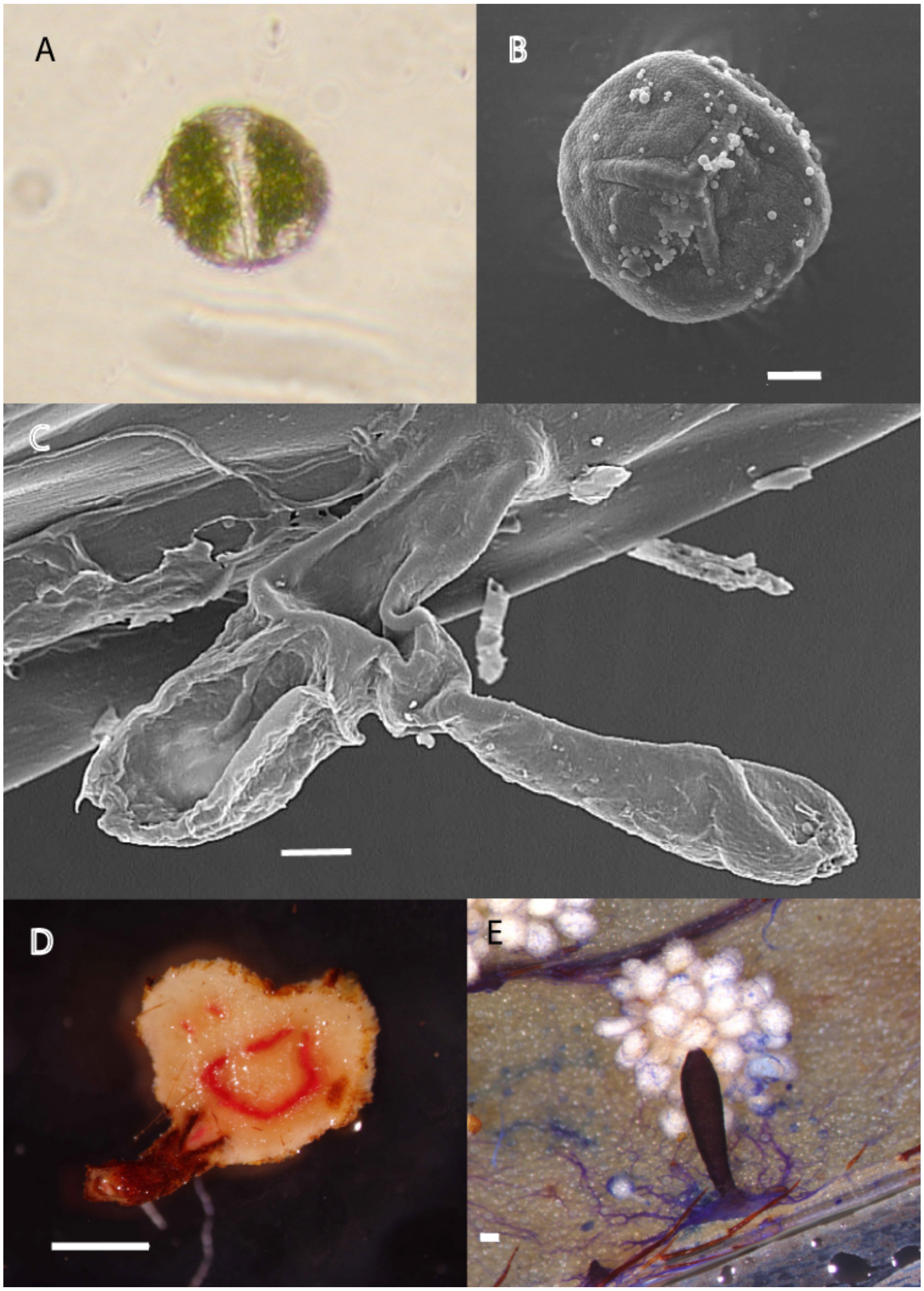

A
B
C
D
E

FIG. 2. Distribution of *Ascogrammitis alan-smithii*.

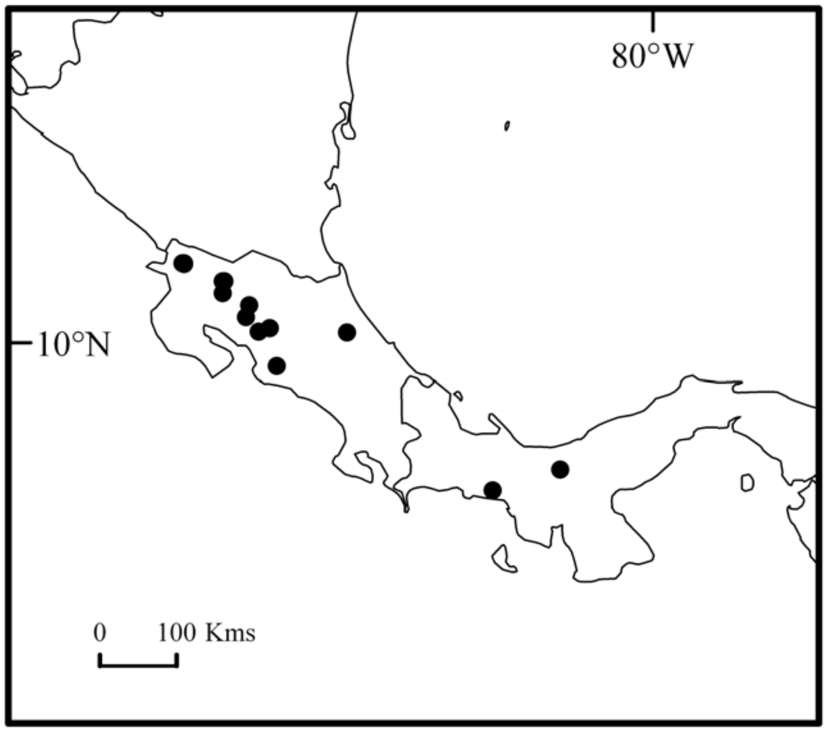


FIG. 3. Distribution of *Ascogrammitis anfractuosa*.

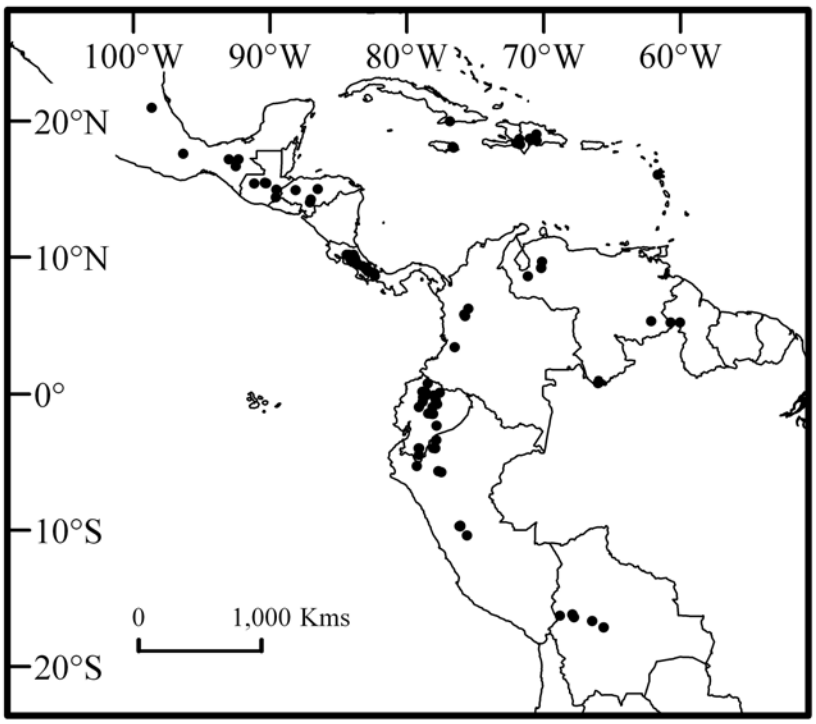


FIG. 4. Distribution of *Ascogrammitis athyrioides*.

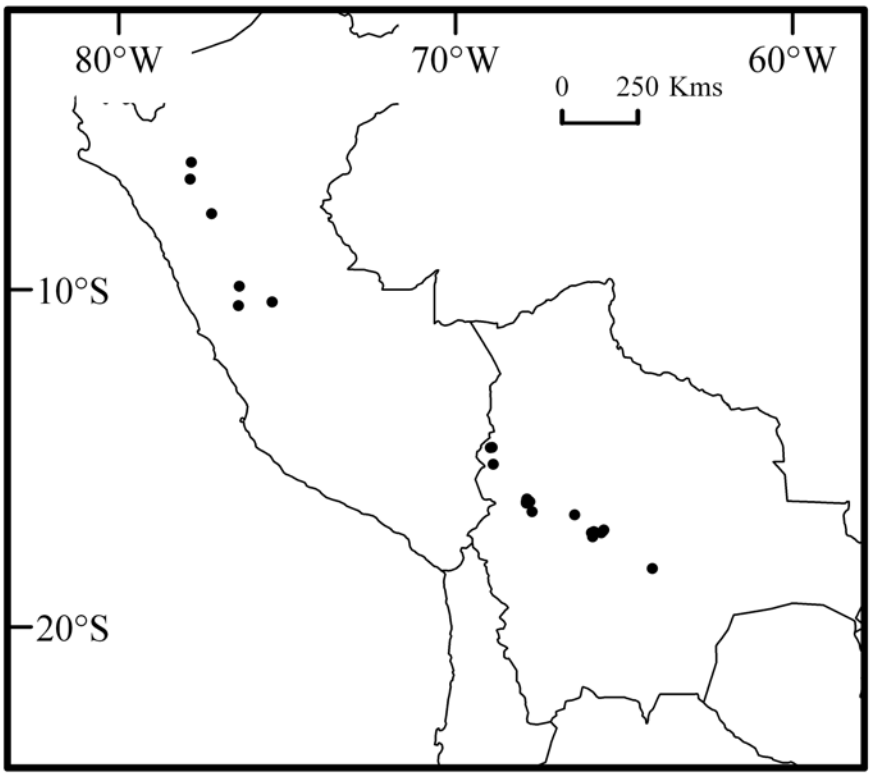


FIG. 5. Distributions of *Ascomphora oxapampensis* (circle) and *A. clathrata* (plus).

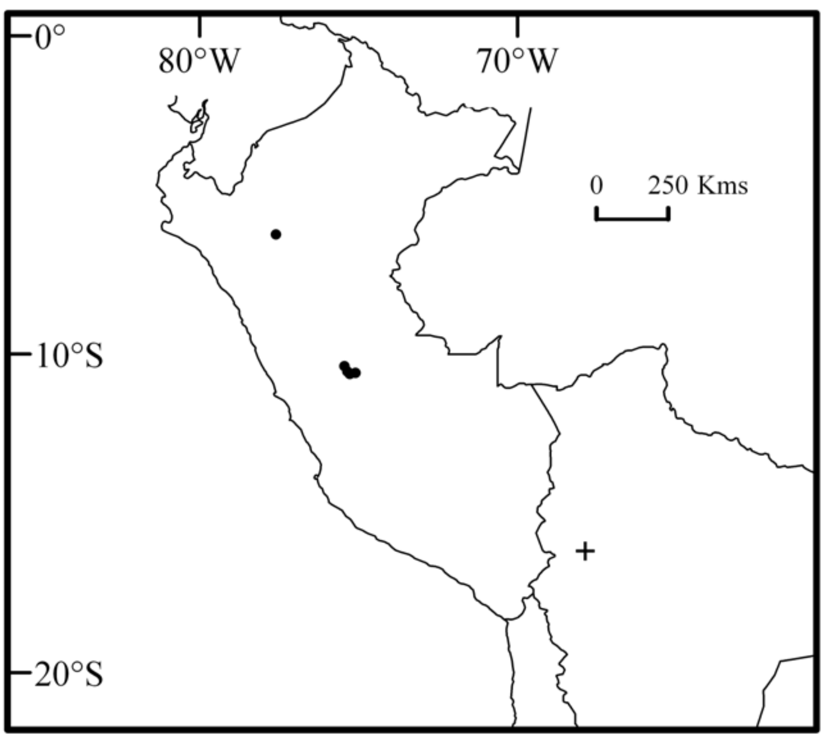


FIG. 6. Distributions of *Ascogrammitis clavigera* (circle), *A. angustipes* (triangle), and *A. colombiensis* (plus).

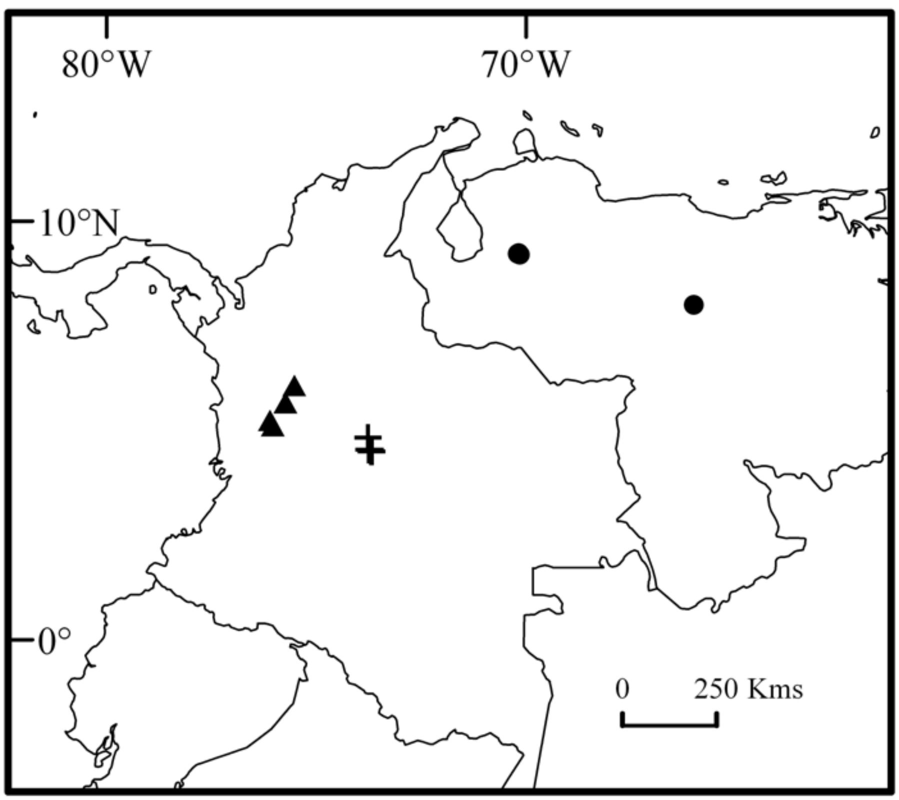


FIG. 7. Distribution of *Ascogrammitis david-smithii.*

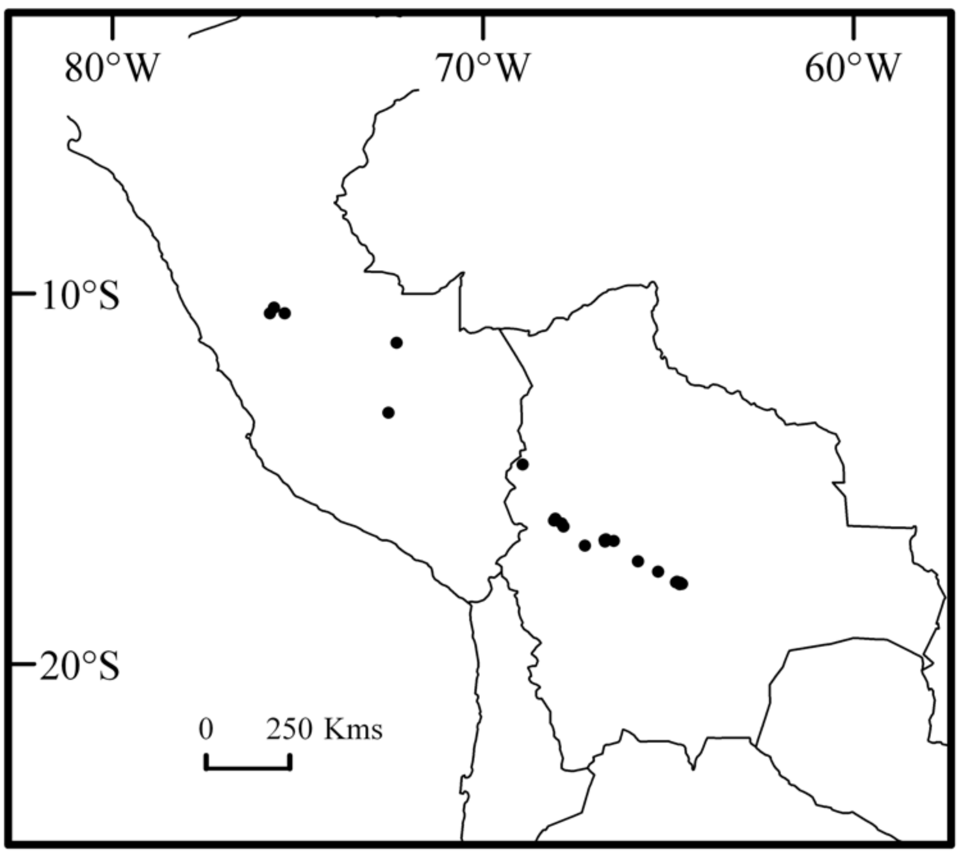


FIG. 8. Distribution of *Ascogrammitis dilatata*.

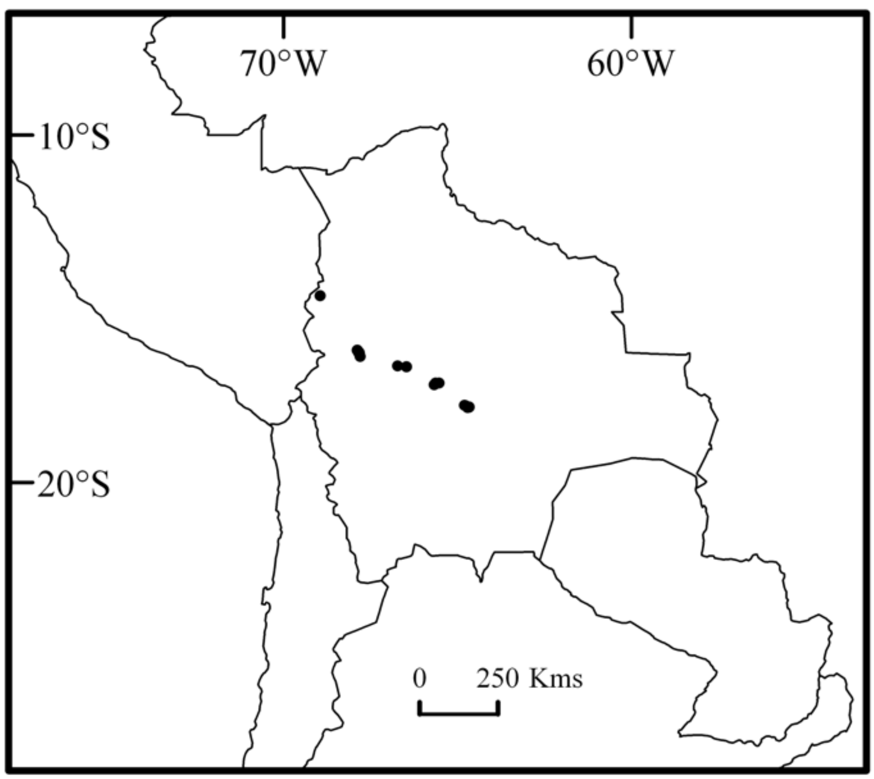


FIG. 9. Distributions of *Ascogrammitis loxensis* (plus) and *A. pichinchensis* (circle).

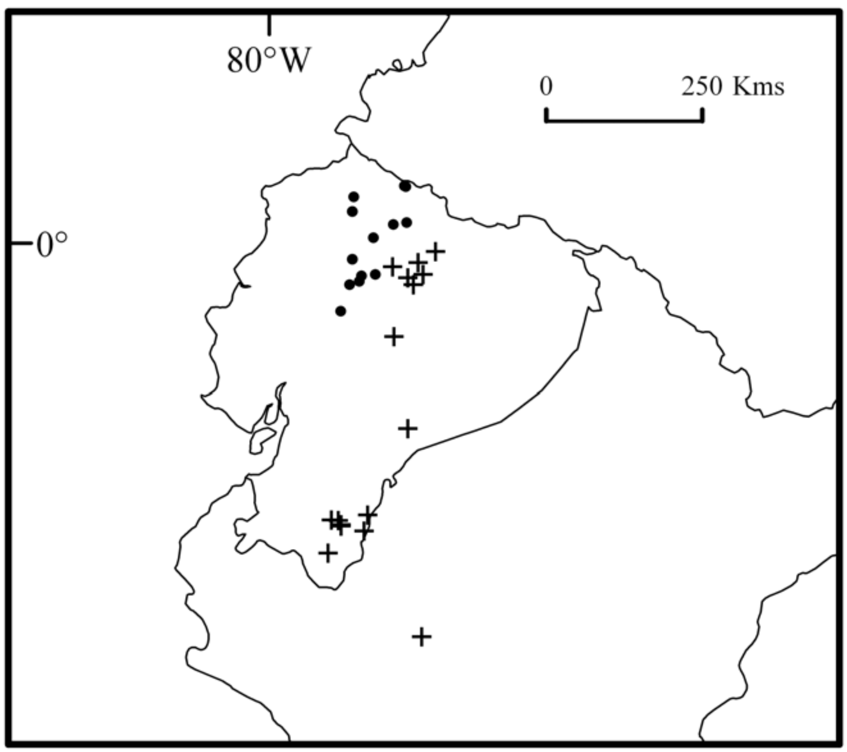


FIG. 10. Distribution of *Ascogrammitis nana*.

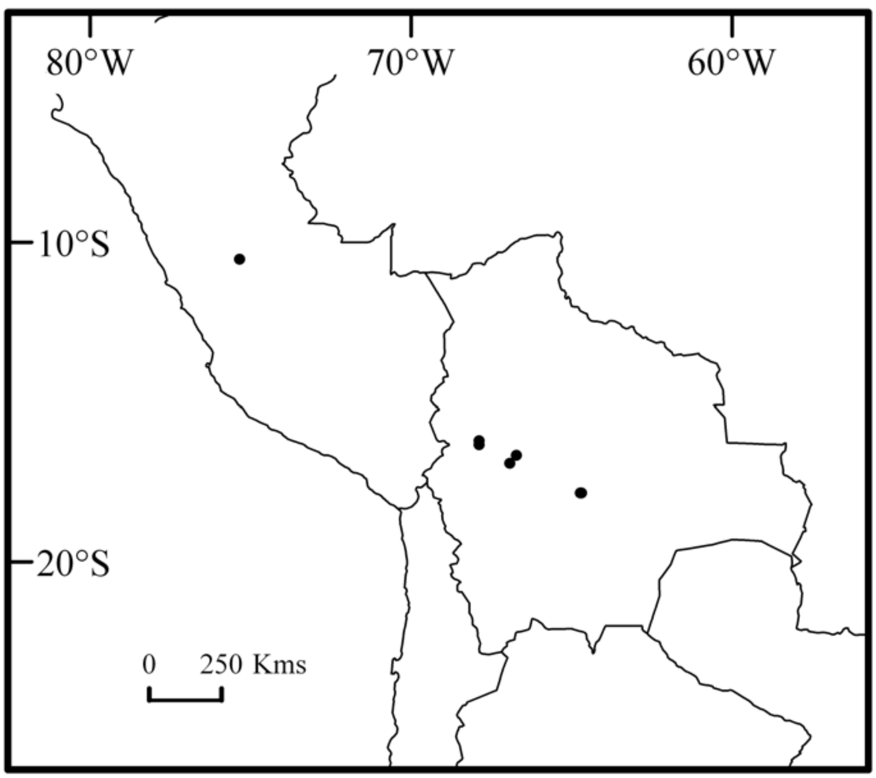


FIG. 11. Distribution of *Ascogrammitis pichinchae*.

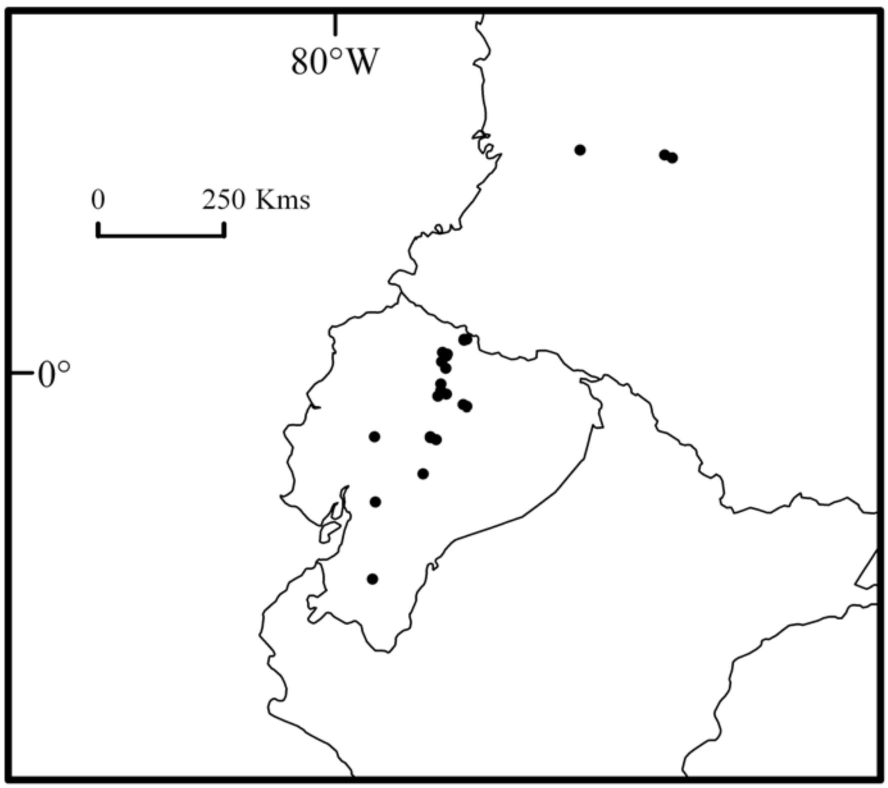


Fig. 12. A. *Ascogrammitis anfractuosa* with hyphae of *Acrospermum maxonii* growing over stomate, from the type of *A. anfractuosa*, scale bar = 10 µm, *Maxon 2770* (NY). **B.** *Ascogrammitis dilatata*, rhizome scale, scal bar = 1 mm, *Nuñez 644* (NY). **C.** *Acrospermum maxonii*, ascome growing over *Ascogrammitis anfractuosa*, from the type of *A. anfractuosa*, Maxon 2770 (NY). **D.** *Ascogrammitis dilatata*, petiole section, *Nuñez 644* (NY).

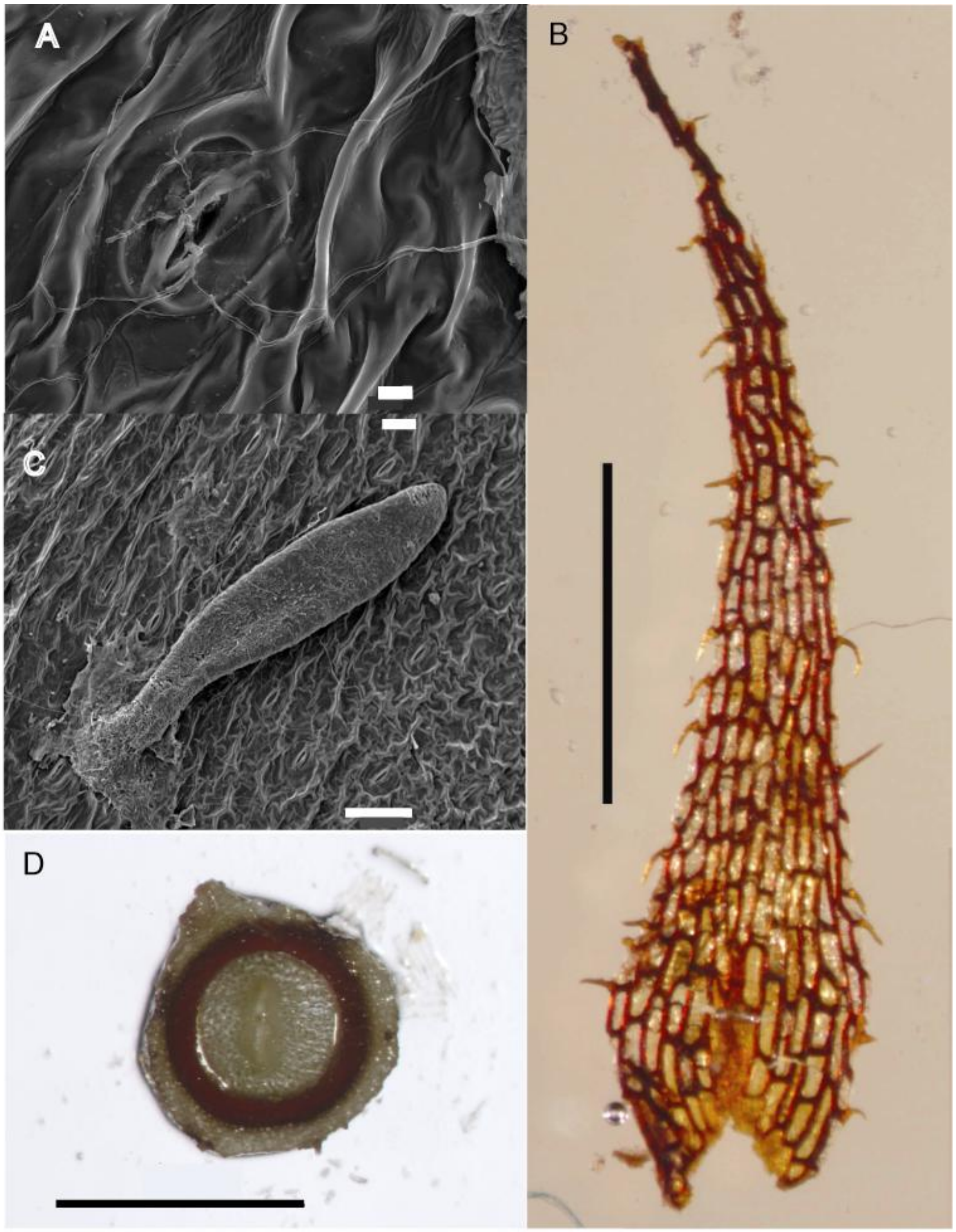

A
B
C
D

Fig. 13. A. *Ascomopora loxensis*, (*Sundue & Werner 1164*); **B.** *Ascogrammitis pichinchensis* (*Sundue, Martin & Sheer 1070*); **C.** *Ascogrammitis colombiensis* (*Sundue & Vasco 1334*); **D.** *Ascogrammitis anfractuosa* (*Sundue & Martin 1035*).

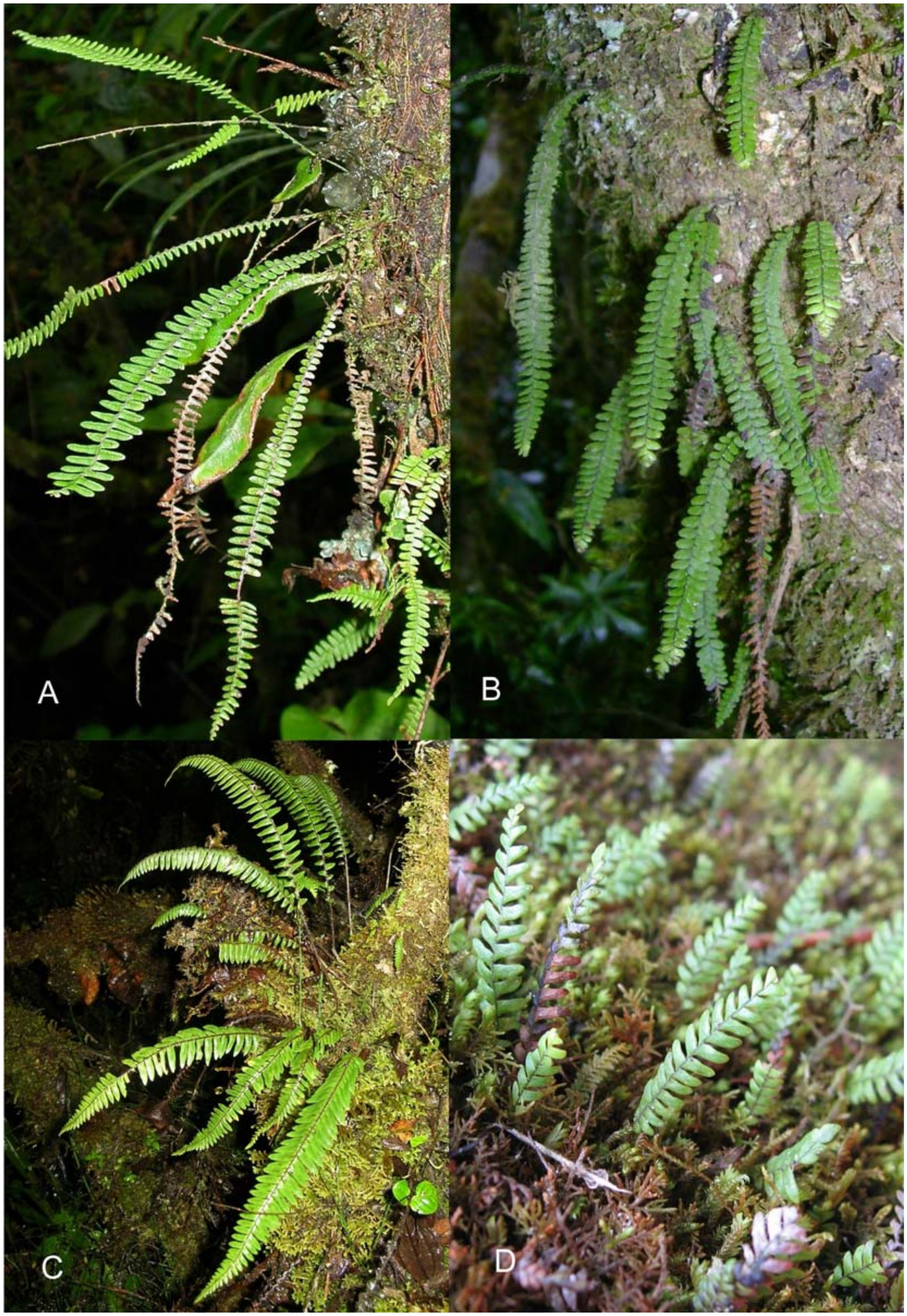

A
B
C
D

Fig. 14. **A–C** *Ascogrammitis pichinchsensis* **A.** Habit. **B.** Rhizome scale. **C.** Detail of abaxial lamina (*Sundue, M. 1070*). **D–E** *Ascogrammitis clavigera* **D.** Habit. **E.** Rhizome scale (*van der Werff, H. et al. 8822*). **F–H** *Ascogrammitis loxensis* **F.** Habit. **G.** Rhizome scale. **H.** Detail of rhizome scale apex with a single papillate cell (*Sundue, M. & Werner, F. 1164*).

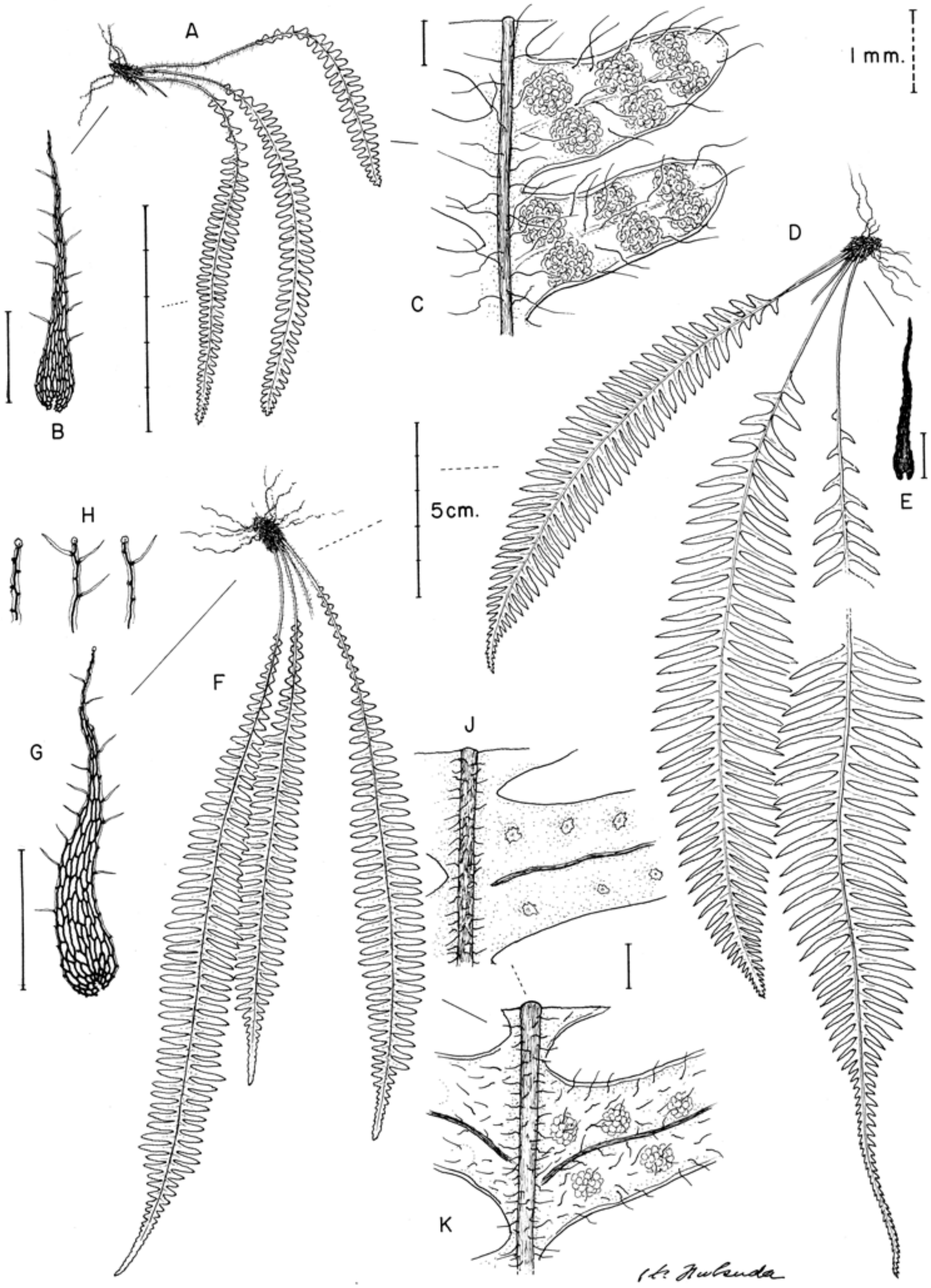

A
B
C
D
E
F
G
H
J
K
1 mm.
5 cm.

Fig. 15. A–D *Ascogrammitis athyrioides* **A.** Habit. **B.** Rhizome scale. **C.** Detail of petiole with setae and 1-furcate hairs. **D.** Detail of 1-furcate hairs (*Kessler, M. et al. 6723*). **E–H** *Ascogrammitis angustipes* **E.** Habit. **F.** Rhizome scale. **G.** Detail of petiole. **H.** Adaxial lamina surface (Rodríguez, *W. D. et al. 5126*). **J–M** *Ascogrammitis oxapampensis* **J.** Rhizome scale. **K.** Rhizome scale showing setae on adaxial surface. **L.** Detail of petiole. **M.** Detail of abaxial lamina surface (*van der Werff, H. et al. 8451*).

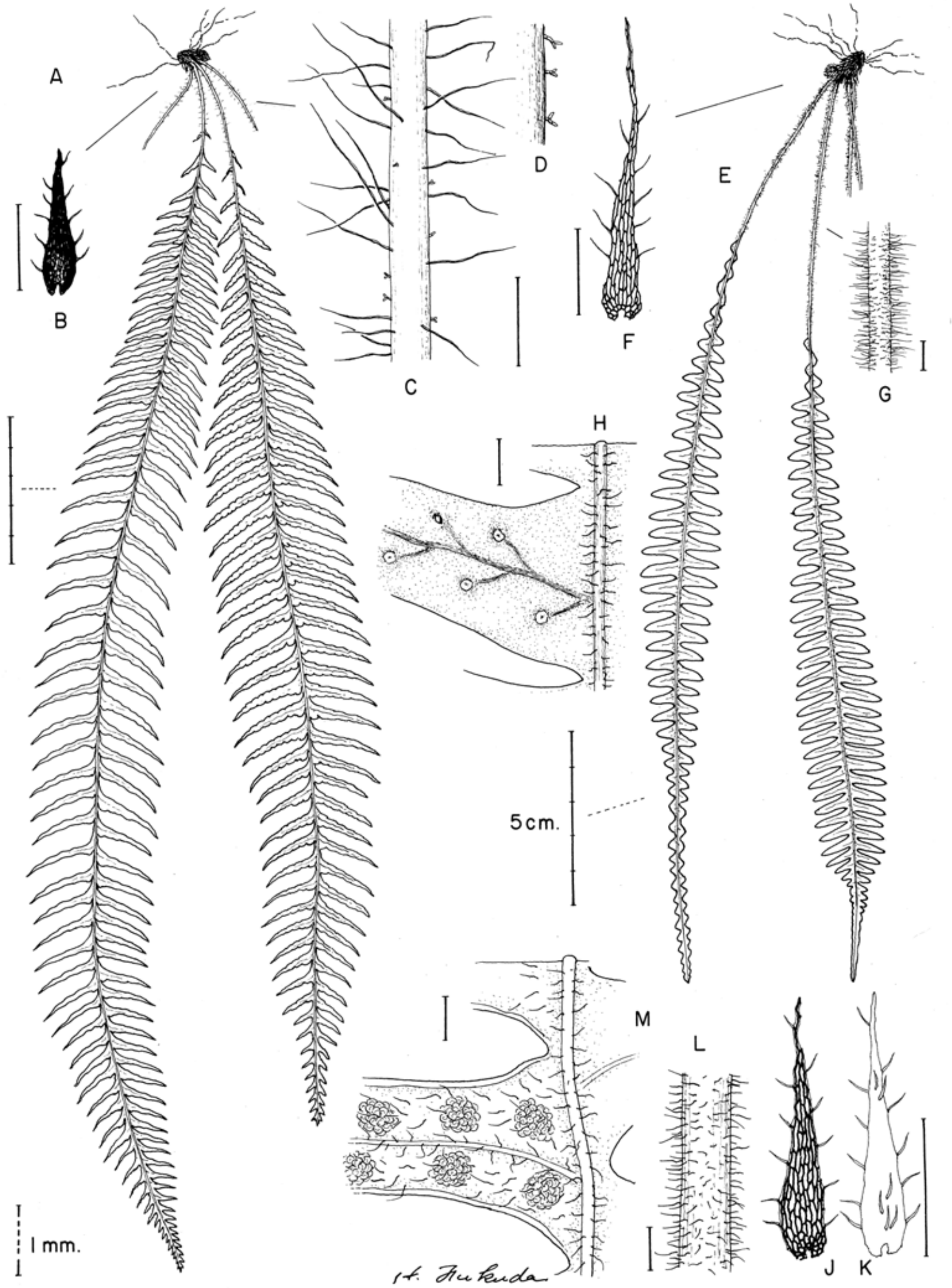

A
B
C
D
E
F
G
H
5cm.
M
L
J
K
1 mm.
H. Fukuda

Fig. 16. A–C *Ascogrammitis david-smithii* **A.** Habit. **B.** Rhizome scale. **C.** Detail of abaxial lamina surface including ascomes of *Acrospermum* (*Jiménez, I. 1215*). **D–F** *Ascogrammitis colombiensis* **D.** Habit. **E.** Rhizome scale. **F.** Detail of abaxial lamina surface including ascomes of *Acrospermum* (*Sundue, M. & A. Vasco 1335*). **G–J** *Ascogrammitis cuencanana* **G.** Habit. **H.** Detail of adaxial lamina surface. **J.** Detail of abaxial lamina surface including ascomes of *Acrospermum* (*Bishop, E. 1990*).

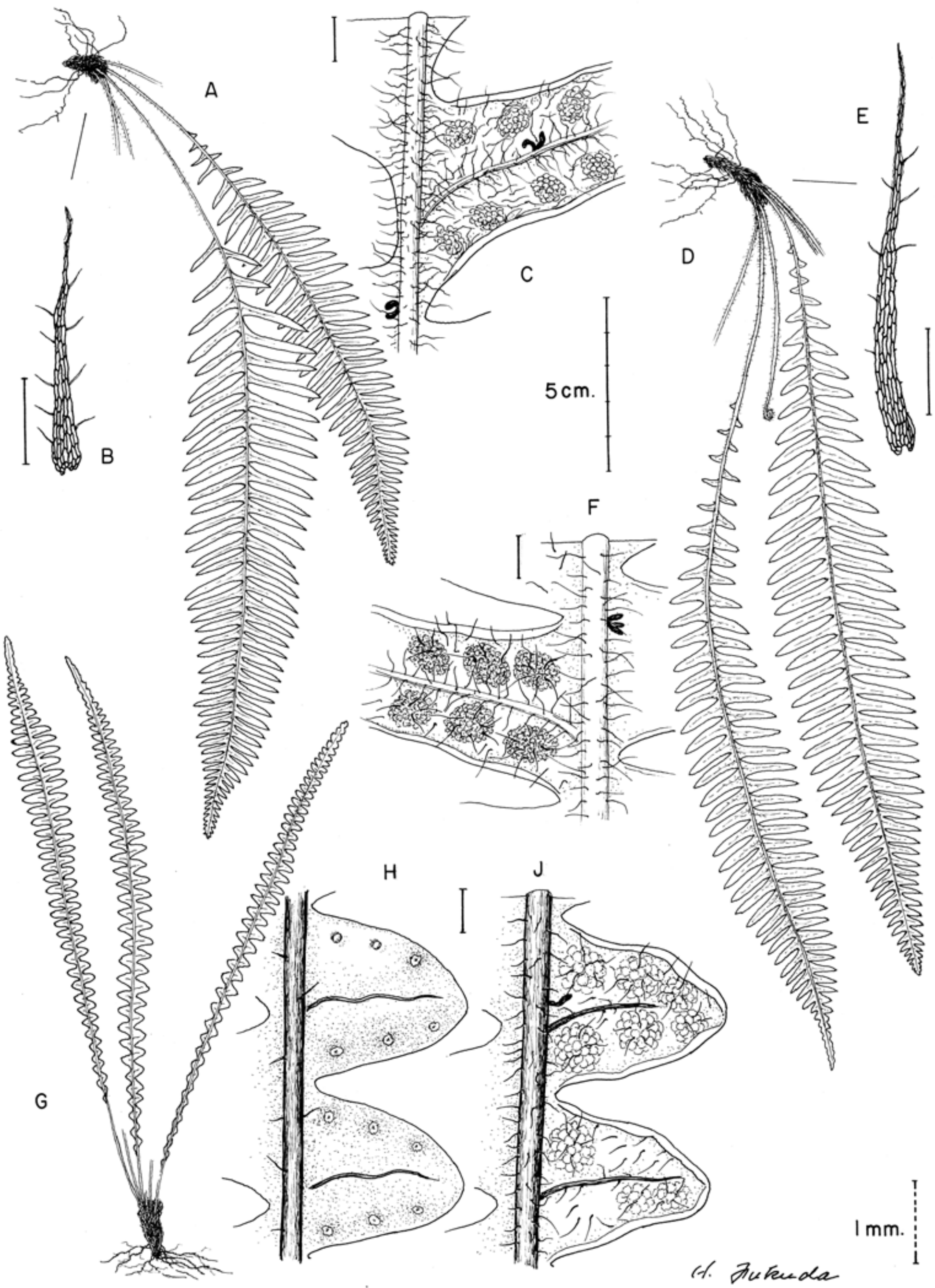
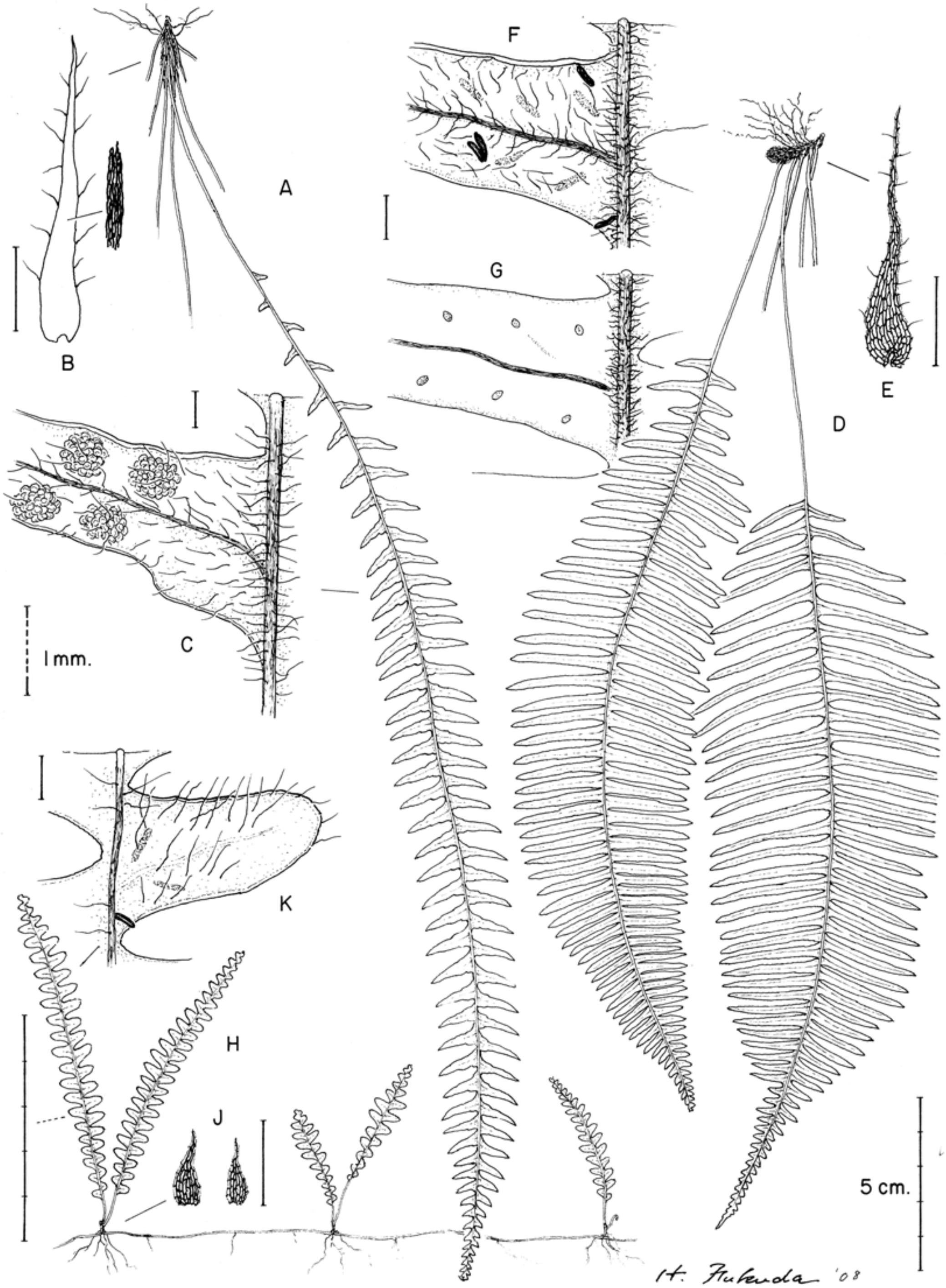

A
B
C
D
E
5 cm.
F
G
H
J
1 mm.
H. Fukuda

Fig. 17. **A–C** *Ascogrammitis tungurahuae* **A.** Habit. **B.** Rhizome scale. **C.** Detail abaxial lamina. (*Rimbach, A. 22*). **D–G** *Ascogrammitis clathrata* **D.** Habit. **E.** Rhizome scale. **F.** Detail abaxial lamina with *Acrospermum* ascomes. **G.** Detail adaxial lamina (*Kromer, T. & Aceby, C. 1237*). **H–K** *Ascogrammitis anfractuosa* **H.** Habit. **J.** Rhizome scales. (*Sundue, M. & Schuettpelz, E. 1075*) **K.** Detail abaxial lamina with *Acrospermum* ascomes (*Sundue, M. 1176*).


A
B
C
1 mm.
D
E
F
G
H
J
K
5 cm.
H. Fukuda '08

CONCLUSION

The present dissertation addresses the systematics of a primarily neotropical clade of ferns. Morphological and molecular DNA sequence data are used together in phylogenetic analyses to resolve problems in the circumscription of some prominent grammitid genera. Chapter 1 reviews morphology of grammitid ferns in order to build a character matrix for use in cladistic analyses. Analysis of the data demonstrates that *Terpsichore* is not monophyletic as originally defined. Additional results are difficult to determine because of lack of resolution in the strict consensus tree, but several assumptions about grammitid morphology are overturned by the results of the morphological study. Chapter 2 combines this data with DNA sequence data from three chloroplast regions. Focus here is upon circumscription of genera within one clade identified in previous analyses that includes the monophyletic *Melpomene*, plus portions of two polyphyletic genera, *Lellingeria* and *Terpsichore.* Phylogenetic analyses resolve this ingroup as monopyletic and sister to a clade that includes Ceradenia, *Enterosora*, and *Zygophlebia*. *Melpomene* is monophyletic, but is nested within *Lellingeria* in most trees. Ingroup species of *Terpsichore* form three well supported monophyletic groups that together are paraphyletic with regards to *Melpomene* plus *Lellingeria*. The value of the combined analysis is demonstrated as each of these clades are well supported by and diagnosable by morphological characters. Two clades of species currently combined in *Terpsichore* are recognized as new genera. In chapter 3, one of these clades, referred to as the *Terpsichore anfractuosa* clade, is described as the new genus *Ascogrammitis*. In this monograph, sixteen species of *Ascogrammitis* are recognized, including five new ones, and new combinations are made for the previously recognized species.

APPENDIX

Character	*T. anfractuosa grp.*	*Lellingeria myosuroides* grp.	*Lellingeria* pro parte	*Melpomene*	*T. taxifolia grp.*	*T. subscabra grp.*
Root insertion	ventral	ventral or radial	usually ventral	ventral	ventral	ventral
Rhizome symmetry	dorsiventral	radial	dorsiventral	dorsiventral	dorsiventral	dorsiventral
Rhizome scale shape	lanceolate or ovate	ovate	lanceolate	lanceolate	lanceolate	lanceolate
Rhizome scale color (cell wall color if clathrate)	dark reddish to blackish	dark reddish	dark gray to blackish	reddish brown	orange to castaneous	orange
Rhizome scales concolorous vs. clathrate	clathrate	clathrate	clathrate	clathrate	concolorous	concolorous
Rhizome scale cells turgid vs. flattened	flattened	flattened	flattened	flattened	turgid	flattened
Rhizome scale, # of apical papillate cells	singular	singular	singular	multiple	singular	singular
Rhizome scale margin	setose	setose or entire	setose	entire	setose or entire	glandular
Rhizome scale marginal setae color	reddish (whitish in 1 sp.)	whitish	whitish	--	orange to castaneous	--
Fronds monomorphic vs. dimorphic	usually dimorphic	usually dimorphic	monomorphic	usually dimorphic	monomorphic	monomorphic
Fronds, type of monomorphy	fertile portions more setose	fertile portions less dissected	--	rtile portions more seto:	--	--
Setae	present	absent	absent	present	present	present or absent
Hairs, typical number of cells	3	3	3 or more	3 or more	3	3
Hairs, typical number of branches	1	1	1 or more	1	1	1
Hairs, typical type of specialized cells	setae or none	acicular	acicular	none	setose or none	glandular
Veins, presence of blackish sclerenchyma	absent	absent	absent	absent	present	
Hydathodes, cretaceous vs. non-cretaceous	cretaceous or non-cretaceous	non-cretaceous	ısually non-creataceou:	non-cretaceous	cretaceous or non-cretaceous	non-cretaceous
Sorus shape	elliptical	usually elliptical	round	round or elliptic	round	round
Sori, distribution on lamina	distal portion of blade	distal portion of blade	distal portion of blade	distal portion of blade	even	even
Sori, position on segment	inframedial	inframedial	medial or inframedial	medial or inframedial	supramedial	inframedial

Table 3. Summary of diagnostic characters for major ingroup clades.

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BIOGRAPHICAL SKETCH

Michael Andrew Sundue was born on 29 November, 1975, in Weymouth, Massachusetts. His formative years were spent in Lexington, MA where he was raised with one sibling. He attended Fiske Elementary School, Diamond Middle School, and subsequently Lexington High School, from which he graduated in 1994. In the fall of 1995, he began undergraduate studies at the University of Colorado in Boulder as geology major, following an interest in mineralogy that he had developed at a young age. After completing his preliminary coursework, he left the University of Colorado and enrolled in the University of Vermont in Burlington, where he began a major in Botany. While attending UVM, exposure to the tropical fern and Lycophyte collections at the Pringle Herbarium led him to develop a strong interest in the systematics and taxonomy of these plants. Upon graduation in 1999, he spent six months living in Mexico, makingextensive collections of ferns and other vascular plants. In 2001, Michael took a research assistant position at the New York Botanical Garden, where he wrote a descriptive flora to the ferns and Lycophytes of Parque Nacional Amboró in Bolivia. When this research position ended, he enrolled in the joint program between the CUNY Graduate Center and the New York Botanical Garden, where he began to study the systematics and evolution of grammitid ferns.